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Aude Verwilghen

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Submitted on 9 Dec 2015

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Rodent pest management and predator communities in oil palm plantations in Indonesia: a comparison of two contrasting systems

Supervisor : Patrick GIRAUDOUX
Co-Supervisor : Francis RAOUUL
Lutte contre les rongeurs et communautés de prédateurs dans des plantations de palmiers à huile en Indonésie: comparaison de deux systèmes contrastés

Directeur de thèse : Patrick GIRAUDOUX
Co-directeur de thèse : Francis RAOUL
First of all, my sincere and great thanks to my two supervisors, Patrick Giraudoux and Francis Raoul, who took the risk to be part of this adventure, supported me all along, and motivated me to not only think about adequate questions but also to think in scientific ways to address those questions. You are indeed a complementary and successful supervising team, with the “bad cop” challenging me and pushing me to my limits, and the “good cop” being so nice, patient and a continual source of encouragement.

I would like to thanks Jean Pierre Caliman, Jean-François Cosson, Michel Gauthier-Clerc and Eric Gohet for their time and very useful inputs as committee members. I am also grateful to Marie-Lazarine Poulle and Ed Turner, as well as to Alain Rival and Dawn Scott for agreeing to respectively be rapporteurs and/or jury members for this work.

I am most grateful to Geraldine Veron and Andy Jennings for their fruitful collaboration, discussions and advice. Their great expertise on small carnivores was fully appreciated. A special thanks also to Geraldine for her help in investigating molecular issues for small carnivores, which were finally and unfortunately not developed in this study (I truly hope that, in the future, we might have the opportunity to valorize samples collected).

My gratitude is also extended to Yannick Chaval, Dominique Rieffel and Pak Ucok: thank you for your collaboration and for sharing your knowledge and expertise on rodent trapping/dissection/identification, on pellets or faeces preparations, and/or many other topics. Thanks also to Maxime Galan for discussions on molecular biology issues related to diet.

I appreciated the outputs of the work carried out by Julie Andru on rodents in the framework of her PhD; it was a valuable input to build on. This study benefited also from the kind information and advice shared by other people, such as Eric Meijsaard, Yves Laumonier, and many others who I hope will forgive me for not citing them.

Many thanks to Michel Arnaud, Albert Flori and Philippe Letourmy for their support in statistics and/or with R software, in addition to the one of my supervisors (thanks for your patience: statistics are less a closed book for me now!). The help of Thierry Chapuset for database issues was also very much appreciated; more generally, thanks to him and to Didier Snoeck for IT support in all its aspects!

I acknowledge the support of State Ministry of Research and Technology of Indonesia, which issued and renewed my research permits. In this process, the cooperation of LIPI, notably of Pak Ucok, was fully appreciated.

I would like to thank also PTSMART and CIRAD for funding and support, and notably Eric Gohet and Jean Pierre Caliman who have facilitated the overall research project in so many ways. A special thanks to PTSMART and SMARTRI who provided access to their plantations and/or excellent facilities. All plantation and SMARTRI staff are fully thanked for their kind assistance at different stages of the study, may it be for data collection in the field, for laboratory work, for plantation data gathering, or for fruitful discussions. It would be too long to mention everyone individually, but I would like to thank especially Pak Sudartha, Pak Naim, Pak Agung, and Pak Advenito, as well as Jek, Kurniadi, Imron, Bambang, Rini, and all drivers. A special thanks to those who participated to faeces collection and night spot counts, for putting so much of their energy and good willing for field work, even during ramadan, walking hours under the sun or staying awake till late in the night. Without all of you, this work would not have been possible.
Thanks also to all trainees and visitors who made Libo research stations even more busy, lively and cosmopolitan. A wink at Madame Bisou for her inestimable and priceless help during spotlight counts. And a special thought for the Hippopotamus Water-Polo Team of the Hyatt Mickey Club. I cannot forget to mention “la bande de l’UR34” at Montpellier: thanks to all for good times spent together (with a special thought to Vero for the benefit of our talkative and relaxing picnics on the grass). Thanks also to other friends who put up with me, and sorry to those who I have neglected during my busy times.

Finally, I would like to thanks my husband for his ineffable love, for being so patient and tolerant during my « hard time », and for careful reading of this manuscript before editing. Thanks also to my parents, who gave me the liking for adventure and the willingnes to discover other worlds, and who helped me to get where I am today.
ABSTRACT

Rapid expansion of oil palm cultivation in Southeast Asia raises concerns about biodiversity conservation. Moreover, rats are invasive pests in oil palm plantations, often causing substantial damage. In Indonesia, rat control is generally based on field treatment using anticoagulant rodenticides and/or on reinforcement of predation by barn owls (Tyto alba), by providing nest boxes within the plantation. Rodenticide use is costly for the producer and can indirectly poison non-target species such as rat predators. Thus, biological control of rodent pests should be promoted, both from a conservation and a production points of view. Within the assemblage of rat predators, small carnivores may contribute to rodent population regulation. However, persistence of small carnivores within oil palm plantations, their habitat use, their diet and their contribution to rodent control have been poorly investigated.

We conducted a 3-year comparative study (2010-2012) in well-established oil palm plantations in Riau and Bangka provinces, in Indonesia: in both areas barn owls have been successfully introduced, but in Riau rat populations have been maintained at an acceptable level without the use of rodenticide for more than 10 years, whereas in Bangka intensive rodenticide applications did not prevent high levels of rat damage.

We compared these two contrasted systems in term of predators community (barn owls and small carnivores) abundance and/or diet. Using a kilometric abundance index yielded from spotlight and faeces counts, we found that small carnivores were much more abundant in Riau plantations than in Bangka, and that the leopard cat (Prionailurus bengalensis) was the dominant species in Riau and absent from Bangka. We investigated the diet at community level and found no significant differences in frequency of occurrence or volume of small mammal’s food items in the faeces of small carnivores between Bangka and Riau; however, we found that the importance of vegetal food items in the diet of small carnivores was greater in Bangka than in Riau, thereby reflecting differences in predator community composition between both areas. Moreover, analyzing barn owls pellets content and number of eggs laid in nest boxes, we found that 1) the proportion of rats in barn owls diet was slightly less in Bangka than in Riau and prey taken as food were more diverse in Bangka, 2) breeding season was limited to one peak in Bangka comparatively to two peaks in Riau, thereby probably leading to a lowest food requirement in Bangka. Broadly, our results suggested that rat prey intake from the barn owl population and the small carnivore community would be less in Bangka plantations than in Riau. To further investigate barn owl selective predation on rat populations, we developed a model to assess the relative age of Rattus tiomanicus (the main barn owl prey in Riau plantations) from barn owl pellet macremains.

We also investigated spatial distribution of small carnivores within the oil palm habitat. We found no attractive effect of forest habitat or oil palm edge for the leopard cat and the common palm civet (Paradoxurus hermaphroditus), which may be encountered deep within the oil palm habitat, whereas the Malay civet (Vivera tangalunga) was always observed in the edge of the oil palm habitat. At the community level, our analysis of faeces spatial distribution showed an attractive effect of forest and oil palm edge habitats. These results support the hypothesis that, although the oil palm habitat may be habitable for some wild small carnivores species such as the leopard cat, where they supposedly forage at night, most species still need forest habitat for their survival in oil palm landscapes.

Prey-predators relationship in agricultural landscape is a complex issue. Broadly, our results suggest that barn owls cannot regulate rodent population on their own, and that small carnivores probably play an important role, in the framework of a multi-factor hypothesis. To enhance small carnivores within oil palm plantations, the producer should adapt agricultural practices (e.g. rodenticide use and understorey vegetation management) and favor appropriate land-use such as retaining forest fragments within and surrounding the plantation.

Keywords: oil palm plantation, rodent pest control, Rattus, predators, small carnivores, Prionailurus bengalensis, Paradoxurus hermaphroditus, Vivera tangalunga, Arctogalidia trivirgata, Felis catus, barn owl (Tyto alba), abundance, diet, spatial distribution.
La culture du palmier à huile a eu ces dernières décennies une expansion spectaculaire, surtout en Malaisie et en Indonésie ; dans ce dernier pays les surfaces en palmiers ont atteint plus de 10 millions d’hectares en 2014, ce qui représente presque un doublement des surfaces sur les dix dernières années (USDA-FAS, 2015). La demande en huile de palme ne devrait pas s’essouffler, suite à l’augmentation de la population conjuguée à celle du niveau de vie (Corley, 2009). La culture du palmier à huile est indéniablement un moteur de développement économique au niveau national et local (Susila, 2004 ; IFC, 2011). Cependant c’est aussi l’une des principales menaces pour la biodiversité en Asie du Sud Est (Wilcove and Koh, 2010). Son impact écologique dépend en majeure partie de sa contribution à la déforestation, mais aussi de sa capacité à maintenir la biodiversité associée au cours de son cycle de vie (Fitzherbert et al., 2008). Pour réduire l’impact des plantations de palmiers à huile sur la biodiversité et favoriser leur intégration dans les équilibres écologiques locaux et régionaux, l’adaptation des pratiques culturales et l’aménagement du territoire à l’échelle de l’exploitation, mais aussi à une échelle plus large, sont des leviers essentiels, favorisant ainsi la multifonctionnalité de ces paysages (production et conservation). Selon les principes de l’agro-écologie, favoriser la biodiversité au sein de l’agroécosystème palmeraie peut aussi représenter un atout pour le producteur, en fournissant des services écosystémiques tel que la lutte contre les rongeurs. Les pullulations de rats peuvent provoquer des dégâts importants dans les palmeraies, avec des pertes de production pouvant atteindre 10 % (Wood and Chung, 2003). La lutte contre ces pestes agricoles se base en général sur l’introduction de chouettes effraies (Tyto alba) dans la plantation (avec mise à disposition de nichoirs) et/ou l’usage de raticides (anticoagulant). Les chouettes sont communément perçues par les planteurs comme des éléments essentiels de la lutte intégrée contre les rats en palmeraies, et la littérature grise abonde sur le sujet. Toutefois, le rôle des chouettes dans le maintien de populations de rats à des niveaux de dégâts jugés acceptables demeure incertain ou du moins complexe (Chia et al., 1995 ; Kan et al., 2014) : ainsi, certaines plantations où les chouettes abondent depuis plusieurs années subissent encore des dégâts de rats conséquents. La plantation peut également abriter des petits carnivores, prédateurs potentiels de rats, qu’il s’agisse d’espèces relativement communes, tel le chat léopard (Prionailurus bengalensis) ou bien d’autres espèces plus rares et/ou en danger (Scott et al., 2004 ; Maddox et al., 2007). L’écologie de ces petits carnivores est relativement peu connue, qu’il s’agisse par exemple de leur régime alimentaire ou de leur utilisation de l’habitat ; un grand champ d’étude reste ainsi à explorer portant d’une part sur l’impact du développement des palmeraies sur ces espèces (déforestation, intoxication indirecte par les raticides, etc.) et par conséquent la persistance de ces espèces dans ce type de paysages agricoles, et d’autre part sur leur rôle dans la lutte contre les rats en palmeraie. Il apparaît ainsi nécessaire de comprendre dans quelle mesure le paysage et les pratiques culturales impactent la structure trophique et spatiale des communautés de proies (rats) et prédateurs (petits carnivores et chouettes) en plantation de palmier à huile.

Dans ce cadre, nous avons donc comparé sur trois ans (2010-2012) deux agroécosystèmes contrastés, représentés par deux palmeraies agro-industrielles dans la province de Riau (Riau_1 et Riau_2), sur l’île de Sumatra (473,604 km²) et deux autres dans la province de Bangka (Bangka_1 et Bangka_2), sur l’île du même nom (11,910 km²). Dans tous les sites, les chouettes ont été introduites avec succès, et à Riau les dégâts sont maintenus à un niveau acceptable sans usage de raticide depuis au moins une dizaine d’années, tandis qu’à Bangka les plantations subissent des dégâts de rats plus élevés et les raticides sont utilisés de manière intensive depuis de nombreuses
années. La question centrale qui a guidé notre recherche est celle des facteurs pouvant contribuer aux différences observées de niveau de dégâts de rats, et donc de niveau de populations de rats, entre les deux agroécosystèmes, Riau versus Bangka. La ressource alimentaire ainsi que la prédation sont en général les deux facteurs principaux influençant la dynamique des populations de rongeurs (Krebs, 2013). Dans le cadre de cette étude, après avoir suggéré que la ressource alimentaire n’était a priori pas un facteur discriminant dans notre contexte, nous nous sommes donc focalisés sur le facteur prédation, gardant en mémoire l’hypothèse de « predation-as-limitation » selon laquelle les densités maximum de rongeurs sont observées dans les habitats les plus pauvres en prédateurs (Krebs, 2013). Notre premier objectif est ainsi d’étudier les prédateurs des rats, chouettes et petits carnivores (Felidae, Viveridae, Herpestidae, etc.), dans ces plantations, notamment leur abondance et leur régime alimentaire, avec l’hypothèse/prévision que ces prédateurs sont plus abondants (et plus diversifiés en ce qui concerne la communauté de petits carnivores) dans les plantations de Riau comparées à celles de Bangka, et qu’à Riau la part des rats dans leur régime alimentaire est plus importante qu’à Bangka. Cela ne nous permet pas d’en déduire l’impact des prédateurs sur la dynamique de population des rats, puisque cet impact dépend aussi, entre autres, de la réponse fonctionnelle et numérique des prédateurs, de l’âge et du sexe des proies prélevées (qui peut avoir des répercussions sur la structure de la communauté de proie et donc sa dynamique de population), ainsi que de la capacité de recrutement de la population de proies (Holling, 1959; Dickman et al., 1991; Korpimaki and Krebs, 1996; Gervasi et al., 2012). Toutefois, si ces prédictions s’avèrent exactes, cela appuierait plutôt l’hypothèse/prévision générale selon laquelle les prédateurs contribueraient de manière plus significative à la lutte intégrée contre les rats dans les plantations de Riau comparativement dans celles de Bangka. Par ailleurs, nous avons également pour objectif d’explorer la distribution spatiale des petits carnivores au sein de la plantation. Notre hypothèse est que les petits carnivores ne sont pas distribués uniformément au sein de l’habitat palmeraie et que l’utilisation de l’habitat varie en fonction des taxons: les petits carnivores sauvages s’observeraient plutôt à proximité des habitats forestiers et de la bordure de l’habitat palmeraie, tandis que les chats domestiques s’observeraient plutôt à proximité des implantations humaines. Dans une première partie, nous avons analysé les niveaux de dégâts de rongeurs dans chaque plantation afin de s’en servir comme indicateur de niveau des populations de rats, confirmant ainsi une plus grande abondance de rats à Bangka par rapport à Riau. Nous avons aussi caractérisé les agroécosystèmes (paysages, environnement, pratiques, communautés de micromammifères) afin de mettre en évidence leurs différences éventuelles pouvant influencer les relations proies-prédateurs. Les pratiques culturales (hormis l’usage des raticides) et les conditions environnementales au sein de chaque plantation sont relativement similaires, si ce n’est des palmiers en moyenne plus jeunes (et donc une canopée plus basse), ainsi qu’un réseau de drainage plus important dans certains blocs de la plantation de Riau. Ces dernières caractéristiques, ainsi qu’un trafic routier plus important à Riau, pourraient influencer la distribution des petits carnivores au sein de ces deux plantations. La production de fruits (en tant que ressource alimentaire des rats) et le couvert végétal (en tant que micro-habitat à la fois des rats et des petits carnivores) étant comparables dans les quatre plantations, ce ne sont a priori pas des facteurs pouvant expliquer la différence de niveaux de populations de rats entre Bangka et Riau. La richesse spécifique des micromammifères (estimée par piégeage) au sein des plantations est très pauvre, comparé aux habitats environnants, même en périphérie de plantations (cline abrupt d’espèces à l’écotone). A Riau, l’espèce de rat dominante est Rattus tiomanicus, tandis qu’à Bangka, il s’agit de R. tanezumi, qui est relativement tolérant au
coumatretalyl, anticoagulant utilisé à Bangka (Andru et al., 2013). Cette tolérance pourrait, du moins en partie, expliquer les hauts niveaux de populations de rats sur les plantations de Bangka.

Le contexte paysager régional a été décrit à partir de la littérature et des cartes existantes, mais pour plus de précision nous avons cartographié l’habitat dans et aux alentours des plantations. Il est apparu que le contexte paysager régional et intra plantation était différent suivant les régions (Bangka versus Riau) et également entre les plantations à Riau. A Riau, dans et autour des plantations, le paysage est très homogène, avec une large dominance de plantations de palmiers à huile, qui couvrent plus de 80% du territoire cartographié. Cela reflète la situation au niveau régional, puisque Riau est la province où les palmeraies couvrent la plus grande partie de la surface (BPS, 2014) ; toutefois, dans la province de Riau, on retrouve encore de grands massifs forestiers intacts, potentiels refuges de faune (Uryu et al., 2008). A Bangka par contre, les environs des deux plantations, qui reflètent le contexte régional, représentent un paysage beaucoup plus diversifié (cultures vivrières mixtes, mines d’étains, agroforêts, etc.), incluant jusqu’à 15 % d’habitat forestiers ou assimilés, tels les agroforêts complexes à hévéa. Même au sein des deux plantations à Bangka, il existe plusieurs petites enclaves d’habitats forestiers ou assimilés (une vingtaine au total, représentant chacune 4 ha en moyenne), alors que sur les plantations de Riau, la seule enclave non cultivée est une zone de conservation de 112 ha constituée essentiellement de marécages, au sud-est de Riau_1. Comparé à Riau_1, Riau_2 a un paysage environnant plus diversifié, mais aucune enclave non cultivée ne subsiste en son sein (si ce n’est une petite expansion marécageuse d’environ 5 ha au nord-est).

En ce qui concerne les chouettes, nous avons comparé leur abondance entre plantations de manière indirecte, via le relevé de la présence/absence des pelotes dans les nichoirs, sur une période d’étude de trois ans. Nos résultats suggèrent que les chouettes sont au moins aussi abondantes à Riau qu’à Bangka. Nous avons également exploré le régime alimentaire des chouettes à travers l’analyse des macrorestes dans les pelotes récoltés dans les nichoirs au cours de notre période d’étude (3196 pelotes analysées). Même si les rats constituent l’essentiel du régime alimentaire de la chouette sur chacune des plantations (>90%), il apparaît toutefois des différences entre régions : la proportion de rats dans les macrorestes est un peu moindre à Bangka qu’à Riau, et les proies sont plus diversifiées à Bangka (incluant également des reptiles et des batraciens, en sus des insectes et oiseaux comme sur les plantations de Riau). Par ailleurs, à partir de données préalablement récoltées par les gestionnaires des plantations, nous avons calculé le nombre moyen mensuel de pelotes par nichoir (pour l’ensemble des nichoirs), sur deux années consécutives préalables à notre période d’étude, ce qui nous a apporté des informations sur la saison de reproduction des chouettes, et donc sur leurs besoins alimentaires puisque en saison de reproduction les chouettes consomment beaucoup plus de proies (Lenton, 1984; Small, 1990). Ces analyses ont révélé l’existence de deux pics de reproduction sur les plantations de Riau, ce qui est communément relevé dans la littérature (concernant les palmeraies), tandis qu’à Bangka on ne retrouve qu’un seul pic de reproduction ; ce résultat suggère par ailleurs un impact potentiel négatif de l’utilisation des raticides (via intoxication indirecte des chouettes). Ces deux types de résultats (différences de régimes alimentaires et de besoins alimentaires) vont dans le sens de notre prédiction de départ selon laquelle la prédation sur les rats par les chouettes serait moindre à Bangka qu’à Riau. En outre, comme indiqué plus haut, une éventuelle sélection de prédation en fonction de l’âge (ou taille) des rats pourrait influencer la dynamique des populations de ces derniers. Nous avons donc développé un modèle statistique afin d’estimer, à partir des macrorestes retrouvés dans les pelotes des chouettes, l’âge relatif des rats de l’espèce Rattus tiomanicus, majoritairement consommés par les chouettes sur Riau_1. La comparaison de la structure d’âge relatif des proies consommées avec la structure d’âge des proies
disponibles sur le site permettra dans le futur d’identifier une éventuelle prédation sélective de la chouette sur *Rattus tiomanicus* à Riau_1. Une démarche similaire pourrait être effectuée sur les autres sites.

En ce qui concerne les petits carnivores, nous avons estimé et comparé leur abondance entre plantations grâce à des indices kilométriques d’abondance, calculés à partir d’observations faites lors de comptages nocturnes à bord d’un véhicule d’une part, et d’autre part à partir de comptage de faeces le long de transects pédestres sur les routes de la plantation. Les observations issues des faeces nous ont apporté de l’information à l’échelle de la communauté, puisque nous n’avons pas pu discriminer les différents taxons, tandis que l’identification des espèces a été possible lors des comptages nocturnes, nous apportant ainsi de l’information sur la diversité et la richesse de la communauté petits carnivores dans les plantations. D’après nos résultats, les petits carnivores sont beaucoup moins abondants sur les plantations de Bangka que sur celles de Riau : les indices kilométriques issus des comptages nocturnes sont deux fois moins élevés à Bangka, et ceux issus des comptages de faeces dix fois moins. De plus, à Riau, la communauté est plus diversifiée et comprend une grande abondance de chat léopard, qui, d’après la littérature, se nourrit essentiellement de rats lorsque ces derniers sont disponibles en abondance (Rajaratnam *et al.*, 2007; Lorica and Heaney, 2013). Par contre, à Bangka, les chats léopards et d’une manière générale les Felidae sauvages sont absents, et parmi les petits carnivores sauvages, la civette palmiste commune, une espèce essentiellement frugivore, est dominante. Les autres espèces sauvages observées sur les plantations, mais beaucoup plus rarement, sont la civette malaise (*Vivera tangalunga*) et la civette à petites dents (*Arctogalidia trivirgata*) ; à notre connaissance, il s’agit de la première observation répertoriée de civette à petites dents dans l’habitat palmeraie. Outre les espèces sauvages, les chats domestiques sont également relativement abondants dans les palmeraies, notamment à Bangka. Nos résultats montrent une corrélation négative entre le niveau de dégâts des rats et l’abondance des petits carnivores : dans les plantations où les petits carnivores, et notamment les chats léopards sont abondants, les dégâts de rats sont moindres, tandis que dans les plantations où les petits carnivores sont moins abondants, et notamment où les chats léopards sont absents, les dégâts de rats sont plus élevés.

Le régime alimentaire des petits carnivores à l’échelle de la communauté a été étudié via l’analyse des macrorestes dans les faeces recoltés lors des comptages. Nos résultats montrent l’importance des micromammifères dans le régime alimentaire des petits carnivores (fréquence d’occurrence dans les faeces allant de 41.7% à 81.2%), et nous ne détectons pas de différences significatives entre les régions ni entre les plantations en terme de fréquence d’occurrence ou de volume dans l’ensemble des faeces. Il est à noter toutefois que ces analyses de régime pourraient être biaisées par le très faible nombre d’échantillons analysés à Bangka comparativement à Riau. Par contre, l’importance dans le régime de la catégorie alimentaire regroupant les végétaux (à l’exclusion de l’herbe) n’est pas la même à Bangka qu’à Riau : cette catégorie alimentaire arrive en tête à Bangka_1 en terme de fréquence d’occurrence et de volume dans les faeces, avant les micromammifères. Ces résultats relatifs au régime de la communauté de petits carnivores semblent refléter la composition de cette même communauté au sein de chaque plantation, et ne contredisent pas notre prédiction de départ selon laquelle la prédation sur les rats par les petits carnivores serait moindre à Bangka qu’à Riau.

Les observations réalisées lors des comptages nocturnes ou des comptages de faeces nous ont également permis d’explorer la distribution spatiale des petits carnivores au sein de la plantation, dans l’habitat palmeraie. Nous avons d’une part identifié l’existence d’agrégats d’observations, et
d’autre part analysé l’attractivité de certains habitats focaux types forêts, bordures de palmeraie et implantations humaines (via l’analyse des distances euclidiennes des observations à l’habitat focal), et ceci à l’échelle de la communauté et aussi par espèce lorsque c’était possible (observations nocturnes). Pour le chat léopard et la civette palmiste, nos analyses ne permettent pas de détecter une attractivité significative de l’habitat forestier ou de la bordure de palmeraies, et ces deux espèces peuvent être observées relativement loin à l’intérieur de la plantation (plus de 2 km de la bordure de l’habitat palmeraie). Pour la civette à petites dents et la civette malaise, le nombre d’observations est trop faible pour des analyses statistiques fiables, toutefois il est à noter que l’ensemble des observations de civette malaise (quatre au total) ont été réalisées en bordure de l’habitat palmeraie. En ce qui concerne les chats domestiques, nous avons observé une attractivité des implantations humaines, mais uniquement sur les plantations de Riau. Nos résultats indiquent donc une utilisation de l’habitat différente en fonction des espèces, et, d’une manière générale, ils confirment les quelques rares études antérieures sur l’utilisation de l’habitat par les petits carnivores dans les palmeraies (Rajaratnam et al., 2007; Nakashima et al., 2013; Azhar et al., 2014a; Jennings et al., 2015). A l’échelle de la communauté, nos résultats montrent une attractivité de l’habitat forestier uniquement pour les comptages de faeces. L’apparente contradiction entre les résultats issus des comptages de faeces (qui reflètent à la fois les activités diurnes et nocturnes) avec ceux issus des comptages nocturnes, semble confirmer d’une part que la palmeraie est un habitat largement utilisé la nuit par certains petits carnivores comme le chat léopard et la civette palmiste, qui y trouvent une abondante ressource alimentaire, et, d’autre part, que la conservation de fragments forestiers dans et autour des palmeraies est un élément essentiel au maintien des petits carnivores au sein de ces paysages.

Pour conclure, d’une manière générale, nos résultats sur l’abondance et le régime alimentaire des prédateurs, chouettes et petits carnivores, vont dans le sens de l’hypothèse globale de « prédation-as-limitation », et suggèrent une contribution potentiellement non négligeable des petits carnivores dans la lutte contre les rats en palmeraies, et notamment du chat léopard, qui peut être relativement abondant dans ce type d’habitat. Il semble donc important dans le futur d’étudier l’impact de prédation de ce petit carnivore sur les rats en palmeraies. Nous estimons toutefois que la régulation des rats en palmeraie tient plutôt d’un cortège de prédateurs que de l’effet d’une seule espèce. Par ailleurs, la prédation n’est en général qu’un facteur parmi d’autres de régulation du niveau de population des proies, et, dans nos cas d’étude, même si c’est une condition potentiellement nécessaire, elle n’est sans doute pas suffisante (Krebs, 2013). Ainsi par exemple, l’impact de l’usage des raticides, soit directement sur les rats (mortalité, résistance), soit indirectement (intoxication indirecte des prédateurs) devrait être analysé. Pour cela, et afin également de confirmer et préciser nos résultats, il semble essentiel d’étudier la dynamique de population des rats sur nos sites d’études, à la fois sur le court et le long terme. Par ailleurs, étant donné l’importance suggérée du chat léopard dans la lutte contre les rats en palmeraie, il s’avère important de mieux caractériser l’utilisation de l’habitat de cette espèce dans les paysages où les plantations de palmiers à huile dominent : le chat léopard peut-il survivre dans l’habitat palmeraie ou bien est-il dépendant des fragments forestiers ou d’autres types d’habitats non cultivés, et si oui dans quelle mesure ?

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<td>BEFTA</td>
<td>Biodiversity and Ecosystem Function in Tropical Agriculture</td>
</tr>
<tr>
<td>BPS</td>
<td>Bandan Pusat Statistik</td>
</tr>
<tr>
<td>CBGP</td>
<td>Centre de Biologie et de Gestion des Populations</td>
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<tr>
<td>CIRAD</td>
<td>Centre de Coopération International en Recherche Agronomique pour le Développement</td>
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<tr>
<td>CPO</td>
<td>Crude Palm Oil</td>
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<tr>
<td>CITES</td>
<td>Convention of International Trade in Endangered Species of Wild Fauna and Flora</td>
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<tr>
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<tr>
<td>FAO</td>
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<tr>
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<td>Kilometric Abundance Index (KAI$<em>{FAE}$ / KAI$</em>{SPL}$: yielded from faeces or spotlight counts respectively)</td>
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- **Co-author of a publication based on research related to the thesis**
  (I have initiated the research, contributed to the protocol, participated to its field implementation and follow-up, and lastly I have contributed to revise drafts of the manuscript produced):


- **Oral communication (seminar):**

- **Co-author of an oral communication (international conference):**

- **Poster (international conference):**
Oil palm is one of the world’s most rapidly expanding crops. Though it definitely plays an important role in the economic development of some tropical countries, it also represents a big threat to biodiversity, especially in Southeast Asia, a hotspot for biodiversity. Intensification of production in oil palm plantation could potentially reduce the pressure on land from new development. However, wildlife-friendly management practices can and should go hand in hand with yield enhancement, notably through the optimization of the functional value of biodiversity. For example, enhancing natural enemies of rats, invasive species which cause a lot of damage to oil palm plantations, could have benefits for the control of this pest. Rodent population regulation and prey-predator interactions in agricultural landscape have been analyzed mostly in temperate or polar environments. According to Krebs (2013), in the framework of a multifactor hypothesis, the predation-as-limitation hypothesis, which states that small rodent maximum density should be lower in predator-rich habitats, is generally accepted for many taxa. Barn owls (Tyto alba javanica Gmelina) and small carnivores are two potentially important rat predators. There is an abundant grey literature on barn owls in oil palm plantations, and enhancement of barn owl populations within oil palm plantation for rat control is widely practiced in Southeast Asia. In contrast, small carnivore persistence in oil palm landscape and their potential role in rodent pest control are poorly studied.

In this study, we compare two contrasting agroecosystems, one with “acceptable” rat damage and no rodenticide use, and the other with high rat damage (and presumably a higher rat population) and intensive use of rodenticide; barn owls being present at similar population levels in both systems. We investigated which assumptions could be made to explain such a difference in rat abundance in both agroecosystems, with respect to the small mammal community, agricultural practices, landscape characteristics, and the predator community. We focused our research on the predator hypothesis, and notably on the small carnivore community, by exploring its abundance, diversity and diet. In addition, we assessed the food intake of barn owls, given that it may also have an impact on rat population dynamics. Our main hypothesis is that the success of rodent control in oil palm plantations might be explained not only by barn owl predation on rats, but rather by an assemblage of predators of which small carnivores play an important role. It is generally assumed that landscape configuration can change predator community composition, thus the way the predator community impacts rodent small mammal populations. Therefore, in the second part of the study, we investigated the spatial distribution of small carnivores within oil palm plantations and its correlation to habitat.

We hope our results will contribute to increase the knowledge about small carnivores in oil palm landscapes and their potential for rodent pest control, in a view to enhance biodiversity in oil palm plantations in a win-win strategy for both production and conservation.
I.1. OIL PALM EXPANSION AND IMPACT ON BIODIVERSITY

I.1.1. Oil palm expansion, “good for some, bad for others”

I.1.1.a. Production, consumption and land use

The oil palm (*Elaeis guineensis* Jacq.) is a monocotyledon belonging to the Arecacea family. Although it is considered as a perennial crop and can grow to over 20 m high, it is not a tree but rather a giant grass (Jacquemard, 2011).

The oil palm fruit contains two oils of different composition: fruit pulp provides palm oil, and the oil palm almonds provide kernel oil; the palm oil is the main product, and the kernel oil increases the total yield by about 10% (Rival and Levang, 2014). These oils are widely used in the agri-food industry (80%), oleochemicals (19%) and biodiesel (1%) (Omont, 2010).

Oil palm is the world’s fifth most rapidly expanding crop\(^1\) (Phalan *et al*., 2013), and within 25 years, the total plantation area of oil palm has tripled, reaching a global estimate of over 15 million ha in 2010 (Gilbert, 2012).

The main palm oil producing countries are Malaysia and Indonesia (Figure 1). In 2013/2014, Indonesia accounted for more than half of supplies, and the area of oil palm plantations reached a total of 10.3 million ha, almost doubling within 10 years (Figure 2) (Ministry of Agriculture, 2013; USDA-FAS, 2015b, a). Oil palm development in Indonesia is mainly located in two regions: Sumatra and Kalimantan\(^2\) (Figure 2) (Gunarso *et al*., 2013).

Oil palm accounts for about 4% of the total land area planted for oil-producing crops, but it produces more than 30% of all vegetable oils in the world (Meijaard, 2014). Oil palm cultivation is one of the most profitable land uses in the humid tropics (Sayer *et al*., 2012). Palm oil has undeniable advantages compared to others vegetable oils: it has the lowest production costs\(^3\) and it has

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\(^1\) considering the period from 1999 to 2008.

\(^2\) Kalimantan is the Indonesian part of Borneo island.

\(^3\) By the end of 2014, palm oil was valued as the vegetable oil with the lowest production costs by the international commodity market (Barcelos *et al*., 2015).
exceptional yield, reaching a global average of 3.8 tonnes per hectare (about 4t/ha if considering also palm kernel oil), that is about six to ten times more than other vegetable oils (Figure 3); moreover it can replace most other vegetable oils and has a very wide range of uses as mentioned previously (Rival and Levang, 2014).

![Figure 4: Oil yield (t/ha/year) of the main oil producing crops (Source: Rival and Levang, 2014)](image)

Oil palm consumption is mainly driven by the countries in the South (India: 17.9%; Indonesia: 19.2%; China: 12.3%); European and United States consumption accounts for 14.7% and 2.6% respectively (USDA-FAS, 2015b).

Global demand for oil palm is predicted to double by 2050 (Corley, 2009), due to demographic growth and increase in the standard of living in emerging countries. Consequently, the area under oil palm cultivation is expected to increase further. Projections of oil palm expansion for Indonesia range from 8 to 14 million hectares, depending on scenarios (Harris et al., 2013).

Within the oil palm industry, two broad types of plantations and management systems may be distinguished (Colchester et al., 2006; McCarthy et al., 2012): industrial plantations, also called industrial estates, and smallholder plantations, also called smallholdings. Industrial plantations are large commercial estates owned by either private companies (on state land under long term leases) or government. Smallholdings are usually owned by family based enterprises but may be managed either in association with an oil palm company private or state owned (supported smallholdings, also called scheme smallholdings, or plasma in a nucleus estate scheme), or independently by the farmer (independent smallholders).

In Indonesia, industrial plantations cover on average 5000-6000 ha in size (a minimum of 4,000 ha of oil palm being needed to supply a single oil palm mill), but they may be as large as 20,000 or 40,000 ha (Casson, 1999; Lee et al., 2014a). They are intensively managed, and the oil palm is generally the only crop cultivated. In contrast, smallholdings are much smaller: on average at 2 ha

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4 In reality, a diversity of systems does exist, from entrepreneurial agriculture to family agriculture. Marzin et al. (2015) proposed a typology including the multiplicity of forms of smallholder plantations, as a composite category that includes family farms, family business farms and managerial farms.

5 Nucleus estate scheme is a system in which part of the fields, called the “nucleus” estate is managed directly by a state owned or private company, while another part is allocated to smallholders as “plasma (satellite)” plantations.
but they may range up to 50 ha (Vermeulen and Goad, 2006; Baudoin et al., 2014), and when independently managed, they may associate oil palms with other crops, notably when the palms are young (Cheyns and Rafflegeau, 2005).

Approximately 60% of Indonesia’s oil palm plantations are industrial estates, and within smallholdings about half are in schemes (Colchester et al., 2011).

### I.1.1.b. Driver of development or curse?

On one hand, oil palm production plays an important role in the economic development of some tropical countries: in Indonesia, it accounts for 46% of agricultural exports and brings in 18.3 billion US$ of foreign exchange (FAO, 2015); it may offer a route out of poverty for some small-scale farmers, and is seen as a real driver of development, as it generates substantial social benefits, including improved infrastructure, wealth and job creation for many people (Susila, 2004; IFC, 2011; World Growth, 2011; Edwards, 2015). According to Murphy (2014), in Indonesia, 25 million people livelihood depend one way or another on oil palm production. But palm oil may also be an instrument of impoverishment and threaten the livelihood of indigenous people, with land conflicts and serious human rights abuses being widespread (Colchester et al., 2006; Mingorance, 2006; Colchester, 2011).

It is thus a complex issue, and the oil palm controversy needs to move beyond a simple polarity between those two advocacies (Sheil et al., 2009; Feintrenie et al., 2010; McCarthy, 2010; Rist et al., 2010; Sayer et al., 2012; Obidzinski et al., 2014; Rival and Levang, 2014), similarly as for biodiversity conservation issues (Koh et al., 2010).

### I.1.1.c. One of the main issues: deforestation

Palm oil production also raises many environmental concerns, such as water pollution by mill effluent discharge or leaching of nutrients from agrochemicals inputs, green house gas emissions from deforestation or peatland conversion, biodiversity losses from deforestation or agricultural practices, etc. (Proforest, 2003; Fitzherbert et al., 2008; Comte et al., 2012; Obidzinski et al., 2012; Savilaakso et al., 2014). Health consequences of palm oil consumption are also questioned (FFAS, 2012; Rival and Levang, 2014). But one of the main issues of oil palm expansion in Southeast Asia is undeniably deforestation (WWF, 2002, 2003; Boucher et al., 2011; Greenpeace, 2011; Koh et al., 2011).

Globally, Indonesia exhibits the largest increase in forest cover loss (Hansen et al., 2013b) with an annual loss rate of respectively 1.15 Mha (0.98%) in the 1990s and 0.82 Mha (0.76%) in the 2000s (Stibig et al., 2014). In Sumatra, the forest cover was reduced from 58% in 1985 to 29% in 2008/9 (Figure 4), the forest was thus cleared at an average annual rate of 542,000 ha (2.1%) (Uryu et al., 2010). In the period 2000-2010, Miettinen et al. (2012) reported an annual rate of 2.7%. Riau province has lost more than 4 million ha of forest (65%) in the period 1982-2007. By comparison, Bangka-Belitung Islands lost approximately 294,600 hectares of forest from 2001-2012, representing about 17.5% of its land area (Global Forest Watch, 2013).

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6 As defined by the Rountable on Sustainable Palm Oil, smallholders are family based enterprises producing palm oil from less than 50 ha of land.
According to Koh and Wilcove (2008), during the period 1990-2005, at least 55% of plantation expansion in Indonesia and Malaysia occurred at the expense of forests. A recent study (Abood et al., 2015) found that oil palm plantations accounted for less than 3% (≈1Mha) of forest loss in Indonesia between 2000 and 2010, and that it was ranked third in terms of deforestation in Indonesia, after fiber plantations and logging concessions which accounted for the largest forest loss (≈1.9 Mha and ≈1.8 Mha respectively).

In Riau province, the total forest loss in the period 1982-2007, 29% was cleared for oil palm plantation (Uryu et al., 2008). Over a longer period, between 1982 and 2010, oil palm plantation accounted for 44% of the total forest loss (Susanti and Burgers, 2012).

Whatever the scenarios considered (moratorium on peat or on high carbone stock forest, yield improvements, preferential expansion on available degraded land, smallholder or agroindustrie development model, etc.) (Koh and Ghazoul, 2010; Carlson et al., 2012; Harris et al., 2013; Lee et al., 2014b), expansion of oil palm cultivation in Southeast Asia is expected to increase greatly, as discussed previously, and will thus continue to raise environmental concerns, notably about deforestation and biodiversity conservation.

### 1.1.2. Impact on biodiversity

Due to its biological requirements, oil palm is mainly grown in the equatorial tropics (Turner and Gillbanks, 2003), where most biodiversity hotspots occur. Sundaland is considered a top biodiversity hotspot because it features an exceptional concentration of endemic species and experiences very high loss of habitat (Myers et al., 2000; Brooks et al., 2002; Sodhi et al., 2010; Mittermeier et al., 2011; Corlett, 2014). Oil palm thus represents a major threat to biodiversity by driving forest clearance in those areas (Koh and Wilcove, 2008; Wilcove and Koh, 2010; Wilcove et al., 2013).
In reaction to oil palm expansion, the number of publications related to oil palm and biodiversity has increased exponentially in the last decade, though relatively few data existed ten years ago (Donald, 2004; Fitzherbert et al., 2008; Turner et al., 2008). However, the growth of publications is markedly slower compared to research linked to technologies and oil palm processing waste/by-products valorization (Hansen et al., 2015), and most research linked to biodiversity focused on insects and on birds (Hansen et al., 2015). Among the few publications dealing with the impact of oil palm production on mammals, almost all focused on large flagship species such as elephants and orangutans (Hansen et al., 2015). Moreover, during a search using Web site literature database (Web of Science) and an internet search engine (Google scholar), we found less than 10 published reports or articles and short communications published in peer-reviewed journals more specifically interested in small carnivores within oil palm landscapes (Scott et al., 2004; Rajaratnam et al., 2007; Nakashima et al., 2013; Ross et al., 2013; Silmi et al., 2013b; Gumal et al., 2014; Jennings et al., 2015), among others dealing on mammals in general (Maddox et al., 2007; Wahyudi and Stuebing, 2013; Azhar et al., 2014a; Bernard et al., 2014). Basically, very little is known about small carnivores within oil palm landscapes (see section I.3.3.).

I.1.2.a. About conversion of natural or semi-natural habitat to oil palm plantation

As pointed out by Fitzherbert et al. (2008), the ecological impact of oil palm depends crucially on the extent to which its expansion causes deforestation. Conversion to oil palm of other land cover types, such as pasture, may have only limited impact on biodiversity (Gilroy et al., 2015), but a great impact occurs when the previous land cover was forest.
Oil palm is often reported as the major contributor to forest fragmentation, thereby impacting on ecological connectivity which is strategic for conservation (Hilty et al., 2006; Abdullah and Nakagoshi, 2007; Reza and Abdullah, 2010).

In addition, many studies have demonstrated the negative impact of conversion of native forest to oil palm plantation for most species or animal assemblages in terms of their diversity and species composition, as summarized by Foster et al. (2011) in Figure 6. For a synthesis about effects of oil palm cultivation on biodiversity, see Fitzherbert et al. (2008), Turner et al. (2011), Foster et al. (2011) and Savilaakso et al. (2014).

![Figure 7: The impacts of converting primary rainforest into an oil palm plantation on the abundance and species richness of different taxa. Arrow tails denote primary forest communities and arrow head oil palm communities. More details on data sources may be found in Foster et al., 2011 (Source: Foster et al., 2011).](image)

Not all species decline following forest conversion to plantation, some species may thrive in the oil palm habitat thanks to an increase in food resources and/or loss of predators and competitors. However, as reported by Luskin and Potts (2011), though current research does indicate that oil palm plantations can sustain high abundances and a diverse array of species, these assemblages are distinct from those in natural forests and lack most native species. Moreover, as emphasized by (Fitzherbert et al., 2008), plantation assemblages are dominated by a few abundant generalists, non-forest species and invasive pests such as rats (Wood, 1984) or wild boar (Koh and Gan, 2007). The establishment of oil palm plantations has also increased the abundance of snakes such as cobras and pythons (Shine et al., 1999b; Shine et al., 1999a).

In response to a change in species diversity and composition following conversion from rainforest to oil palm plantations, ecosystems functioning may be significantly altered within oil palm habitats.

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7 An assemblage is usually defined as a taxonomically related group that occurs in the same geographic area (Ricklefs and Miller, 2000). However, this term may also be used for a group of taxa that are not specifically phylogenetically related, but rather geographically or “ecosystemically” related; i.e that occurs in oil palm plantations.
(Foster et al., 2011; Turner et al., 2011). However, studying trophic interactions between ant populations and their prey, Konopik et al. (2014) found that predator-prey interactions can be mostly maintained in oil palm plantations despite significant changes reported in the community composition of potential prey, and they suggest that predators are capable of exploiting new prey sources in novel ecosystems.

1.1.2.b. About the biodiversity value of existing plantations

Though the greater impact on biodiversity might definitely occur at the planting stage, depending on the previous land cover and the scale of the plantation, the ecological impact of oil palm plantation also depends on the extent to which it is able to support biodiversity and ecological services (Fitzherbert et al., 2008; Foster et al., 2011).

Biodiversity in agricultural landscapes is strongly influenced by compositional and structural landscape heterogeneity, i.e. the number and proportion of different cover types and their spatial arrangement (Burel and Baudry, 2003; Fahrig et al., 2011). The farming or management system itself, and the diversity of agricultural practices should be taken into consideration (Cawsey and Freudenberger, 2008; Burel et al., 2013a). In tree plantations, stand structural complexity, including understory and windrow composition, was shown to be of importance for fauna (Lindenmayer and Hobbs, 2004; Ramirez and Simonetti, 2011).

Therefore, we assume that the biodiversity values of oil palm plantations may depend on:
- stand age: immature versus mature, height and canopy closure;
- management practices adopted on site: 1) cropping system (e.g. monospecific versus agroforestry), 2) planting material (which influences notably canopy closure), 3) agricultural practices: windrow spatial arrangements and composition (e.g. persistent land clear or pruning residues), pesticide and herbicide usage, drainage, cover crop, etc.;
- the landscape context of the plantation (e.g. scale of the plantation, remnant of natural or semi-natural habitat patches within the plantation, presence of nearby forests within or in areas surrounding the plantation, etc.).

A sample of diverse situations is illustrated in Figure 7.

Compared to studies comparing species richness and abundance of various animal taxa between forest and oil palm plantations, little is known about the effect of different oil palm production systems (e.g. smallholdings versus industrial plantations) and management practices on biodiversity and ecosystem functions (Foster et al., 2011; Savilaakso et al., 2014).

As pointed out by Foster et al., 2011, dramatic losses of species are almost certainly due to the simplification of habitat that occurs when a forest is converted to oil palm. Indeed, compared to forest habitat, oil palm plantations are characterized by a rather low structural habitat complexity: uniform stand age and canopy height, and low ground layer vegetation cover (Luskin and Potts, 2011; Teuscher et al., 2015). Although oil palm plantations will never reach the complexity of an undisturbed or lightly disturbed rainforest, habitat features change throughout the plantation life cycle: when oil palm grows, the habitat increases in complexity, creating a more heterogeneous habitat through time (Luskin and Potts, 2011). Indeed, compared to young plantations, older plantations possess habitat features such as a more dense and complex understory (above ground structural and species complexity) and closed canopy which may provide cover and support wildlife movement, thereby being more hospitable for fauna, notably mammals, than young plantations.
(Burel and Baudry, 2003; Hilty et al., 2006; Ramirez and Simonetti, 2011). Agricultural practices such as management of ground layer vegetation cover and epiphyte persistence on oil palms will also influence habitat complexity and therefore biodiversity. Najera and Simonetti (2010), analyzing results in 14 countries, have shown that the removal of the understorey vegetation in oil palm plantations reduces bird richness and abundance. Results of Koh (2008b), in Borneo, also suggest that ground cover percentage and composition in oil palm habitat was the most important predictors of species richness for butterfly and birds. Azhar et al. (2013b) demonstrated that, for birds, each foraging guild exhibited unique responses to different stand-level attributes such as stand age, vegetation cover, epiphyte persistence and canopy cover in Malaysian oil palm plantations.

Habitat and landscape complexity might also differ among management regimes and cropping systems. Smallholding management systems are expected to be more compatible with conservation interests than large areas of oil palm plantation exploited by the agro-industry. Indeed, complexity at habitat and landscape scale has been shown to be more favorable to biodiversity (Benton et al., 2003; Lindenmayer and Hobbs, 2004; Foster et al., 2011), and smallholdings usually represent a more diverse matrix of oil palm interspersed with other habitats, such as forest remnants, while industrial plantations may cover several thousand hectares of uniform oil palm habitat with few or no patches of other vegetation types. Moreover, smallholders may practice crop association or polyculture, while industrial plantations are usually oil palm monoculture. However, the differences between industrial plantations and smallholdings largely depends on the type/characteristics of the smallholdings, which are very diverse and may vary among and within regions. In Riau province for example (in the center of Sumatra), where some of our study sites are located, many smallholdings are managed by or in association with the agroindustry or the government, and biophysical characteristics (structural habitat complexity) of smallholdings are quite similar to those of the industrial plantations.

We found only very few studies addressing how different oil palm production systems affect biodiversity, and they almost all focused on birds. According to Azhar et al. (2011, 2013b), industrial estates and smallholdings supported similar bird assemblages, but the latter support significantly more species, notably more forest species, and smallholdings supported a higher foraging guild diversity than industrial estates. Comparing the effects of monoculture (i.e. monospecific plantation) versus those of polyculture practices in oil palm smallholdings in Peninsular Malaysia, Azhar et al. (2014b), found that bird abundance was significantly greater in polyculture, but that the opposite was true for species richness as well as for abundance of insectivores and frugivores. Only one study has focussed on forest mammals, and reported more carnivores species in smallholdings than in industrial plantations (Azhar et al., 2014a).

For industrial plantations, given that oil palm is a long term pluriannual crop, with no crop rotation, and that replanting occurs about every 25 years, there is generally no issue such as habitat complementation and/or supplementation in space and time due to a crop mosaic, so called the “hidden heterogeneity” by Vasseur et al. (2013). However, landscape heterogeneity may be measured considering non-cropped areas versus crop areas (Burel and Baudry, 2003). Indeed, oil palm plantations, either smallholding or industrial, may retain forest fragments or semi-natural vegetation patches within their boundaries, thereby increasing the biodiversity within the oil palm habitat, as demonstrated for birds and some insects (Koh, 2008b; Azhar et al., 2011; Gervais et al., 2012; Lucey and Hill, 2012; Gray et al., 2014; Lucey et al., 2014). For mammals specifically, Azhar et al. (2014a) found that the number of all species, irrespectively of their conservation status, was influenced by the amount of natural forest cover within the boundaries of the plantation.
Figure 8: Photos of various oil palm plantations more or less favorable to biodiversity (various management systems, stand age and landscape context) (Source: A. Verwilghen)
As seen previously, oil palm production may undeniably have great social and environmental negative impacts. However, quoting a conservationist scientist (Meijaard, 2014), “oil palm is not the evil we think it is”, and rather than demonize the oil palm producers, some authors have advocated a constructive approach addressing the issues related to oil palm production (Rival and Levang, 2014), and more generally to conservation efforts (Tallis and Lubchenco, 2014). According to Rival and Levang (2014), “it is no longer a question of halting the expansion of the oil palm but of finding a smart way to manage it”. And, as emphasized by many authors, there is no single approach for dealing with the oil palm issue in Southeast Asia: there is a need for a broad-based, interdisciplinary and multi-pronged strategy, dealing at different scales, with a mixture of regulations and incentives, a need for research, and requiring efforts of all stakeholders from producers to governments (Fitzherbert et al., 2008; Koh and Wilcove, 2009; Wilcove and Koh, 2010; Yaap et al., 2010). Efforts to mitigate the environmental and social impacts of the oil palm industry have emerged as a result of the civil society push; the RSPO (Roundtable on Sustainable Oil Palm; see Box 1) is a good example of this. RSPO have been repeatedly criticized and the credibility of its certification has been questioned (Greenpeace, 2009; Angerand, 2011; McCarthy, 2012). Yet, some authors reported that though there is still a lot to do, it is to its credit to have initiated a process of fundamental change in policy and practice throughout the oil palm commodity chain, and the work is in progress (Laurance et al., 2010; Paoli et al., 2010; Yaap et al., 2010).

Following RSPO, the government of Indonesia has developed its own national sustainability standard, ISPO, in 2009. Compared to a voluntary initiative like the RSPO, the ISPO certification system is mandatory and applies to all oil palm growers operating in Indonesia (http://www.sustainablepalmoil.org).

**Box 1: The RSPO initiative (Source: Omont (2005), RSPO (2015))**

Established in 2004, the RSPO is a global, multi-stakeholders organization promoting the production and use of sustainable palm oil. It was initially a business-to-business initiative, bringing together private actors in the oil palm commodity chain and NGOs, in reaction to the virulent attacks against the oil palm industry. Today, RSPO has over 2000 members, representing 40% of the oil palm industry, and divided in seven categories: growers, processors and traders, manufacturers, banks and investors, retailers, environmental/nature conservation NGOs and social/development NGOs. RSPO has developed principles and criteria for sustainable production, which were approved in November 2005 (and revised in 2013), leading to certification of the first plantations in 2008. By April 2015, 3.32 million hectares were certified, representing a volume of certified sustainable palm oil of 12.27 million tons, corresponding to 18% of global palm oil production.

To minimize the adverse impacts of agriculture on biodiversity, two seemingly opposed approaches of land management have been proposed and their effectiveness are still under debate. One is land-sparing, which seek to maximize yield on intensively farmed lands thereby reducing pressure on land and facilitating the protection of natural habitat from conversion to agriculture. The other one is land-sharing, which aims to integrate biodiversity conservation and food production on the same land using wildlife-farming friendly methods (Green et al., 2005; Matson and Vitousek, 2006; Fischer et al., 2008; Koh et al., 2009; Struebig et al., 2010; Phalan et al., 2011; Law et al., 2015).
This ties up with the question of choice of development models, between smallholders or agro-industry (Rival and Levang, 2014).

Though contrasting, the two approaches of land-sparing and land-sharing are not exclusive, and a kind of “middle path” may be found. As pointed out by (Ghazoul et al., 2010) “it is necessary to consider new approaches to land management that integrate rural livelihoods and conservation with intensive production systems”.

It is clear that, to avoid major biodiversity losses, the key issue is deforestation, and appropriate strategic land-use planning at macro level is mostly needed (Struebig et al., 2010). The High Conservation Value Forests (HCVF) concept, which appears in the RSPO standard, is an important tool for this, as it aims to identify and manage areas within forest landscapes that contain ecological, social or cultural values of exceptional importance for local and global stakholders.

Intensifying the production and raising yields in plantations could potentially reduce the need for land area under oil palm.

In addition to setting aside protected areas and avoiding conversion to oil palm of forest and high conservation value habitats, it is also important to find ways of making oil palm plantations more wildlife friendly. Indeed, conservation outside protected areas, notably in agricultural lands, is essential for the survival of many wildlife species populations. Considering that these lands cover an increasingly large fraction of the globe, the agriculture landscape should represent an essential component of any conservation strategy (Perfecto and Vandermeer, 2008). Franklin and Lindenmayer (2009) reported that, to a large extent in many regions, the future of biodiversity depends on how productive areas are managed; this is truly the case for oil palm expansion in Southeast Asia. Indeed, the oil palm industry is one of the key users of agricultural lands in Southeast Asia, with a potentially large effect on conservation and biodiversity as developed above.

And thus the effort of the producer to reduce its ecological impact at the agroecosystem level, by improving agricultural practices and land use at the micro level of the estate, must be commended and supported by more research.

Moreover, wildlife–friendly management practices can go in hand with enhancement of yields according to the concept of agro-ecology and ecological intensification (Altieri, 1995, 1999; Chevassus-Au-Louis, 2006; Bonny, 2011; Griffon, 2013). Conserving the benefits of auxiliary predator and parasite biodiversity in agroecosystems, therefore maximizing the ecosystem services of natural pest suppression, has been widely studied, but research focused mainly on predatory arthropods (Straub et al., 2008; Letourneau et al., 2009; Finke and Snyder, 2010). The issue is sometimes controversial as biodiversity enhancement may in some cases negatively affect production (Tylianakis and Romo, 2010). But, on average, meta-analytical syntheses have shown that reduction in species richness can negatively affect ecosystem functioning and services, and thereby productivity (Balvanera et al., 2006; Maas et al., 2013).

Functional values of biodiversity in oil palm plantations could definitely be optimized (Anderson, 1996). For example, the maintenance of some elements of the biota within plantations could have benefits for key ecosystem processes such as pest control (Mohd Hashim et al., 2000; Lindenmayer and Hobbs, 2004). In the field of biological control, this practice of enhancing natural enemy efficacy through modification of the environment (i.e. the habitat), called conservation biological

\footnote{The HCVF or HCVs (High Conservation Values) concept was originally developed by the Forest Stewardship Council (FSC) for certification in the forestry sector.}
control, is under the spotlight (Barbosa, 1998; Tscharntke et al., 2007; Fiedler et al., 2008; Deguine and Ratnadass, 2013). Foster et al. (2011) stressed the importance of conserving biodiversity and ecosystem processes within the oil palm habitat itself. And Tscharntke et al. (2005), pointed out the often-neglected influence of landscape context on local field processes and ecosystem services in agroecosystems. However, little is known on the importance of local and landscape management for biodiversity and its relation to ecosystem services or dis-services (Tscharntke et al., 2005; Tscharntke et al., 2007; Zhang et al., 2007), specifically in the oil palm agroecosystems (Foster et al., 2011). To our knowledge, little research on this topic has been carried out in oil palm landscapes: the current SAFE (The Stability of Altered Forest Ecosystems) and BEFTA (Biodiversity and Ecosystem Function in Tropical Agriculture) projects carried out in Borneo and Sumatra respectively, are major research initiatives on this topic. The first one aims to investigate the impacts of forest conversion to oil palm and of forest fragmentation on biodiversity and ecosystem functioning at the landscape scale (Ewers et al., 2011; Turner et al., 2012); while the second focus more at the plot scale and aims to quantify the effect of habitat complexity on biodiversity and the role of this biodiversity on ecosystem functioning and crop productivity (Foster et al., 2014). More specifically related to pest control, Koh and Gan (2007; 2008) provided some examples of reptile, bird and mammal species that could potentially be providing beneficial services for oil palm cultivation in Southeast Asia. Koh (2008a) findings suggested that insectivorous birds deliver a natural pest control service for oil palm agriculture, and Azhar et al. (2013b) study demonstrated the influence of agricultural system, stand structural complexity and landscape context on foraging birds in oil palm landscapes. Considering other pest control services, there is quite a lot of literature on barn owls and their role in rodent control within oil palm plantations, but almost none on the potential role of small carnivores and on the related prey-predator interactions (see next section). Yet, rodent pest management by enhancement of small carnivores within oil palm landscapes might be a good example of win-win strategy to reconcile conservation and production.

I.2. RODENT POPULATION REGULATION AND PREY-PREDATOR INTERACTIONS IN AGRICULTURAL LANDSCAPES: LESSONS FROM EUROPEAN EXPERIENCE

I.2.1. The multifactor hypothesis and the role of predation in rodent population dynamics

Rodent population dynamics have been described mostly in temperate and polar environments; there is almost no long-term quantitative data on population fluctuations of rodents in tropical ecosystems (Krebs, 2013). However, as reported by Krebs (2013), “the conventional wisdom is that rodent fluctuations show a latitudinal gradient with strongly variable fluctuations at high latitudes and, less variable fluctuations at temperate and tropical latitude”. In particular, rodent populations in productive tropical ecosystems should be relatively stable in density, compared to the more pronounced population cycles in the less complex ecosystems of northern regions (Odum, 1971). Which environmental factors may cause rodent population changes and whether vertebrate predators can regulate their prey or not has long been a controversial question (Erlinge et al., 1984; Batzli, 1996). Some suggested that predators merely consumed the “doomed surplus”, i.e. the excess
production of a prey population which were about to die from starvation (Errington, 1946; Banks, 1999), and others that predators have a greater impact on their prey (depending on the balance between generalist and specialist predators), thereby being a significant limiting or regulating factor for small mammal populations (Pearson, 1971; Erlinge et al., 1983; Pech et al., 1992; Korpimaki and Krebs, 1996; Hanski et al., 2001; Gilg et al., 2003). “Most evidence support the hypothesis of an important role of predation in accelerating population declines and prolonging the low phase of population cycles, but there is no strong evidence that predation is sufficient to stop population growth at peak densities” (Batzli, 1996). Newsome (1990) reported that, in most cases, decline in rodent population was caused by interactions between various factors including food shortage or poor weather and predation, rather than predation alone, supporting the hypothesis that there is a limited range of population densities at which predator control is effective, known as the concept of “predator pit”. Indeed, as reported by Krebs (2013), the simple predator-prey cycles of ecological theory have become outdated, and most researchers now link predation with other limiting factors to provide a multifactor explanation for rodent population changes. The main factors or mechanisms that could cause population fluctuations or influence relative average densities are: weather, food supply, predators, parasites (macro-parasites, bacteriae, viruses, etc causing diseases), and social behavior (e.g. social mortality) (see Figure 8); these factors may be broken down into three broad types: 1) contingency causes, which may be present or absent in any particular population fluctuation, 2) necessary causes, which must be present, and 3) sufficient causes, which by themselves can cause a population fluctuation (Krebs, 2013). Anthropogenic intervention might of course also affect population dynamics, directly (e.g. hunting/harvest, rodenticide use) or indirectly.

According to Krebs (2013), two problems must be distinguished: what sets the average density of a population, and what determines the population growth rate. Average density is most likely explained by food resources (or by primary productivity in general), whether population rates of growth are affected by many factors affecting survival probability and recruitment rate, of which predation and social behavior appears to be the dominant mechanisms of regulation (Krebs, 2013).

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**Figure 9**: Factors influencing rodent population dynamics (Source: adapted from Krebs, 2013)

A hypothesis, known as the predation-as-limitation hypothesis and which is generally accepted for many animals (Krebs, 2013), suggests that rodent maximum density would be lower in predator-rich...
habitats, i.e. would be inversely related to the abundance of their predators. The best way to test the role of predators in rodent population changes is by reducing predator abundance (removing predators) or reducing their efficiency at the population peak (Korpimaki and Krebs, 1996). However, such experiments are very difficult to implement “because of the large scale at which most predators operate and because of ethical constraints on harming wildlife” (Krebs, 2013). Moreover, controlled experiments produce stronger inferences than do observations alone (Sih et al., 1985).

As reported previously, the hypothesis that predation is necessary and sufficient to produce prey population fluctuations is rejected, but other hypotheses might be valuable for some systems and are yet to be confirmed (Krebs, 2013): 1) predation is necessary but not sufficient to produce prey population fluctuations (i.e. predation mortality is one necessary component of a multifactor explanation), 2) predation is neither necessary nor sufficient to produce prey population fluctuations (predation mortality is both too sporadic and too weak to generate population changes).

The impact of predation in prey population dynamics depends notably on the numerical and functional responses of predator to prey density, and whether these responses are directly density-dependent or delayed density dependent (Holling, 1959; Andersson and Erlinge, 1977; Korpimaki and Krebs, 1996; Sinclair, 2003; Turchin, 2003; Krebs, 2013). The functional response describes the effect of individual predators in terms of the number of preys eaten per predator as a function of prey densities, and the numerical response describes how the whole predator population density responds to changes in prey density. Direct or delayed responses are a critical factor determining whether predation promotes prey stability or instability. Moreover, because specialist predator numbers decline as prey numbers decline, regulation may be determined by the presence or absence of alternative prey for the predator. It brings us to the generalist predation hypothesis, which predicts that prey communities may be stabilized by a dominant generalist predator community, whereas specialist predators would generate and/or maintain population fluctuations (Andersson and Erlinge, 1977). This hypothesis was supported by results of a long term study in a mixed farmland and woodland landscape in a temperate zone of Europe, where a rich predator community dominated by generalist carnivores showed a rapid functional response to high density of vole prey, and switch to alternative prey during low density of the main prey species (Dupuy et al., 2009).

Whatever hypothesis, one should keep in mind some key points, as emphasized by Krebs (2013) : “if prey population can compensate for predation mortality, predator kill rates may not dictate rodent population response to predation”, and “the demonstration that predators kill many individuals is not sufficient for understanding the role of predators in any system”.

Indeed, difference in predation impact is often poorly predicted by kill or predation rate and species abundance, but could rather be caused, for example, by variation in the type of selective predation occurring (Gervasi et al., 2012; Hoy et al., 2015). Undeniably, predators that demonstrated a predatory preference, among age or sex classes, may affect prey community structures, thereby causing a variety of demographic responses to predation (Dickman et al., 1991; Andreassen and Gundersen, 2006; Boukal et al., 2008). For example, if selective predation disproportionately affects individuals with low survival and/or reproductive value, such as young or senescent individuals, it may mitigate the overall impact of predators on prey population dynamics (Hoy et al., 2015).
To conclude,

1) Small mammal population dynamics are generally driven by bottom up food resources and top-down predator community processes (Krebs, 2013).

2) Predation rate, which affects survival probability and thus population growth, may be broken down in several components, as illustrated in Figure 9 below, adapted from Gervasi et al. (2012).

![Figure 10: Structural diagram illustrating the demographic processes leading to observed growth rate in prey populations, with more detailed level for predation rate (Source: adapted from Gervasi et al., 2012).](image)

3) Generalizations cannot easily be drawn when dealing with predator-prey interactions, as the potential demographic impact of a predator on its prey is influenced not only by the characteristics of the prey population (density, recruitment, etc.), but also by the characteristics of the prey and predator species/individual (reaction to predators, efficiency of attack, etc.) and by a variety of ecological factors such as the climate and productivity of the ecosystem, predator-prey body size relationships, availability of alternative prey, composition of predator community, and habitat heterogeneity (Sinclair et al., 2003; Gervasi et al., 2012; Krebs, 2013); the last two factors will be detailed below.
I.2.2. About predators interaction: competition or facilitation

It is assumed that a diverse predator guild⁹ would be more effective at controlling rodent prey populations. However, many mechanisms strongly impact predator-diversity effects, and interactions among multiple carnivorous predator species may have neutral or negative consequences for prey suppression, either directly because of their effect on carnivore demography through intraguild predation, or indirectly through behavioral effects on either the predator or the prey (Linnell and Strand, 2000; Ritchie and Johnson, 2009; Finke and Snyder, 2010). Indeed, multiple predators have effects that cannot be predicted simply by summing their individual effects (Sih et al., 1998). For example, in predator-prey foraging games, the prey’s reaction to one type of predator may either facilitate or hinder the hunting success of another predator (Embar et al., 2014), as detailed below. In addition, competitive interactions among predators may result in diet modification, as a result of a shift in space and habitat use to avoid other guild members (Caro and Stoner, 2003; St-Pierre et al., 2006).

Basically, in their competitive interactions, two different predators may be exploitative competitors or interference competitors for each other (Linnell and Strand, 2000). Exploitative competition occurs when species share the same limited resources, and one can potentially outcompete the other, either through numerical or behavioral superiority in acquiring this resource; in contrast, interference competition is the result of direct interactions such as spatial exclusion, harassment or mortality (Vanak and Gompper, 2009).

Finke and Snyder (2010) synthetized the different mechanisms behind predator-diversity effects:

- Niche complementarity: when different predator species prey on different species or stage, or attack prey in different locations in the environment or at different times or period.
- Functional facilitation: when one predator facilitates another’s hunting success.
- Sampling effect: when predators differ in their voracity and/or foraging efficiency.
- Dilution effect: when density dependent harm to a species increases with increasing single-species densities; may occur for example when greater predator diversity acts to dilute cannibalism risk.
- Intraguild predation: when a predator feeds heavily on another, or in case of interspecific killings.
- Non-consumptive effects: when predator presence alone alters the behavior, physiology, or life-history of the surviving prey.

All those interaction mechanisms within the predator guild may have more or less important implications on rodent prey demography. For example, Embar et al. (2014) reported that owls and viper facilitate each other’s hunting success through their combined effects on their main prey behavior (owls forced gerbils into the bushes where vipers preferred to ambush, while viper presence chased gerbils into the open areas where they were exposed to owls). Vanak and Gompper (2009) showed that dogs are in general not exploitative competitors with wild carnivores, but they may be effective interference competitors, especially with medium-sized and small carnivores and in areas where the native large carnivore community is depauperate. Moreover, dogs may spread diseases among wildlife (Young et al., 2011; Hughes and Macdonald, 2013). Domestic/feral cats, potential rat predators, may also have a negative impact on wild small carnivores, through

⁹ A guild is a group in an assemblage that use a suite of resources in a similar manner (Ricklefs and Miller, 2000), here it is rat predators.
competition and/or disease transmission (Nishimura et al., 1999; Izawa et al., 2009; Duffy and Capece, 2012; Medina et al., 2014).

1.2.3. The importance of landscape configuration

Spatial heterogeneity can also affect ecological systems (Wiens, 2002), notably biodiversity in agricultural landscapes. More specifically, landscape configuration (mosaic of habitat patch, edge effects, corridors, proportion of favorable to marginal habitats, etc.) can be critically important factors in influencing population dynamics, and predation and dispersal are key mechanisms linking landscape and small mammal demographic patterns (Lidicker, 1995, 2000, 2002; Krebs, 2013; Berthier et al., 2014). As predicted by Lidicker (1995), the average population density of a small rodent within one habitat patch, even a “high quality habitat”, can depend critically on the surrounding habitat and the predators this contains. Durant (1998) has shown that the concept of predator refuges, in which prey can seek respite from predation, is also applicable to interspecific competition, and can thus be crucial for the persistence of both prey and predators.

Landscape configuration may also play an important role in agroecosystems for “ecosystem balance readjustment” after rodenticide treatment. Indeed, rodenticide can induce indirect toxic effects on non-target species, such as small mammal predators (Berny et al., 1997; Berny, 2007). In such cases, treatment may have an adverse and durable effect, leaving the system more vulnerable to small mammal outbreaks in a context of decreased predator population densities and impoverished communities (Delattre and Giraudoux, 2009). The potential for predator re-colonization may depend on: (1) source habitats in the neighbouring area (e.g. natural forest, areas untreated, etc.), (2) the diversity of alternate prey that may keep predator populations more stable during periods of small mammal population decrease, those alternate prey potentially being found in or immigrating from surroundings habitats. Burton et al. (2012) highlighted the frequently complex relationships between landscape heterogeneity and carnivores ecology. It is generally assumed that a more diverse/complex landscape may enhance fauna diversity by providing a diversity of habitats, especially in agricultural landscapes (Benton et al., 2003; Scherr and McNeely, 2008; Fahrig et al., 2011; Burel et al., 2013b), as shown for some non-mammal taxa in Europe (Weibull et al., 2003; Purtauf et al., 2005), for mammalian communities in Indian coffee plantations (Bali et al., 2007) or wildlife in Australian plantation forests (Lindenmayer and Hobbs, 2004). When examining the relationship between diversity (of either plant, pollinator and predator) and productivity in real world ecosystems (i.e. non-experimental), Tylianakis et al. (2008) found a positive relationship between diversity and productivity only when a diverse array of niches is available to be portioned among species. It is to say that “biodiversity may have its greatest impact on the functioning of diverse, naturally heterogeneous ecosystems”.

The fact that landscape composition and structure can affect population dynamics of small rodents, directly (habitat and food resource) or indirectly by changing predator community composition (thus the way these predator communities impact rodent small mammal populations), is well documented in temperate countries (Delattre et al., 1992; Giraudoux et al., 1997; Duhamel et al., 2000; Morilhat et al., 2007; Morilhat et al., 2008). See Figure 10.
As discussed previously (section I.1.2 and I.1.3.), some studies showed a link between biodiversity, ecosystem function and habitat heterogeneity in oil palm landscapes. In tropical areas, White et al. (1997) found that adjacent habitats play a role in *Rattus rattus* damage levels in macadamia orchard systems, probably linked to food availability. Lindenmayer and Hobbs (2004) suggested that the maintenance within tree plantations of some elements of biota\(^\text{10}\) from the original forest could have benefits for key ecosystem processes like pest control. But in fact little is known on the influence of landscape configuration on prey-predator interactions in tropical agricultural environments, and especially within oil palm landscapes.

\[\text{We define biota as the total collection of organisms from a space delimited area (from local geographical scale up to the whole planet): flora, fauna and other forms of life such as fungi are collectively referred to as biota.}\]
I.3. INTEGRATED RODENT PEST MANAGEMENT IN OIL PALM PLANTATIONS

I.3.1. Rodent pest and damage

Expansion of large scale oil palm plantations is favorable to rodent proliferation, and some of them became invasive pests, causing serious and persistent damage (Wood and Chung, 2003; Fitzherbert et al., 2008).

In oil palm plantations in Southeast Asia, three species are dominant and represent major pests for the crop (Liau et al., 1993; Corley and Tinker, 2003; Wood and Chung, 2003): the Malaysian field rat, *Rattus tiomanicus* Miller; the ricefield rat, *Rattus argentiventer* Robinson and Kloss; and the oriental house rat, *Rattus tanezumi* Temminck -- considered as a synonym of *Rattus rattus diardii* Jentink (Musser and Carleton, 2005) and associated with the lineage of unclear taxonomic status called *Rattus R3*.

*R. tiomanicus* predominates in most mature estates, whereas *R. argentiventer* is found in immature and young plantations (Hafidzi and Saayon, 2001; Wood and Chung, 2003; Chia, 2005). A change in rat assemblage composition was reported in some localities, notably the Malaysian peninsula, as from the 80s: *R. tiomanicus* was progressively replaced by *R. tanezumi*, which is now the common rat in some places (Liau et al., 1993; Wood and Chung, 2003). Aplin et al. (2011) illustrated this regional movement of *R. tanezumi*, spreading from the IndoMalayain region Mainland Asia (Laos, Thailand, Vietnam, Malaysia) into Indonesia, overlapping on the natural range of *R. tiomanicus* on the Sundaic islands (Figure 11). Results of Andru (2012), who sampled about 380 rats in 24 mature oil palm plantations across Indonesia, showed a longitudinal gradient in the distribution of *R. tiomanicus* and *R. tanezumi*, the first being dominant in the West of Indonesia (notably in Sumatra), while the second is more present in the East of Indonesia (Bangka, Borneo, Iryan Jaya).

Figure 12: Geographical distribution and dispersion of the six lineages of the *Rattus* complex: (B) inferred natural range and (C) inferred direction of regional movement; *R. tiomanicus* is part of lineage VI, *R. tanezumi* is part of lineage II and IV. (Source: Aplin et al., 2011).

Rodent pests are a major source of crop damage worldwide, specifically in Asia, thereby highly impacting food security (Stenseth et al., 2003; Singleton et al., 2010; John, 2014). In Indonesia, they...

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11 Pagès et al. (2010; 2013) revealed the presence of an additional *Rattus* mitochondrial lineage, called R3, which include specimens identified as *R. r. diardii* (Robins et al., 2007) and was referred to as the *Rattus* lineage IV by Aplin et al. (2011). The *Rattus* R3 is morphologically indistinguishable from *R. tanezumi*, and both were found to be conspecific by Pagès et al. (2013). Therefore, in the latter, we referred equally to *R. tanezumi*, R3 and *R. r. diardii* as *R. tanezum* species.
are the most important agricultural pre-harvest pest, and loss due to this pest would be enough to feed 39 million people (Meerburg et al., 2009). In oil palm plantations, rodents, mainly rats, cause significant damage (Wood and Liau, 1984b; Turner and Gillbanks, 2003), sometimes reaching an estimated potential loss up to 10% of the production (Liau, 1990; Wood and Chung, 2003). They feed predominantly on the pericarp of oil palm fruit, whether directly on the fruit bunches on the palm tree or on detached fruit that fall to the ground when ripe; they are also found to eat apical tissues of oil palm seedlings in the nursery, the petiole bases of immature palms, and to seriously damage inflorescences; in addition, they supplement their diet by feeding on the pollinating weevil Elaeidobius kamericus, which lay its eggs in male inflorescences (Wood, 1976; Chiu et al., 1985; Hoong and Hoh, 1992; Chung, 2013). Therefore rats may also negatively affect pollination efficiency.

Rat control in oil palm plantations is generally based on field treatment using anticoagulant rodenticides and/or on the reinforcement of predation by barn owl in the plantation by providing nest boxes (Wood and Chung, 2003), as it is detailed later. The aim of this control is to maintain rat population at an acceptable level (cost of losses versus cost of control). Rodenticides may represent a significant part of all pesticide applications in oil palm plantations; for example, they make up a ¼ for plantations of the Golden Agri-Ressources (GAR) group, and this amount may be significant in terms of environmental impact and in terms of financial cost.

The annual losses associated with rat damage were estimated, ten years ago, to be from $US 48 to 288/ha, and poison baiting, estimated to $15/ha, is also costly for the oil palm industry (Wood and Chung, 2003). In addition, rats become more resistant to rodenticide following exposure (Andru et al., 2013; Chia, 2005; cf section II.2&3), and the use of rodenticides causes secondary poisoning on non-target wildlife, such as barn owls and small carnivores (Duckett, 2008; Naim et al., 2011). Thus, for a more sustainable oil palm production, predation should be enhanced and monitored to better understand its impact on rodent population dynamics.

I.3.2. Barn owls in oil palm plantations: a long story

The barn owl, which has an almost global distribution, feeds primarily on rodent species (Taylor, 1994), many of which are agricultural pests. Barn owls are potentially effective in rodent control because of a combination of behavioral characteristics and life history traits such as their ability to reproduce rapidly as prey abundance increases, their high foraging efficiency and their low territoriality in foraging ranges, as well as to the possibility to manipulate their density by providing them with nest boxes (Martin, 2009).

The barn owl (Tyto alba javanica) in Sumatra and Peninsular Malaysia was initially a migrant originating from Java. It built up from rare populations to a common status, as a consequence of oil

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12 Golden Agri-Ressources Ltd (“GAR”) is the owner of the plantations where the current research was carried out. It is a company listed on the Singapore Exchange since 1999; shareholds are held by the Widjaja family for about 50% and about 50% are publicly held. GAR’s primary activities include cultivation, harvesting and processing of oil palm products; the company is operating mainly in Indonesia and also has integrated operations in China. In 2012, GAR managed 463,426 ha of oil palm planted area (366,914 ha of nucleus and 96,512 ha of plasma) and produced 2.36 million tonnes of CPO (Crude Oil Palm), which accounted for about 9% of Indonesia’s CPO production and brings the company as the world’s second largest producer of palm oil. (GAR, 2012).

13 about 0.4 kg of commercial products/ha/year, representing about 0.001 kg of active ingredient/ha/year (GAR, 2012).
palm plantation expansion which provides an ideal ecological niche for this rat predator (Duckett and Karuppiah, 1990; Duckett, 2008). *Tyto alba javanica* can deal with larger prey than the European barn owl, and it consumes large numbers of prey: in oil palm plantation, each adult consumes one rat a day (equivalent to about 90 g of prey per day), and a breeding pair with young can consume on average 1200 to 1500 rats per year (Duckett and Karuppiah, 1990; Small, 1990).

Introduction of barn owls into oil palm plantations for rodent control was first developed in West Malaysia in the late 70s. Provision of nest boxes within plantation lead barn owl population to rapidly build up, as the shortage of suitable nesting sites was a major factor limiting population growth (Duckett, 1976; Lenton, 1980). In oil palm plantations in Southeast Asia, nest box density reported in the literature commonly range from 10 to 30 ha for one box (Small, 1990; Ho and Teh, 1997; Heru et al., 2000; Duckett, 2008; Noor Hisham and Cik Mohd Rizuan, 2013), with a high initial number of nest boxes usually progressively being reduced to a lower density following visible success of rat control. Based on predictive modelling, the rate of about 1 box per 10 ha is approximately the density which is considered by Small et al. (1990) as the preferable density when rodenticide is used. Territoriality appears negligible and barn owl have been demonstrated to be tolerant to a closer proximity to each other (Small, 1990), however higher density appears useless for further enhancing pest control. Indeed, although first trials carried out in Peninsular Malaysia with approximately one box to every 2-5 ha were reported to be successful (Duckett and Karuppiah, 1990; Small, 1990; Small et al., 1990; Duckett, 1991, 2008), Wood and Chung (2003) considered this density to be high and hypothesized that owls may in fact have been foraging far out of the site where they are nesting.

The barn owl was long been reported to be effective in controlling rats in oil palm plantations and barn owl enhancement through provision of nest boxes is now widely practiced by large oil palm companies in Indonesia. Many results showed a drop in rat damage subsequent to increased numbers of breeding barn owls and/or occupancy rates of nest boxes (Duckett and Karuppiah, 1990; Ho and Teh, 1997; Heru et al., 2000; Hoong, 2000; Adidharma, 2002; Duckett, 2008; Noor Hisham and Cik Mohd Rizuan, 2013). Most of these authors reported an efficient control by barn owls for many years without rodenticide baiting (or with baiting only at the initial stage of barn owl introduction, while waiting for barn owl population to grow). However, the relationship between the level of control and the reduction in pest abundance or the level of control and the reduction in pest damage is complex and often under examined (Hone, 2007).

For example, all these studies are based on rodent damage only, not on an estimate of rat population size. To the best of my knowledge, only two studies, by Heru et al. (2000) and Small (1990), reported that rat abundance significantly decreased after the introduction of barn owls. Moreover, most often, only damage on fruit bunches was considered, though it is not the only damage occurring. Rodents have been shown to change their habits when predators are around (Abramsky et al., 1996), and it is possible that, as soon as barn owls are introduced, rats spend more time in frond piles, consume more detached fruits and do less damage to fruit bunches still on the palm, as reported by Corley and Tinker (2003). If damage done is mostly on detached fruit, then damage rate based only on the fruit bunches still on the palm, the usual assessment method, might underestimate the actual damage and thus overestimate the real predation impact of the barn owl on rat populations.

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14 i.e. to an acceptable damage level for which the economic benefit of control exceeds the economic costs of control.
Moreover, existing modeling and field studies which investigate the relationship between barn owls and rat numbers (Small et al., 1990; Lim et al., 1991) give conflicting results as pointed out by Chia et al. (1995), Wood (2001), and Wood and Chung (2003). These authors state that “evidence of exact effect [of biological control of rats by barn owls] is inconsistent” or that “the effect on rat population size is presently inconclusive”, as supported by Kan et al. (2014).

Undeniably, the use of barn owls for biological control has many positive effects, not least effect on wildlife preservation and less environmental risk, thanks to reduction in rodenticide use, as well as cost reduction compared with chemical treatments (in cases when chemical treatment is abandoned). However, there are still some plantations where rodent damage is very high, although barn owls were introduced and their population grew. Chia et al. (1995) raised the question whether barn owls can exert a significant impact on the size of populations of their prey in oil palm plantations. Obviously, when rat density is high, barn owls alone are unable to reduce rat populations to low numbers (Chia, 2005; Noor Hisham and Cik Mohd Rizuan, 2013), as reproductive capacity of rodent might far outpaces removal of rodents via predation. From their results in a young oil palm plantation in Honduras, Padilla et al. (1995) showed that the population of some hawks appears to be affected by the amount of prey, but not the other way around, and suggested that predatory birds simply act as a regulator of prey which are above the "carrying capacity" of the environment, as predicted by the “doomed surplus” hypothesis (Errington, 1946). In Europe, studies indicated that bird of prey may only play an incidental role in regulating micromammal populations in case of outbreaks and were unable to regulate prey populations at high density (Lockie, 1955; Blondel, 1967; Sinclair et al., 1990).

Therefore, though it is largely assumed that barn owl introduction for rodent control in oil palm plantation in Malaysia and Indonesia was a success (Lenton, 1980; Small, 1990; Ho and Teh, 1997), it is likely that barn owls would be unable to keep rat populations at low numbers on their own when rat infestation is very high, and the real effect of barn owl predation on rat populations still remains inconclusive.

The demographic consequences of barn owl predation on rat populations is mediated notably by selective predation, either related to prey species or to prey body mass or sex (Sih et al., 1985; Dickman et al., 1991; Lim et al., 1991). Although barn owls where shown to feed predominantly on small mammals, notably rodents, they are mainly opportunistic and may shift towards other prey such as birds, batrachians or insects when their main prey becomes less available (i.e. when the prey declines in abundance or becomes less vulnerable to predation) (Taylor, 2009). Previous research worldwide, including in oil palm landscapes, has tried to determine whether there is selective predation according to size, weight or age of the rodent prey, but there is a lack of clear pattern: studies show a tendency for barn owls to feed on either larger (Hafidzi and Naim, 2003; Trejo and Guthmann, 2003); in Malaysian oil palm plantations: Lim et al. (1993) for R. tiomanicus or smaller/younger prey (Dickman et al., 1991; Granjon and Traore, 2007; Bueno and Motta-Junior, 2008) than expected by random selection, and sometimes demonstrate no selection (in Malaysian oil palm plantations: Puan et al. (2011b) for R. tanezumi; Small (1990) for R. tanezumi and R. tiomanicus). Some authors have suggested that differential predation by barn owl may be site specific, according to phytogeographic units (Leveau et al., 2006) and microhabitats (Trejo and Guthmann, 2003). Therefore, there is a need to investigate selective predation locally, in order to adapt pest control strategies to each site.

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Low damage in plantations where barn owls are used for biological control, without rodenticide treatment, is taken as evidence of barn owl effectiveness; but we may question what the exact part of barn owls is: are they really doing most of the job? Results of Sumantri and Wood (2012, 2013) also raised this question as they found important differences in rat populations, between different fields and over time, in plantations without barn owl introductions in the locality (no nest boxes provided) and with no chemical application for some years. We hypothesize that success of rodent control might be explained not only by the barn owls, but by an assemblage of predators, of which small carnivores may play a non-negligible role. Moreover, in some areas such as in Kalimantan, where most new oil palm plantation developments occur (Wakker, 2006; Sandker et al., 2007; Carlson et al., 2012), attempt to introduce barn owls in nest boxes have failed (Modh Naim and Sudartoho Ps, pers. com.). Furthermore, our work will show a case (Bangka island) where a rat population (rat damage) escapes control although nest boxes are provided at “optimal” densities and are well occupied by barn owls. It seems, therefore, even more important to understand, assess and enhance the role of predators others than barn owls on rodent population, in order to minimize rodenticide use.

**Figure 13**: Photos illustrating barn owl introduction in oil palm plantations. (Source: A. Verwilghen, unless otherwise mentioned)
I.3.3. Small carnivores in oil palm plantations: a story yet to be written

I.3.3.a. Small carnivores, a priority group for conservation: distribution and status overview

The term “small carnivores” is used herein for small-bodied (weighing < 15 kg) members of the order Carnivora as categorised by IUCN (Schipper et al., 2008), to which we also include small felids and small-to-medium-size canidae\(^{15}\) such as dholes (Cuon alpinus) and foxes. For Asia, the “small carnivore” group therefore includes the following families: Herpestidae (mongooses), Mephitidae (skunks and stink-badgers), Mustelidae (weasels, martens, otters, badgers and allies), Prionodontidae (linsangs), Procyonidae (raccoons, coatis and allies), Viverridae (civets), Canidae (dholes and foxes) and Felidae (“wild” cats\(^{16}\)).

The second greatest number of small carnivore species (47 species, 26%) occurs in the Indomalayan realm (Schipper et al., 2008) and Sumatra has been identified as a priority area for small carnivore conservation (Schreiber et al., 1989).

According to Wearn et al. (2013), we still do not have a clear picture of small carnivores distribution and abundance in Southeast Asia, though the proliferation of camera-trapping studies has led to an increased knowledge on many species, notably rare or cryptic ones (Holden, 2006; Veron et al., 2006; Zaw et al., 2008; Mathai et al., 2010; Wilting et al., 2010; Sunarto et al., 2013; McCarthy and Fuller, 2014; Rode-Margono et al., 2014; Sollmann et al., 2014; McCarthy et al., 2015; Sunarto et al., 2015). McCarthy and Fuller (2014) and McCarthy et al. (2015) reported that there have been few studies on small carnivores and small-to-big-size felids (except for the Sumatran tiger) in Sumatra, the majority of information on the species being taken from studies occurring on Borneo or in Mainland Southeast Asia. Consequently, little is known of their ecology, habitat use and distribution on the island (Holden, 2006; Pusparini et al., 2014; Sollmann et al., 2014), except a publication providing present knowledge on Non-Panthera cats in Southeast Asia (Duckworth et al., 2014). In Riau or Bangka province, to our knowledge, only two studies related to small carnivores have been published, and both were carried out in Riau: Sunarto et al. (2015) studied cat coexistence in four protected area in Southern Riau, and Jennings et al. (2015) (a study in which we were associated) investigated small carnivore species distribution in oil palm plantations, on two of our study sites.

A list of small carnivores (including also medium and large carnivores) potentially present in Sumatra or Bangka islands, with their IUCN Red List Status, is provided in Appendix 1. At least 4 of the 5 living small to mid-size wild cats known to be distributed in Indonesia have been recorded in Sumatra (Duckworth et al., 2014; Pusparini et al., 2014; Sunarto et al., 2015). Those recorded in Riau major protected areas were: the leopard cat Prionailurus bengalensis Kerr, the Asiatic golden cat Pardofelis temminckii Vigors and Horsfield, and the marbled cat Pardofelis marmorata Martin (Sunarto et al., 2015). The flat-headed cat Prionailurus planiceps Vigors and

\(^{15}\) The domestic dog (Canis familiaris) is not included, however we have assessed its abundance given the potential interactions of this species with small carnivores.

\(^{16}\) The domestic/feral cat (Felis catus) is usually not included in the category “small carnivores”. However, we have assessed its abundance given its potential high predation on rats and interactions with wild small carnivores.
Horsfield may be present, as this species was previously recorded in Riau (Wilting et al., 2010). Whether the fishing cat Prionailurus viverrinus Bennett occurs or not in Sumatra is still under question (Duckworth et al., 2009; Duckworth et al., 2014; Sunarto et al., 2015). To our knowledge, wild felids were never recorded as present in Bangka Island in the regional distribution database nor in any other published or unpublished occurrence recorded (Sody, 1937; Heaney, 1984, 1986; Corbet and Hill, 1992; Meijaard, 2003; Meiri, 2005; van Strien, 2011; Louys, 2014). Possible reasons for the absence of wild felids from Bangka Island will be discussed in section III.2.1.

Not less than eighteen species of small carnivores from families other than felids have been recorded in Sumatra. Due to a lack of recent occurrence records, status for the small Indian civet Viverricula indica Geoffroy Saint-Hilaire is under question and, if occurring, the species range in the island is probably restricted to the far North (Duckworth et al., 2008a; Jennings and Veron, 2011). Similarly, the range of the small Asian mongoose (also called the Javan mongoose, Herpestes javanicus Geoffroy Saint-Hilaire) in Sumatra would also be restricted to the north of the island (Wozencraft et al., 2008). According to Veron et al. (2015), the status of the collared mongoose Herpestes semitorquatus Gray in Sumatra is uncertain, due to the very low number of confirmed occurrence records for the island; however, the bright reddish-orange mongoose that may predominate in Sumatra might be misidentified with the Malay weasel Mustela nudipes Desmarest, as suggested by Ross et al. (2012). In Bangka, only six species were confirmed as present, but this may be due to paucity of surveys relative to the rest of Sumatra.

Of the 26 species of small carnivores occurring or potentially occurring in Sumatra and Bangka, according to the IUCN red list category (IUCN, 2014), 12 are regarded as least concern and the 14 other species are categorized as near threatened (3), vulnerable (5), endangered (4), or data deficient (2). Although some species of small carnivores thrive in human-dominated landscapes and have proven to be resilient, small carnivores are increasingly impacted by habitat conversion as well as by overexploitation, contamination and disease (Schipper et al., 2008). Actually, little is known about the impact of human modified habitats, such as oil palm plantations, on most species. The leopard cat, which is widespread in Southeast Asia (Sunquist and Sunquist, 2002; Duckworth et al., 2014) and regarded as of “Least Concern” (IUCN, 2014), was reported to be highly tolerant to disturbed habitat and commonly found in agricultural landscapes (Scott and Gemita, 2004; Belden et al., 2007; Lorica and Heaney, 2013; Mohamed et al., 2013; Rode-Margono et al., 2014). The common palm civet Paradoxurus hermaphroditus Pallas is also listed as Least concern (IUCN, 2014), reflecting its large population size, wide distribution, and adaptability to human-modified habitat including cultivated areas (Duckworth et al., 2008c; Jennings and Veron, 2009).

Others species are never or more rarely found in human modified habitats (IUCN, 2014) and, in the literature, we found only few occurrence records of these species in tree plantations or cultivated areas in Southeast Asia (Harrison, 1968; Scott and Gemita, 2004; Duckworth et al., 2006; Giman et al., 2007; Koh and Gan, 2007; Maddox et al., 2007; Veron et al., 2007; Jennings and Veron, 2009; McShea et al., 2009; Jennings et al., 2010a; Wilting et al., 2010; Eng, 2011; Willcox et al., 2012; Ross et al., 2013; Wahyudi and Stuebing, 2013).
I.3.3.b. And what about small carnivores in oil palm landscapes?

The interest in studying small carnivore use of oil palm landscapes is quite recent. It came first from the “conservationists”\(^\text{17}\), who were worrying about the dramatic expansion of oil palm plantations in Southeast Asia and therefore questioned the persistence of high priority conservation species or group, including small carnivores, in oil palm landscapes (Donald, 2004; Brown and Jacobson, 2005; Maddox et al., 2007; Fitzherbert et al., 2008). At that time, emphasis was placed more on the impact of oil palm development on flagship species or critically endangered species than biodiversity per se. Gradually, interest in maintaining biodiversity and ecosystem function in oil palm landscapes was raised, not only from a conservation point of view but also from a production point of view (Foster et al., 2011), and emphasis was put on the potential economic benefit of small carnivores to oil palm growers, notably cats, as predators of pest species (Scott and Gemita, 2004; Rajaratnam et al., 2007; Koh and Gan, 2008).

As a matter of fact, small carnivores play an important role in ecosystems, not only as seed dispersers (Rabinowitz, 1991; Zhou et al., 2008; Nakashima et al., 2010a; Nakashima et al., 2010b; Chakravarthy and Ratnam, 2015) but also as predators of small mammals. Indeed, though small carnivores exhibit a wide range of feeding habits, most of them include small vertebrates in their diet. Felids are the most carnivorous, sometimes called hypercarnivores; they mainly feed on small mammals, but frequently include birds, reptiles, amphibians, and insects in their diet (Sunquist and Sunquist, 2009). Viverrids have a varied diet, and their vertebrate prey is generally small in comparison to felids (Corlett, 2011); most Asian species are omnivores, consuming vertebrates, invertebrates and plant foods, particularly fruits (Jennings and Veron, 2009). Herpestidae are mainly carnivorous, but the diet can be variable between and within species (Gilchrist et al., 2009); Asian mongooses are generally considered as opportunistic predators of large invertebrates and small vertebrates (Corlett, 2011). Mustelidae and Prionodontidae are more carnivorous than most members of the Viverridae and Herpestidae family (Ray and Sunquist, 2001).

In Table 1 we summarized all occurrence records of small carnivores within oil palm landscapes or oil palm habitats, from a literature review. Nineteen species were reported. As pointed out by Maddox et al. (2005), the use of the oil palm crop itself is limited and most species are restricted to the unplanted habitat surrounding the oil palm habitat. Within the oil palm habitat, the common palm civet and the leopard cat were the most frequently recorded species, followed by the Malay civet Viverra tangalunga Gray. Five other species were recorded within the oil palm habitat, though rarely: smooth-coated otter Lutrogale perspicillata Gray, yellow-throated marten Martes flavigula Boddaert, Malay weasel, and marbled cat. Other species were also recorded within oil palm landscapes, but outside the oil palm habitat or in unknown habitats: undetermined otter species, masked palm civet Paguma larvata Gray, banded linsang Prionodon linsang Hardwicke, small Indian civet, large Indian civet Viverra zibetha, binturong Arctictis binturong, short-tailed mongoose Urva brachyuran (Herpestes brachyurus) Gray, collared mongoose, and flat-headed cat. Some authors (Scott et al., 2004) quoted the asiatic golden cat as a species showing potential for survival in oil palm. Those authors, as well as Maddox et al. (2005), also cited the fishing cat as tolerating human-altered habitat and being sighted in degraded forest habitat within oil palm landscape; however misidentifications are suspected and the presence of this species in Sumatra is still under question (Duckworth et al., 2009).

\(^{17}\) Members of the conservation movement or scientists and/or practitioners working in the field of conservation biology.
Table 1: Small carnivore species reported as occurring within oil palm-dominated landscapes in Southeast Asia. Records are differentiated according to the location of the record: within the oil palm habitat (OPH), within an oil palm plantation but outside the oil palm habitat (outside OPH), unknown area within an oil palm-dominated landscape (OPL).

<table>
<thead>
<tr>
<th>Species</th>
<th>Within OPH</th>
<th>Outside OPH</th>
<th>OPL</th>
<th>Methods</th>
<th>Location</th>
<th>Source</th>
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<tr>
<td>Smooth-coated otter (<em>Lutrogale perspicillata</em>)</td>
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<td>SS+DS</td>
<td>SU</td>
<td>Maddox <em>et al.</em> (2007)</td>
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<td>Otter sp. (<em>Lutra sp.</em>, <em>Lutrogale sp.</em>, <em>Aonyx sp.</em>)</td>
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<td>Azhar <em>et al.</em> (2014a)</td>
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<td>Yellow-throated marten (<em>Martes flavigula</em>)</td>
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<td>Malay weasel (<em>Mustela nudipes</em>)</td>
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<tr>
<td>Small-toothed palm civet (<em>Arctogalidia trivirgata</em>)</td>
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<td>Scott and Gemita (2004)</td>
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<tr>
<td>Common palm civet (<em>Paradoxurus hermaphroditus</em>)</td>
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<td>Maddox <em>et al.</em> (2007)</td>
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<td>Nakashima <em>et al.</em> (2013)</td>
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<td>Jennings <em>et al.</em> (2015)</td>
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<td>Masked palm civet (<em>Paguma larvata</em>)</td>
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<td>Azhar <em>et al.</em> (2014a)</td>
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<td>Banded linsang (<em>Prionodon linsang</em>)</td>
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<td>Azhar <em>et al.</em> (2014a)</td>
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<td>Small Indian civet (<em>Viverra indica</em>)</td>
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<td>Azhar <em>et al.</em> (2014a)</td>
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<td>Malay civet (<em>Viverra tangalunga</em>)</td>
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<td>Jennings <em>et al.</em> (2010b)</td>
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<td>Large Indian civet (<em>Viverra zibetha</em>)</td>
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<td>Azhar <em>et al.</em> (2014a)</td>
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<td>Banded civet (<em>Hemigalus derbyanus</em>)</td>
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<td>Wahyudi and Stuebing (2013)</td>
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<td>Binturong (<em>Arctictis binturong</em>)</td>
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<td>Rustam <em>et al.</em> (2012)</td>
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<td>Short-tailed mongoose (<em>Urva brachyura</em>)</td>
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<td>Ross, 2011 (pers. com.)</td>
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<td>Collared mongoose (<em>Urva semitorquatus</em>)</td>
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<td>Ross <em>et al.</em> (2012)</td>
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<td>Flat-headed cat (<em>Prionailurus planiceps</em>)</td>
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<td>BO</td>
<td>Wahyudi and Stuebing (2013)</td>
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<td>Leopard cat (<em>Prionailurus bengalensis</em>)</td>
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<td>Scott and Gemita (2004)</td>
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<td>X CT+DS+SS</td>
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<td>Maddox <em>et al.</em> (2005, 2007)</td>
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<td>Rajaratnam <em>et al.</em> (2007)</td>
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<td>Silmi <em>et al.</em> (2013a)</td>
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<td>X CT+DS+FA</td>
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<td>Azhar <em>et al.</em> (2014a)</td>
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<td>Marbled cat (<em>Pardofelis marmorata</em>)</td>
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<tr>
<td>Fishing cat (<em>Prionailurus viverrinus</em>)</td>
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<td>Maddox <em>et al.</em> (2005, 2007)</td>
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*a,b* Provisional identification and records (see Ross *et al.* 2012 for a; see Duckworth *et al.* 2009 for b).

We use the genus *Urva* for the Asian mongoose, according to Veron *et al.* (2015)

Abbreviations used:
- for methods: CT: camera trapping; RT: radio telemetry, LT: live-trapping, DS: direct sightings, FA: faeces survey; SS: sign survey (excluding faeces survey); IN: interviewed (unconfirmed records) ; UN: unpublished field record
- for location: SU: Sumatra; PM: Peninsular Malaysia; BO: Borneo
Given the potential beneficial role of small carnivores for rodent pest management, as well as the question of their persistence within oil palm landscapes, a global research programme was developed in collaboration with oil palm growers (PT Smart company\textsuperscript{18}) and researchers in the field of agronomy, ecology and conservation biology from Indonesian and French research Institutes or Universities (CIRAD, UFC, SMARTRI, LIPI, MNHN, CBGP)\textsuperscript{19} (Verwilghen et al., 2012). This study took place as part of this programme. The objective of this programme is to improve knowledge on rodent prey and their predators (prey-predator relationships) within oil palm landscapes, dealing with production and conservation issues. Another research project, aiming at assessing the effectiveness of the leopard cat in controlling rat populations in an oil palm plantation in Central Kalimantan, was also initiated more recently (Silmi \textit{et al.}, 2013a) by other oil palm growers (PT Surya Sawit Sejati) in collaboration with Copenhagen Zoo.

\begin{table}[h]
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\begin{tabular}{|c|c|}
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\textbf{I.4. SUMMARY OF KEY ISSUES AND OBJECTIVES OF THE STUDY} & \\
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\textbf{I.4.1. Key issues: from a global to a local perspective} & \\
\hline
To conclude from previous sections, we emphasise the following issues, from a global to a local perspective: & \\
\hline
1) Oil palm plantations will undeniably expand in the future; the footprint of large scale industrial plantations on biodiversity is already huge and will potentially increase. & \\
2) Both from a conservation and a production point of view, it is important to keep as much biodiversity and ecosystem processes as possible within the oil palm habitat. & \\
3) There is a knowledge gap related to these ecosystems functions, for example concerning prey-predator interactions in oil palm landscapes in connection with pest control, and notably concerning mammals; & \\
4) Rats are causing significant damage to oil palm production. Rodenticide use is costly for the oil palm industry and has harmful effects on the environment, including indirect intoxication of non-target (possibly auxiliary) wildlife. Promoting biological control of rat pests would reduce the ecological impact of oil palm cultivation. & \\
5) In the framework of a multifactor hypothesis to explain rat population dynamics, predation by natural enemies is a good candidate. & \\
6) Though the success of barn owls for rat control have been widely acknowledged, barn owl effects on rat population dynamics remains inconclusive, and owls are presumably unlikely to regulate rat populations on their own. & \\
7) Within the assemblage of rat predators, small carnivore predation may contribute to rodent population regulation or limitation. & \\
8) They are few studies on small carnivores within oil palm landscapes. & \\
\hline
\end{tabular}
\end{table}

\textsuperscript{18} PT SMART Tbk (PT Sinar Mas Agro Resources and Technology Tbk) has been developing and managing oil palm plantations in Indonesia since the mid-1980’s. PT Smart Tbk is a subsidiary of Golden Agri-Ressources Ltd (“GAR”).

\textsuperscript{19} CIRAD (Centre International de Recherche Agronomique pour le développement) ; UFC (University of Franche Comté), LIPI (Indonesian Institute of Sciences), MNHN (Muséum National Histoire Naturelle), CBGP (Centre de Biologie pour la Gestion des Populations), SMARTRI (PT Smart Research Institute).
Consequently, there is a need to investigate the contribution of small carnivores to rodent pest control, specifically within large scale industrial oil palm plantations, in a view to promote biological control of those pests and thereby reduce the ecological impact of oil palm cultivation.

Moreover,
9) Landscape configuration may be critical for the persistence of small carnivores in oil palm landscapes

Therefore, a better understanding of small carnivore habitat use within oil palm plantations is necessary to suggest appropriate land-use/land-management, in order to enhance small carnivore persistence in oil palm landscapes.

**I.4.2. Objectives of the study**

Many situations do exist in terms of rodent pest management and success in oil palm plantations. We will study two contrasted systems. In the first one, being represented by two plantations in the Riau province (Riau_1 and Riau_2), barn owls have been introduced and, according to plantation managers, rat damage, and presumably rat abundance (see below), has been controlled to an acceptable level without the use of rodenticide for many years. In the second case, being represented by two plantations in the Bangka province (Bangka-1 and Bangka_2), barn owl introduction in association with intensive rodenticide application has not prevented high levels of rat damage, as measured by plantation managers.

![Figure 14: Location of study sites in Sumatra and Bangka islands](image)

The precise relationship between rat damage and rat population level is still under question, though relative rat damage may be used as an indicator of relative rat population among our study sites (see section II.2.2).

This raises the following questions: what assumption(s) can be made to explain differences in rat abundance in both agroecosystems (Riau *versus* Bangka), with respect to small mammal communities, agricultural practices, landscape characteristics, and the predator community?
As pointed out in section I.2, many factors potentially affect rodent population dynamics; it is a complex issue and determining to what extent one or another factor predominates remains poorly understood. Predation was often reported as a fundamental cause of regulation, in association with food resources (Krebs, 2013). But we will argue in section II.1.2. that, in our study sites, food shortage is not a good candidate to explain rat population limitation in Riau plantations compared to Bangka. Therefore, in this study, we will focus on the predation factor in the framework of a multifactorial hypothesis, with the general assumption that small carnivores may contribute to the regulation of rat populations, in addition to barn owl predation.

Questions raised in the first part of this work are closely linked to the predation-as-limitation hypothesis, as inspired by Krebs (2013), stating that a particular suit of predators -here small carnivores-, limits population density of the prey species –here R. tiomanicus or R. tanezumi- so that rat density averaged over a few years will be lower if predators are present/more abundant -here in Riau plantations comparatively to Bangka-.

In predation ecology, the estimation of basic predation patterns such as kill or predation rate is often used as an indirect assessment for potential impact (Gervasi et al., 2012). To assess the impact of a predator on a prey population, one needs to know, among other factors (see I.3), the density of the prey population, the proportion of the prey population which is killed by the predator, and if there is selective predation in relation to sex or age of the prey. The proportion of prey which is killed by a predator is influenced, among other factors, by the density/ abundance of the given predator (though not a linear relationship, see notably I.3.2 about predator interactions), by its food intake (feeding requirements may depend on physiological status), and by the relative importance of the prey in its diet. In the core of this study (section III), we will explore the diet (and/or food intake), as well as the abundance and diversity of two predator categories, as represented by barn owls and by the small carnivore community. Although it is not sufficient for understanding the extent to which both predators affect the rat population, it aims to improve our knowledge on the topic.

- For barn owls:
  It is acknowledged that barn owl predation may not regulate a high density rat population on their own; however, a lower rat intake by barn owls in Bangka plantations comparatively to Riau may contribute to explaining a higher rat population level. If barn owl populations are at about a similar level in all plantations, other parameters may influence barn owl rat intake rate and should be explored, such as parameters related to barn owl diet and reproduction, which may contribute to the different number of rodent kills/year between Bangka and Riau plantations. We predict that predation pressure on rats by the barn owl is higher in Bangka plantations than in Riau. In this view, our objectives are:
  - to assess if rats make up a different proportion of the barn owl diet in Bangka plantations compared to Riau;
  - to investigate differences in barn owl breeding season in Bangka comparatively to Riau (given that reproduction intensity influences food intake).

In addition, in order to further investigate barn owl selective predation in relation to prey size or age, one must be able to determine the age structure of the prey items, and to compare it to the age structure of the prey population in the field. No reliable methods were available yet for the main prey species found locally, thus another objective of this study is:
  - to develop a tool for reconstructing rat population age structure from macroremains found in barn owl pellets.
• For small carnivores:

Little is known about small carnivore communities within oil palm plantations. We hypothesize that small carnivores contribute to rat control in oil palm plantations. We predict that small rodent maximum density will be lower in small carnivore-rich habitats. We aim to test this prediction by:

- estimating if the lower rodent density in Riau plantations, compared to Bangka, is associated with a more abundant and diverse small carnivore community, including highly carnivorous species.

In addition,
- we investigated the importance of rodent prey in the small carnivore community diet.

As pointed out by Krebs (2013), we need to link the predation hypothesis with other limiting factors to explain why the average abundance of a particular species of small rodent varies from place to place. Landscape configuration, habitat features and agricultural practices may influence small mammals or small carnivore abundance and diversity within our study sites, as demonstrated for others taxa in northern agroecosystems (Weibull et al., 2003; Aviron et al., 2005; Purtauf et al., 2005; Burel et al., 2013a).

Thus, in section II, before focusing on the predator community, we characterize and compare our study sites in term of the small mammal community (prey resource), landscape configuration, habitat features, as well as agricultural or management practices, i.e. all being factors that may explain, directly or indirectly, the variability of prey-predator dynamics in the two agroecosystems (so-called Riau and Bangka).

More specifically, our objectives are the following:

- to identify the main differences in landscape configuration between Riau and Bangka (large landscape context: provincial and regional) and between plantations (within and surroundings of each plantation);
- to describe the main characteristics of the oil palm habitat in our study sites, and assess if this habitat is different or homogeneous among the plantations;
- to identify what is/are the dominant small mammal species within the oil palm habitat, and point out the main characteristics of those species that may affect estimations of population density. In addition, because it may influence spatial distribution of rodent damage and/or predators, we will investigate if small mammals species diversity exhibits a cline from the interior of the oil palm plantation to the fringes of the neighboring habitats;
- to assess and compare rat population levels and trends between oil palm plantations;
- to analyze the differences in rodent pest management practices between the two systems and assess their relative success. In particular, we aim to investigate whether barn owl population levels are similar in Riau and Bangka, and to characterize rodenticide use in both systems (baiting procedures, rodenticide application) in comparison to the temporal evolution of rodent damage.

As reported previously, a better understanding of small carnivore habitat use in oil palm landscapes is necessary to assess which landscape configuration may enhance carnivore persistence within oil palm plantations, and consequently suggest appropriate land-use or management practices. Therefore, based on our previous landscape characterization within and surrounding the studied plantations (section II), we investigated the spatial distribution of small carnivores within the oil palm habitat, in the second part of this study (section IV). Our aim is:
- to assess the spatial heterogeneity of observations (aggregation of observations), and to investigate whether there is a correlation in spatial distribution of observations to focal habitats such as forest habitat, oil palm edge and human settlements.

In the last section (section V), we synthesize all the results and discuss them, we explore management implications, and we identify research needs.

Figure 14 below synthetizes the organization of the manuscript.
II. AGROECOSYSTEM AND LANDSCAPE: COMPARISONS OF STUDY SITES

As detailed in the general introduction, landscape configuration, habitat features and agricultural practices within the plantation, as well as diversity of the small mammal communities, may explain, directly or indirectly, the variability of the prey-predator dynamics, and thus of the results presented in the following sections.

Selection of habitat by mammals is driven by resource availability, but also by predation risk (e.g.: vegetation provides covers to the animal from predators, and human disturbance is more or less tolerated by different mammal species). Habitat quality can vary among oil palm plantations (Luskin and Potts, 2011), thereby impacting species richness and community composition. It is therefore important to characterize the oil palm habitat in our study sites and to identify potential differences among plantations.

In addition, landscape configuration can be a critically important factor in influencing rodent population dynamics, and, even in a high quality habitat, population density of a small rodent might vary depending on the nature of the adjacent habitat and the predators it contains (Lidicker, 1995; Giraudoux et al., 1997; Duhamel et al., 2000; Lidicker, 2000). Moreover the relative abundance of small carnivores is also known to be influenced by landscape configuration (Rabinowitz and Walker, 1991; Mudappa et al., 2007; Lantschner et al., 2012; Azhar et al., 2014a). Therefore it is crucial to assess landscape configuration not only within but also around the oil palm plantation.

Consequently, the objective of this section is to characterize the plantation agroecosystem of our study sites and their environment. We will focus on the differences between the two systems, i.e. Bangka and Riau, as well as on the differences between the four plantations/study sites.

Landscape will be compared at both the plantation scale (about 4,000 to 5,000 ha) and at a wider scale (regional/provincial level). We will first give details of the land cover in Sumatra/Riau and Bangka, focusing on the relative importance of oil palm and forest cover. Then we will zoom in and around the study sites. Forest habitat cover and fragmentation within and around the plantations will be assessed. The oil palm habitat as well as plantation management practices linked to rodent pest control, including rodenticide treatment and barn owl establishment, will be described. We will also document and discuss small mammal diversity within and surrounding the plantations, as well as rat population level and trends within the four plantations.

II. 1. OIL PALM PLANTATIONS AND LANDSCAPE

The study was conducted within four large-scale mature oil palm plantations in Indonesia, own by the PT Smart company. Two plantations are located in the Riau province, in central Sumatra, respectively named Riau_1 (101°11’38”E – 0°56’45”N) and Riau_2 (101°06’02”E – 0°32’10”N), and two plantations are located in the Bangka-Belitung province, in Bangka Island, respectively named Bangka_1 (105°33’14” E – 1°49’35” S) and Bangka_2 (105°26’11” E – 1°56’1” S); see Figure 13 in section I.4.2). Plantations in Riau are 38 km apart, whereas plantations in Bangka are close to each other (about 10 km).
With a view to identifying factors that could potentially influence small mammals or small carnivore abundance and diversity within our study sites, our objectives in this part are:

- to identify the main differences in landscape configuration between Riau and Bangka (large landscape context: provincial and regional) and between plantations (within and surroundings of each plantation);
- to describe the main characteristics of the oil palm habitat in our study sites, and assess if those habitats are different or homogeneous among the plantations.

We will first give a general presentation of land cover at regional and provincial level, based on a literature review and existing maps. Then, based on our own observations and land cover mapping, the landscape around and within the plantations as well as the oil palm habitat will be described. We will explore the potential of the oil palm habitat and its environment for small mammals and small carnivores, focusing on factors such as vegetation structure and human disturbance. We will also assess forest habitat cover and fragmentation within and surrounding the oil palm plantation, by calculating landscape metrics, and we will identify potential ecological barriers for small carnivores.

Potential links between the results presented in this section (habitat characterization and landscape configuration) and abundance or distribution of small carnivores within our study sites will not be explored here but will be discussed in sections III and IV.

**II.1.1. Landscape level comparisons**

**II.1.1.a. Land cover at Riau/Sumatra and Bangka**

Sumatra is the sixth largest island of the world (473,607 km²), while Bangka is a smaller island, covering 11,910 km². The population density in 2010 was of 63.6 inhabitants/km² in Riau, mainly concentrated in the provincial capital city Pekan Baru, and of 69.5 inhabitants/km² in Bangka (BPS, 2010).

Sumatra supports a wide range of ecosystems, with an uneven distribution of vegetation type between provinces: Riau has the largest area of peat swamp and mangroves, while padang vegetation and heath forest mainly occurs in Bangka (Whitten, 2000). Sumatra’s forest harbors some of the world’s highest biodiversity, but land clearing has occurred at a tremendous rate during the last few decades. Bangka is characterized by even a greater level of human disturbance and past land use change than Sumatra.

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20 From Whitten (2000):
Heath forest is known in Indonesia as ‘kerangas’ or ‘land too poor for rice growing once cleared’. It probably covers much less of Bangka island than that estimated by FAO/MacKinnon (1982) and might even be nowadays restricted to the north of the island. Heath forest usually grows on commonly called white-sand soil and can be notably different in its floral components and structure from usual lowland dipterocarp forest: it generally has a lower biomass than lowland forests; it is poor in tree species and trees of large girth, and it has a sparse ground flora. Heath forest does not seem to regenerate after burning or cultivation, and it is easily degraded into padang.

Padang is open savanna of shrubs and low trees (of which the tallest usually reach only about 5 m) over sparse grass and sedge. This shrubby vegetation grows on extremely impoverished soils and it is considered as a relatively stable secondary growth, usually deriving from heath forest degradation.
In Sumatra, undisturbed forest (upland and swamp) covered 5.7Mha representing 12% of the island area in 2010 (Gunarso et al., 2013) (see Table 2). In Riau, according to WWF Indonesia (Uryu et al., 2008), the remaining natural forest covered 2,254,118 ha in 2007, representing 27% of the province area, against 78% in 1982. Yet, in 2008/9, Riau was still the second most forested province, with 20% of all forests in Sumatra (Uryu et al., 2010), and the province and its surroundings include some major protected areas (Figure 15). The forest cover in Riau is fragmented into eight major forest blocks (see Figure 15 and 17), of which Tesso Nilo forest complex (167,618 ha), made of Tesso Nilo National Park (83,068 ha) and two logging concessions, is one of the last tropical lowland forests of outstanding conservation value left in Sumatra; in 2007, it still represented about 110,000 ha of contiguous natural forest (Uryu et al., 2008). But WWF-Indonesia (2013) estimated that, up until 2011, encroached areas inside the Tesso Nilo forest complex reached 86,238 ha or about 51% of the total area.

Table 2: Land cover area (10^3 ha) in 2010 in Sumatra (Source: Gunarso et al., 2013).

<table>
<thead>
<tr>
<th>Aggregate class</th>
<th>Area (10^3 ha) in 2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undisturbed Upland Forest</td>
<td>5,321</td>
</tr>
<tr>
<td>Disturbed Upland Forest</td>
<td>5,686</td>
</tr>
<tr>
<td>Undisturbed Swamp Forest</td>
<td>467</td>
</tr>
<tr>
<td>Disturbed Swamp Forest</td>
<td>2,073</td>
</tr>
<tr>
<td>Upland Shrub and Grassland</td>
<td>3,623</td>
</tr>
<tr>
<td>Swamp Shrub and Grassland</td>
<td>2,681</td>
</tr>
<tr>
<td>Agroforest and Plantation</td>
<td>12,012</td>
</tr>
<tr>
<td>Oil Palm Plantation</td>
<td>4,743</td>
</tr>
<tr>
<td>Intensive agriculture</td>
<td>6,700</td>
</tr>
<tr>
<td>Bare Soil</td>
<td>1,194</td>
</tr>
<tr>
<td>Others</td>
<td>3,291</td>
</tr>
<tr>
<td>Total</td>
<td>47,791</td>
</tr>
</tbody>
</table>

Figure 16 Protected areas (darker green) within Riau and surrounding provinces (Source: Eyes on the Forest (2015))
Unlike Sumatra where there is still some extensive undisturbed lowland forests left (though no more left intact according to Laumonier ((1997)), in Bangka, primary forest has totally disappeared and even natural forest is sparse and extremely patchy, as illustrated on Figure 16-a and b showing maps of remaining forest in 1982 (FAO/MacKinnon, 1982) and in 1996 (WWF-USA, from Whitten, 2000). As we can see, those maps are not congruent, and moreover, on recent maps, forest seems to cover broader areas (see Figures 16c and 19). As pointed out by Dong et al. (2014), forest area estimates, even from recent maps based on satellite imagery, vary substantially, due to their respective performance in separating oil palm or tree plantations and natural forest. In Bangka, complex rubber agroforests, which cover a large area, are also a source of misleading land cover interpretation, due to their similarities with natural forest. Indeed, those agroforests, in their mature phase, are very close to secondary forest in terms of biomass and structure, hence their name of “jungle rubber” (Michon and De Foresta, 1992; Gouyon et al., 1993; Penot, 2004; Beukema et al., 2007). According to national statistics, the total area of forest in Bangka (including production forest, protection forest, conservation forest and forest in conversion) was of 472,791 ha in 2012, that is 39.7 % of the island area (BPS, 2014b).

![Figure 17: Variability of forest cover estimations in Bangka. In grey: remaining forest (a) in 1982 (Source: FAO/MacKinnon, 1982) and (b) in 1996 (from WWF-USA, Source: Whitten, 2000); (c) forest cover, in green, as estimates in 2009 with PALSAR 50m mosaic imagery (Source: Dong et al., 2014).](image)

In Sumatra, the area of oil palm plantations reached about 4.7 million ha by 2010, occupying nearly 10% of its total land area (Gunarso et al., 2013) (see Figure 17). Other land cover areas are mentioned in Table 2.

In Riau, oil palm plantations cover a very large area, followed by pulp and paper plantations (see Figure 18). Within Indonesia, Riau is the province with the largest oil palm plantation coverage: oil palm plantations represented about 2,139,800 ha in 2012 (BPS, 2014), that is 24.3 % of the province area. The exploitation of oil and gas resources has also consistently marked Riau landscape.

In Bangka Belitung province, oil palm plantations are less extensive: they covered 192,800 ha in 2012, that is 11.7 % of the province area (BPS, 2014b). In addition to oil palm, main commodities

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21 The study of Gunarso et al. (2013) focused on large scale oil palm plantations including estates and associated scheme smallholders but “probably excluding most independent small holders whose oil palm plantings are mixed with other crops or trees”.

38
crops in Bangka Belitung islands are rubber (77,206 ha\textsuperscript{22}), pepper (45,064 ha), and coconut (11,280 ha) (BPS, 2014b). Rubber and pepper are often cultivated in association with other crops; as is the case in many oil palm smallholder plantations (at least at young age), unlike in Riau, where oil palm smallholdings have similar vegetation profile to agro-industrial plantations.

There is still quite a lot of complex rubber agroforests in Bangka compared to Riau (see remaining forest –or forest like- cover in Figure 16c), though conversion of those agroforests to rubber or oil palm plantations has been extensive in the last few decades. Those complex agroforests (“jungle rubber”) are characterized by a stand structure and a biodiversity similar to that of secondary forests, and are thus valuable habitats for conservation (Gouyon et al., 1993; Schroth et al., 2004).

Extensive areas of padang vegetation can be found in Bangka island, deriving either from land clearing or being a completely natural vegetation type (Whitten, 2000). Savannah and shrubby landscape in Bangka are also derived from mining activities. Bangka is the largest tin producing island of Indonesia, the country being in 2013 the world's biggest producer of tin; Bangka-Belitung contributes to 90\% of Indonesia's tin production (IDH, 2013). The island's is now pockmarked with thousands of moon-like craters and old barren tin mined-land. Natural vegetation regeneration on this type of land is extremely slow, from herb species at 11 years old to shrub species by 38 years-old (Nurtjahya et al., 2009).

Basically, by comparing Riau and Bangka landscapes, one could roughly describe Riau as an ocean of oil palm plantations with some remaining extensive areas of natural forest. Whereas Bangka landscape is more diverse and patchy, with a dominant mosaic of mixed agricultural production systems and forest or “forest like” habitats; though, there is no more extensive areas of natural forest in Bangka, new oil palm plantations are spreading fast and tin mining leaves a degraded savannah and shrub footprint, like oil gas fields in Riau.

\textsuperscript{22} This figure very probably do not include areas covered by “jungle rubber”.  

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\textbf{Figure 18}: Oil palm plantations in 2009 in Sumatra (Source: Gunarso et al., 2013)

\textbf{Figure 19}: Land cover in 2007 in Riau province (estimated using PALSAR FDB 50m orthorectified) (Source: Longépé et al., 2011)
II.1.1.1. Zoom in and out of the study sites

For a landscape comparison at regional or provincial level, we used existing maps and databases. As previously pointed out, these maps may be subject to misclassifications, due to their low performance in separating natural forest and oil palm or tree plantations or even herbaceous crops (Dong et al., 2014; Tropek et al., 2014). Therefore, although these maps may be valuable source of information for analysis at global or regional level, or for areas where local data is lacking (Burivalova et al., 2015), they may not be relevant for analysis at a local scale. For a fine analysis of habitat type and landscape configuration at plantation scale (plantations and surroundings), we needed more detailed data. Thus, we produced our own land cover maps based on visual interpretation of more or less recent satellite images and ground truthed observations, combined with existing PTSmart plantation maps. Those updated land cover maps were used to calculate landscape metrics in order to assess forest habitat cover and fragmentation within and surrounding the oil palm plantation. We also identified potential ecological barriers for small carnivores and assessed land cover change in the recent years.

Material and methods

At the landscape scale, some authors such as Lantschner et al. (2012) in a plantation forest landscape in Argentina, or Azhar et al. (2014a) in an oil palm landscape in Malaysia, have demonstrated that habitat use by carnivores was influenced by patch size and/or proportion of area...
covered with native vegetation. Therefore, in order to better quantify land cover in and around each plantation, we measured various landscape level attributes.

The extent of the area to be taken in consideration around each plantation for a better quantification of habitat quality for small carnivores was chosen based on the home-range of the leopard cat. We chose this species as representative of the small carnivore community because it is frequently encountered in oil palm plantations and data about its home-range size is widely available in the literature (Rabinowitz, 1990; Grassman, 2000; Grassman et al., 2005; Austin et al., 2007a; Rajaratnam et al., 2007; Izawa et al., 2009); whereas actual home range size of other small carnivore species, notably felids, are unknown or less well known (Wilting et al., 2010). Grassman et al. (2005) reported that, in a forest in Thailand, leopard cat exhibits a mean annual home-range size (minimum convex polygon method) of 12.4 km² for males and 14 km² for females. In an oil-palm dominated landscape, prey are much more abundant and the home range size is supposedly much smaller, as confirmed by Rajaratnam et al. (2007) who reported annual home-range sizes ranging from 1.9 to 4 km² in a mixed oil palm and forest landscape in Sabah. From a literature review, 14 km² was the maximum home-range size found for leopard cats; and home-range size reported for other small carnivore such as common palm civet and Malay civet were smaller (Rabinowitz, 1991; Colon, 2002; Jennings et al., 2006; Jennings et al., 2010b; Nakashima et al., 2013). Therefore, for a more accurate land cover mapping, a buffer of 15 km from the border of the oil palm plantation would be sufficient to take into account potential home-range of the small carnivore community encountered in the plantation.

The various landscape level attributes measured were as following:
- the cumulative area of each habitat type : a) within the plantation, b) within 15 km surrounding the plantation border (including the plantation itself) (Table 3);
- indices of forest habitat (or forest like habitat) fragmentation within the plantation area including the number of patch and mean patch area (Table 4);
- the mean of the distances of each point of the plantation to the forest or forest like habitat within 15 km surrounding the plantation border (including the plantation itself);
- the distance from the centroid of the estate to the nearest extensive area of forest (at least 5,000 ha) in the overall landscape (not only within the 15 km buffer around the plantation).

For all landscape metrics except the last one, i.e. for all landscape metrics concerning the inside or surroundings of the plantations, we used our own land cover maps (Figures 19 to 21), which were more accurate and confirmed by our ground truthed observations. The different habitat land cover types are defined further.

For the last landscape metric, we used the 2010 Southeast Asia land cover map from Miettinen et al. (2012), because 1) the nearest extensive forest may not be included in the 15km buffer area covered by our own map, 2) it would have been too time consuming to produce a new land use map for a larger landscape, and 3) global map remains a valuable source of forest cover information when other data are lacking (Burivalova et al., 2015). For this last landscape metric, we grouped as forest habitat the four following land cover classes as used by Miettinen et al. (2012): peatswamp, lowland forest, lower montane forest, and upper montane forest; mangroves were excluded. Lowland forest land cover class did not include the small, scattered patches of secondary forest or complex agroforests that formed part of the mixed habitat mosaic surrounding Bangka plantations.

To create our own land cover maps, the following process was used.
The land cover outside the oil palm plantations was digitalized from visual interpretation of satellite images (American Museum of Natural History, 2004): Spot 2010 and 2011 for Riau area, Spot 2008 for Bangka area, completed by ground truthed observations for the “close” surroundings (up to about 1 or 2 km from the plantation border) and for some specific areas further away (i.e. forest area in the East of Bangka_1). For each plantation, we travelled along the overall plantation border, and we recorded GPS point and took photos (with indication of direction of photo taken) each time habitat type changed; when roads were going out of the plantation, we followed them for few kilometers to broadly record habitat types; we chose to visit some specific areas further away based on questions related to satellite images interpretation (unknown land-use, or habitat to better characterize); in total, we recorded and described at least 200 ground truthed points per plantation area, and for some plantations over 300 points. To ensure consistency in land cover delimitation - notably forest cover- for areas where no ground truthed observations were made, we compared our interpretation to databases from other sources (Miettinen et al., 2012; Dong et al., 2014) and checked satellite images from various acquisition dates (Spot 2008 and Landsat 2005 for Riau area, Google Earth image from 2013 for both areas). For land cover within the oil palm plantations (oil palm block and non-plantated areas such as human settlements, enclaves, water courses, etc.), PTSmart Global Information System (GIS) database was used (integration of PTSmart layers in our own database); we verified land cover of the non-plantated areas by field observations (ground-truth). For river and stream locations in Riau, PTSmart data were completed by I. Comte data and by visual interpretation of the more recent satellite images cited above.

Land cover was classified and defined according to the following habitat types. This classification was oriented based on ecological knowledge on small carnivores: e.g. tree cover and/or vegetation height or complexity are often good predictors of their abundance (Lantschner et al., 2012; Bashir et al., 2013; Kalle et al., 2013; Mohamed et al., 2013), human activity may be repulsive (Azhar et al., 2014a), main watercourses and main roads may represent ecological barriers.

- Oil palm plantations
  - Oil palm: this habitat type groups large scale oil palm plantations, whether agro-industrial ones or smallholder ones. Distinction between these categories was made when possible (see Figure 21) but not taken into account for the analysis because 1) the distinction between agro-industrial and large scale smallholder plantations was very difficult based on interpretation of satellite image, 2) differences within the smallholder plantation category are wider than differences between agro-industrial and smallholders (pers. obs.), and profiles of the two kind of plantations are very similar in the Riau area 24. In Bangka, smallholder plantations are usually quite different from agro-industrial plantations: smallholdings mainly consist of small patches, usually cultivated in association with other crops when young, and scattered in a mosaic of agriculture and forest land use; therefore they were included in the “mosaic” habitat type (see below) and not classified as “oil palm” habitat.
  - Vegetation with a dominance of herbaceous layer
  - Savannah: typical savannah profile, with dominance of herbaceous layer. Swamp and non-swamp category have been split.

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23 In the framework of her PhD entitled “Landscape-scale assessment of soil properties, water quality and related nutrient fluxes under oil palm cultivation: a case study in Sumatra, Indonesia”, Irina Comte has digitalized the hydrographic network in Riau_2 area.

24 Consequently, there might be few errors on Figure 20, in the north of Riau_2, above the river: the area considered as small-holders may include agro-industrial plantations.
- Mining: areas where mining activity still occur or did occur in the past. This habitat is characterized by herbaceous vegetation and bare sand soil dotted with big holes more or less filled with water.
  - Vegetation with a dominance of shrub layer
- Shrub: dominance of vegetation with shrub profile. Swamp and non-swamp category have been discriminated but were not used for the analysis.
  - Vegetation with a dominance of forest layer
- Tree plantation: monospecific tree plantation (acacia, rubber, teck or gmelina). Only large scale tree plantation with homogeneous profile were included in this habitat type; smallholder rubber plantations in Bangka were not classified in this habitat type but included in the “mosaic” ones as part of a mixed agricultural and forest landscape.
- Forest: large woody areas with dense high tree cover (the FAO definition was adopted as a common sense but the notion of “dense” and “high” were quite subjectively assessed based on visual interpretation of satellite image and few ground truthed observations; the qualification of “large” was adapted according to the location, as described below). This habitat includes natural and managed forests, as well as complex rubber agroforests (such as “jungle rubber” in Bangka) and peatswamp forest, but excludind tree plantations such as the habitat type defined above. In Riau, the only forest patches remaining are usually quite large, whereas in Bangka small patches of forest left over may be scattered in a mixed landscape. Therefore, in Riau forest patches were more easily individualized and digitalized, and consequently classified as “forest”. Whereas in Bangka, inside the plantation, tiny areas of forest (less than 0.5 ha) where digitalized individually and classified as forest habitat, but outside the plantation, only larger areas (over about 20 ha) were digitalized individually; the others were included as part of the mixed agricultural and forest landscape habitat named “mosaic”. Whenever possible, swamp forest category have been discriminated within this habitat type (e.g. southeastern of Riau_1 on Figure 21), but were not used for the analysis because identification was not possible everywhere (e.g. in the extreme Southeast of Bangka_2 on Figure 22)
  - Mixed agriculture and forested areas, with dominance of agroforestry practices
    - Mosaic 1: this habitat is a patchwork of agricultural patches, including dominant young oil palm or rubber plantations, within a shrubby matrix. This habitat occurs only in Bangka.
    - Mosaic 2: this habitat is a patchwork of both mixed subsistence crops farms and palm or rubber smallholder plantations, disseminated in Bangka in a forest or forest like matrix including a lot of jungle rubber, and in Riau in a more shrubby matrix.
  - Others
- Human settlement: this habitat groups areas with a relatively high population density, such as villages or village areas, mills and dispensaries. This habitat was precisely mapped only within and in the vicinity of our study sites, and was not mapped when it lies away from the plantation after a large ecological barriers (like over the north the big river in the north of Riau_1 plantation).
- Human various: this habitat is regrouping all areas with human activities but with less human presence than for “Human settlement” habitat type; “Human various” include the following categories: air strip, petroleum or gas exploitation areas, cemetery, effluent pond or water reservoir. It was precisely mapped only within and in the vicinity of our study sites, and was not

25 “Land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent, or trees able to reach these thresholds in situ. It does not include land that is predominantly under agricultural and urban land use” (FAO, 2010).
mapped when it lies away from the plantation after a large ecological barriers (like over the north the big river in the north of Riau_1 plantation).

- Road: roads were differentiated in three categories according to their use and the nature of the road surface, e.g. plantation roads (earth road more or less busy) are considered as road_3, and tarmac roads with a lot of traffic are considered as road_1 or “main road”. Outside the plantation, only roads of category 1 (“main road”) and 2 (“secondary roads”) were digitalized. For the analysis, only the category “main road” (or road_1) was considered.

- Watercourse: rivers and streams were not considered for the calculation of landscape metrics; however, main watercourses were mapped as they may represent an ecological barrier for small carnivores.

We used QGIS version 2.2.0 (R Core Team, 2014), with GRASS and GEarthView extensions, to created our maps. Ground truthed points were located with a GPS (Garmin GPSmap 60CSx), then downloaded and transformed in appropriate format for importation in QGIS using DNR GPS application. Four maps were produced, one for each plantation.

The following process was used to calculated landscape metrics. Cumulative areas for each habitat type as well as the number and respective area of forest patches were calculated from QGIS and Excel: area of each polygon was calculated via the field calculator tool of QGIS; number of polygons, i.e. number of patches, and area of each polygon were retrieved from the attribute table; then the attribute table was converted to an excel file, which was used for summing the number of polygons and cumulative areas for each habitat type. Mean distance to forest or forest like habitat type, for each plantation, was calculated using QGIS associated with R version 3.0.3. and the pgirmess 1.5.9 package (Giraudoux, 2014): for each plantation, using QGIS, we created a vector file with a polygon representing the border of the plantation, as well as a raster file (30x30 pixels) of the shortest Euclidian distance of each point to the forest or forest like habitat within 15 km surrounding the plantation border (including the plantation itself); then we imported both files into R and used the rwhatpoly function (pgirmess package) to extract from the distance file all points included in the plantation polygon; finally we calculated the mean of these distances for each plantation in R. The distance from the centroid of the plantation to the nearest extensive area of forest in the overall landscape was estimated using QGIS from the Miettinen et al. (2012) land cover map: the raster file was converted into vector file for the polygon area calculation via the field calculator tool in QGIS, forest areas over 5,000 ha were retained, then we used the line measurer tool for distance calculation.

**Results and discussion**

Figure 19 and Table 3 show that the landscape around both Riau plantations was largely dominated by oil palm, and that, compared to Riau plantations, the surrounding landscape of both Bangka plantations was much more diverse, with forest or forest like cover more abundant in and around the plantations. For Riau plantations, the landscape in a 15 km buffer included more than 80% oil palm (owned by agro-industrial companies or smallholders), whereas it represented about 14% and 18% for Bangka plantations. The forest or forest-like habitat covered respectively 12 to 15% and 2 to 3% for Bangka and Riau plantations.

Although oil palm dominated, our results (Figure 19, 20 and Table 3) showed that the landscape around Riau_2 was a bit more diverse than around Riau_1. Oil palm habitat represents about 85% of the area around Riau_1 and about 80% around Riau_2. Riau_2 western block is adjacent to a
patch of 230 ha of secondary degraded forest (legally protected forest), and the northern border of both block are fringed with areas of riparian degraded forest or semi-natural vegetation along a large river (Tapung river). An acacia plantation is also located on its west side, whereas the rest of the surrounding landscape consists mainly of others oil palm plantations.

As shown on Figure 19 and 21 and on Table 3, for Bangka plantations the surrounding habitat included a mosaic of agricultural fields, secondary forest patches or forest like habitat such as jungle rubber, tin mining areas (both old or still in activity), shrub and savannah vegetation. From opportunistic sightings during our field surveys, confirmed by Indonesian statistics (Ministry of Agriculture, 2013) agricultural systems in Bangka were various, from monospecific plantations to complex agroforestry systems, and they included both cash crops (rubber, pepper and oil palm) and/or subsistence crops (banana, taro, cassava, yam, pineapple, etc.). In contrast to the Riau study area, where monospecific plantations (mainly oil palm) are dominant (whatever the management system, from independent smallholders to agroindustry), in Bangka study area, cash crops were also cultivated in association with subsistence crops (only at young age for oil palm), or even combined with secondary forest regrowth (jungle rubber). Moreover, in Bangka, field size was globally smaller (as detected on satellite images).

On our land cover map (Figure 19 to 21), habitat type named Mosaic_1 and Mosaic_2 are both patchworks with a dominant agroforestry profile. Mosaic_2 is a patchwork of both mixed subsistence crops farms and palm or rubber smallholders plantations, disseminated in a forest or forest like matrix including a lot of jungle rubber. This habitat covers large areas in the Bangka study areas (57% and 69%), whereas it is absent or very much reduced in Riau study area (0.12% for Riau_1) (see Table 3). With regards to Mosaic_1 habitat, which is only present in Bangka, young oil palm or rubber plantations are the dominant production system, in a matrix of shrubby savannah.

Around both Bangka estates, there are some few patches of secondary forest (including three of them ranging from about 200 to 400 ha); Bangka_2 is also connected in the Southeast to a larger area of dry and swamp forest (Figure 19)

All those characteristics provided a more complex habitat surrounding Bangka plantations than for Riau plantations.

The landscape within the oil palm plantations studied was also different between Riau and Bangka plantations. Our maps (Figure 21) and landscape metrics (Table 4) show that isolated small patches (from 0.1 ha to 25 ha, with average of 4 ha) of rubber agroforests owned by independents were retained within the oil palm cultivation areas in both Bangka plantations, for a total of 75 ha in Bangka_1 and 40 ha in Bangka_2. Riau_2 plantation did not retain any patch of natural vegetation inside the planted area, except a small incursion of swamp forest (less than 5 ha) along its eastern border. In Riau_1, swamp forest was present inside the southeastern part of the plantation (about 112 ha) and has been defined as a “conservation area” by PTSmart management; three small swampy shrub areas also lied in the northern (7.6 ha and 13.3 ha) and the southern area (19.5 ha) of the plantation.

In addition to the network of natural streams and man-made drains lying inside the plantations, a river is bordering the south of the forest patch in the western block of the Riau_2 plantation, representing potential ecological barriers to the distribution of mammals within the plantation. A tarmac road with a lot of traffic is crossing Riau_1 plantation from East to West, and may also disturb mammal movements.
According to our analysis:
- The mean of the distances of each point of the plantation to the forest or forest like habitat within the area covering 15 km surrounding the plantation border (including the plantation itself), was greater for Riau plantations than for Bangka: distances were of 1,574 m, 1,490 m, 405 m and 546 m for Riau_1, Riau_2, Bangka_1 and Bangka_1 respectively.
- The nearest extensive natural forest was about 28 km and 30 km away from Riau_1 and Riau_2 respectively, and is mainly lowland forest. In Bangka, the nearest extensive natural forest was about 9 km and 11 km away from Bangka_1 and Bangka_1 plantations respectively, but it is peatswamp forest. The more extensive area of lowland forest in Bangka, covering about 3,600 ha, was 63 km far away from both plantations. Consequently: compared to Riau, the extensive area of lowland forest in Bangka is of lower size and much more distant from the plantations.

Table 3: Relative cumulative area (in % of total area) of each habitat type a) within the plantation, b) within a 15 km buffer around the plantation, for each of the 4 estates (based on map Figure 19)

<table>
<thead>
<tr>
<th>Habitat type*</th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(a)</td>
<td>(b)</td>
<td>(a)</td>
<td>(b)</td>
</tr>
<tr>
<td>Oil palm</td>
<td>94.21</td>
<td>85.34</td>
<td>98.65</td>
<td>80.65</td>
</tr>
<tr>
<td>Forest or forest like</td>
<td>2.34</td>
<td>2.01</td>
<td>0.11</td>
<td>3.25</td>
</tr>
<tr>
<td>Mosaic 2</td>
<td>0.01</td>
<td>0.0006</td>
<td>0.12</td>
<td>0</td>
</tr>
<tr>
<td>Tree plantation</td>
<td>2.34</td>
<td>2.01</td>
<td>0.11</td>
<td>3.25</td>
</tr>
<tr>
<td>Mosaic 1</td>
<td>0.01</td>
<td>0.0006</td>
<td>0.12</td>
<td>0</td>
</tr>
<tr>
<td>Shrub</td>
<td>0.84</td>
<td>0.03</td>
<td>0.01</td>
<td>0.18</td>
</tr>
<tr>
<td>Savannah</td>
<td>0.84</td>
<td>0.03</td>
<td>0.01</td>
<td>0.18</td>
</tr>
<tr>
<td>Mining area</td>
<td>0.84</td>
<td>0.03</td>
<td>0.01</td>
<td>0.18</td>
</tr>
<tr>
<td>Human various*</td>
<td>0.40</td>
<td>9.27</td>
<td>0.23</td>
<td>8.86</td>
</tr>
<tr>
<td>Human settlement*</td>
<td>1.86</td>
<td>3.32</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Main road**</td>
<td>0.33</td>
<td>NA</td>
<td>0</td>
<td>NA</td>
</tr>
</tbody>
</table>

* see methodology for definition of habitat type.

Table 4: Forest or forest like cover and fragmentation within each plantation

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total forest or forest like area (% of total plantation area)</td>
<td>2.34</td>
<td>0.11</td>
<td>1.90</td>
<td>1.03</td>
</tr>
<tr>
<td>Number of patches</td>
<td>1</td>
<td>1</td>
<td>17</td>
<td>10</td>
</tr>
<tr>
<td>Mean patch area (ha)</td>
<td>112.26</td>
<td>4.89</td>
<td>4.127</td>
<td>3.996</td>
</tr>
<tr>
<td>Minimum patch area (ha)</td>
<td>112.26</td>
<td>4.89</td>
<td>0.1074</td>
<td>0.3125</td>
</tr>
<tr>
<td>Maximum patch area (ha)</td>
<td>112.26</td>
<td>4.89</td>
<td>25.1405</td>
<td>14.3846</td>
</tr>
</tbody>
</table>

During the three years study period, according to satellite images analysis and observations during field surveys, land cover has not much changed close by the plantations, except for Riau_2. Indeed, more than 40 ha of the riparian forest along the northern border of Riau_2 plantation has been deforested by smallholders for oil palm plantation, between 2010 and 2012. Compared to 2008, more than 160 ha of this forest corridor has disappeared (only considering south of the river and along the east-west limits of the plantation). Around and within Riau_1 plantation, we didn’t record any land cover change between 2010 and 2012; however, between 2000 and 2010/2011, a big patch of forest laying less than 7 km away in the north west of the plantation was totally deforested (see Appendix 2). For Bangka plantations, few areas surrounding were deforested and cultivated during our survey period, but no figures are available, owing to no more recent satellite images than the 2008.
Figure 21: Land cover map: 15 km around each plantation (Source: satellite images SPOT 2008 for Bangka and SPOT 2011 for Riau, combined with 2011 field surveys in plantations vicinity).

Legend:
- River and stream
- Landuse
  - Forest or forest like habitat
  - Mosaic_2
  - Mosaic_1
  - Tree plantation
  - Oil palm
  - Shrub
  - Savannah
  - Mining
  - Human settlement
  - Human various

Notes: See previous pages for habitat type description and methodology.
Figure 22: Land cover maps: zoom into the vicinity of each Riau plantation. Numbers refer to photos from Figure 23 and 24 showing characteristic habitat types. For source of data and notes: please refer to Figure 19. Complements to legend with regards to Figure 19: distinction is made between agroindustrial oil palm plantations (including nucleus and plasma) and smallholders oil palm plantations; swamps as well as main roads and secondary roads are mapped.
Figure 23: Land cover maps: zoom into the vicinity of each Riau plantation. Numbers refer to photos from Figures 25 and 26 showing characteristic habitat types. For source of data and notes: please refer to Figure 19.
Figure 24: Photos showing characteristic habitat types within and around Riau_1 (Source: A.Verwilghen). Refer to Figure 21 for approximate locations.
Figure 25: Photos showing characteristic habitat types within and around Riau_2 (Source: A.Verwilghen). Refer to Figure 21 for approximate locations.
Figure 26: Photos showing characteristic habitat types within and around Bangka_1 (Source: A. Verwilghen). Refer to Figure 22 for approximate locations.
Figure 27: Photos showing characteristic habitat types within and around Bangkla_2 (Source: A.Verwilghen). Refer to Figure 22 for approximate locations.
II.1.2. Plantations and oil palm habitat description

After comparison of our study sites at the landscape level, we will now zoom in more deeply within the plantation, and describe the oil palm habitat and the associated agricultural or management practices.

Relief and climate

The relief in the oil palm plantations is flat to slightly undulating, ranging from 10 to 70 m above ground level. The climate is humid tropical. In Riau, the average monthly temperature ranges from 26°C to 32°C, a mean annual rainfall of 2500 mm, and two dry seasons in February and May through to August (average of 140 mm/month in the dry season and 230mm/month in the wet season). In Bangka, temperature is slightly cooler (average monthly minimum of 22°C), and the second dry season is shifted one month forward (from June until September).

Plantation design

Total area for each plantation, including non-planted area (human settlements, mill, conservation areas, etc.) is of 4,743 ha, 4,388 ha, 3,905 ha and 3,846 ha respectively for Riau_1, Riau_2, Bangka_1 and Bangka_2. All plantations are in one piece except Riau_2 which is divided in 2 areas of respectively 2,541 and 1,847 ha. The areas cultivated with oil palm are of 4,386 ha, 4,124 ha, 3,680 ha and 3,658 ha respectively for Riau_1, Riau_2, Bangka_1 and Bangka_2 plantations. Each plantation is divided into cultivation blocks of uniform age, with an average size of 30 ha (1,000 m long x 300 m width), surrounded by unpaved roads. Oil palm density averages 143 palms/ha, oil palm being planted in row in a triangular pattern (palm trees are about 7-8 m apart). The structure of each block presents a harvesting path every other row, while the other row is covered with vegetation waste, including sometimes old fallen logs (during land preparation, vegetation cleared is stacked up in a windrow; later, palm fronds from trimming are piled up). A regular road grid eases access to every block of the plantation (about 45 m road/ ha in flat area). Housing sites as well as the mill are usually located within the plantation (see maps in appendix). The perimeter of each plantation is usually bounded by mound or trenches to deter harvest theft (and occasionally to reduce intrusion of wildlife damaging crops). In some areas such as swamp and peat soils, a network of drainage ditches is layed out in the plantation (see photos Figure 28). This network is particularly dense in the eastern block of Riau_2, notably in its northern and southern areas. Because most small carnivores are reluctant to cross water bodies, those drainage ditches may impedes to various degree the movements of small carnivores within the plantation.

Vegetation profile and oil palm fruiting

Riau_1 is the oldest plantation: it was planted between 1986 and 1990; both Bangka plantations were planted in between 1991 and 1996; and Riau_2 is the youngest, with plantation year ranging

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26 Source: Analysis of PTSmart weather data on Riau and Bangka plantations.
27 Depending on the width of the ditch, the depth of water, and the presence of a very narrow bridge (made of wood trunk or cement pylon) for workers to cross over.
from 1991 to 2002 (see details about proportions per planting year in Appendix 3). Both Riau plantations were planted onto previously forested land (secondary forest, the forest being logged during the seventies) (J.P. Caliman pers. com.). For Bangka plantations, previous land-cover is unknown, but was probably not dense forest cover as in Riau (J.P. Caliman pers. com.).

A plantation has a 25-30-year-life-cycle with palms beginning to fruit at about 3 years. The oil palm is monoecism, that is male and female flowers occur separately on the same plant, usually in distinct male and female inflorescences. Female inflorescences normally develop into fruit bunches after pollination by insects; in South East Asia it is mainly by the weevil *Elaedobius kamerunicis*, which have been introduced from west Africa (assisted pollination may be used when weevil population or male inflorescences are insufficient). Development to ripeness takes between 4.5 and 6 months. The bunch is ripe and ready for harvesting when fruits start to detach and fall on the ground (so called loose fruits). Due to continuous fruiting of the palm tree throughout the year, the yield cycle does not fluctuate very much over the year (see Figure 27), and consequently the monthly number or ripe fruit bunches within a block does not vary appreciably in our study sites, like in almost all Indonesian oil palm plantations. Frequency of harvesting rounds in each block varies around 15 days, leaving fruits available for rodents in their home range at any time, whether still within bunches up the tree or as loose fruits on the ground. (Corley and Tinker, 2003; Jacquemard, 2011).

Therefore, in our study sites, like in most other mature oil palm plantations in Southeast Asia, food availability for rodents is not a limiting factor to population growth (except in case of extreme and unusual climatic conditions), and is thus not a good candidate to explain the different level of rodent population between Bangka and Riau.

Vegetation profile and habitat features within the oil palm cultivated area in the four plantations are very much alike, due to close palm trees age range, as well as to similar planting material and management practices:

- closed canopy cover: Wilson and Ludlow (1991), found that, for standard oil palm plantations (planting interval, non-hybrid planting material, pruning practices, etc), canopy closure occurs at the age of about 8 to 12 years, when light penetration drops below 10%, and afterwards the tree canopies open up slightly and the percentage of light under the canopy increases. Because of quite uniform old stand age and management practices in our four studied plantations, we may consider that canopy closure is high and similar in the four plantations (with an exception to some blocks of younger age in Riau_2).

- palm tree height (stem height) is on average of about 10 m (for a 19 years old palm tree), ranging from about 7 m (for 15 years old palm trees in Riau_2) to about 13 m (for 25 years old palm trees in Riau_1)\(^{29}\);

- stem more or less covered with epiphytes growing in decaying bases of formerly cut fronds: In Riau_1, Combaz (2009) found up to about four different species per m² in stem surface; similar

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\(^{28}\) In more extreme environments, either with a severe dry season or far from the equator, yields become more seasonal, due to the shortening of the palms' productive periods and the increased synchronization of palm production cycles (% bearing palms); monthly production may thus fluctuate a lot, with the peak month reaching 40% of annual production and less than 1% in the lowest month (Nouy *et al*., 1996; Corley and Tinker, 2003). In South of Indonesia, for example in Lampung area, a severe dry season increased by the El Nino phenomenon results in a dramatic drop in oil palm fruit production, and may lead to rats dying from starvation and thus fluctuations in rat population (Lamade E., pers.com.).

\(^{29}\) A mean stem height increase of about 60 cm/year was observed by Cirad in trials in Sumatra on Deli x Yangambi crosses, as from three years old palm tree (there is very little height growth in the first three years); the relation found was: stem height = - 1.6712 + 0.049 age in months (Cochard, 2008).
figures may be found for our others study sites. As an example, total epiphyte density was of 12.35 individuals per m² at stem surface in old plantations in Malaysia (Luskin and Potts, 2011), under similar environmental conditions to our study sites.

- low understory that consisted mainly on pteridophytes and other vascular plants (Combaz, 2009) (see Box 2). On every other row, piles of vegetation waste, sometimes including old fallen logs, are mostly covered with dense ferns or regrowth. At the base of each palm, a circle of about 1.6 meter radius is maintained free of weeds (to ease loose fruit collection). The harvesting path represents a more or less 0.4 m wide bare soil strip in every other row. Roughly, about half of the area is covered with live vegetation.

Box 2: Combaz (2009) have assessed vascular plants diversity in Riau_1, among nine sampling stations located on and around the palm tree (inner circle, interval, harvesting path, windrow, fronds pile, stem, under crown, etc.) as well as in three types of open areas: dead palms, borders (roads around the fields) and rivers banks. His findings were:

- Ninety one species have been found on 150 ha sampled (22 pteridophytes, 45 dicotyledons and 24 monocotyledons); the author estimates that it represents between 75% and 93% of the studies area’s flora biodiversity.

- Pteridophytes, dicotyledons and monocotyledons are unevenly represented among stations. Species more commonly found in the circle, harvesting path and border stations are mainly monocotyledones and herbaceous dicotyledones, e.g Axonopus compressus, Centotheca lappacea, Ottochloa nodosa (Poaceae), Ageratum conyzoides (Asteraceae), Phyllanthus amarus, Croton hirtus (Euphorbiaceae), Peperomia pellucida (Piperaceae). On frond piles and windrows, shade-tolerant species are widespread, mostly big ferns such as Nephrolepis biserrata (Dryopteridaceae), Sphaerostephanos heterocarpus (Thelypteridaceae), Asplenium longissimum and Asplenium tenerum (Aspleniaceae) and a few dicotyledons like Clidemia hirta (Melastomaceae) and the very common Asystasia gangetica subsp. Micrantha (Acanthaceae).

- Species richness and Shanon and Simpson indices are generally higher at the plantation’s border and river bank stations.

Spatial heterogeneity in vegetation structure and richness are mainly due to biotic conditions such as soil type (e.g. leaning oil palm tree on hydromorphic terrain, plant species associated with peat soil or swampy areas), but there are no great differences in the range of heterogeneity among plantations.

Features such as understorey live vegetation, stem epiphytes, or piles of vegetation waste, may provide shelter or refuge for mammals, whether to Rattus spp. (Aplin et al., 2003; Puan et al., 2011a) or to small carnivores (Jennings et al., 2006; Nakashima et al., 2013). As reported previously, those features are similar among our study sites, and would therefore not influence to a high degree small mammals or small carnivore relative abundance within each plantation.
Figure 28: Seasonal oil palm yield (fresh fruit bunches) in the four studied plantations (Source: PTSmart data)
Human disturbance

Our study sites, like other oil palm plantations, are subject to human disturbance coming from the plantation management itself and from surrounding communities.

All plantations are managed intensively by a large workforce which is regularly present in the oil palm habitat to conduct field work such as harvesting and pruning (concomitant to harvesting), fertilization (mineral fertilizers or mill wastes i.e. empty fruit bunches), weeding or pesticide/herbicide application. This leads to high intensity human disturbance. In each of our studied plantations, a field is visited by several workers about every 7 days (not taking into account the more frequent circulation along the perimeter roads). Human disturbance related to these agricultural practices is thus about the same in each plantation (similar management practices), which is important to consider, knowing that it may influence negatively forest mammals abundance within the oil palm habitat, as demonstrated by Azhar et al. (2014a).

Several settlements for plantations workers and a mill are found within each plantation (often in central locations in order to reduce movement and transportation costs), except in Bangka_2 were there is no mill. The workforce/ha is a priori similar among the four plantations, therefore human pressure from this workforce is a priori similar in each plantation.

A difference in human disturbance among the four plantations may come from the influence of surrounding communities or travelers using the plantation as a pathway. Indeed, in Riau_1 for example, a very busy tarmac road crosses the plantation east-west, and literally cuts the plantation into two parts. This kind of roads may affect wildlife movements within the plantation (Austin et al., 2007b) or even cause mortality (Behera and Borah, 2010).

Another source of human disturbance within the studied plantations is hunting and poaching, carried out by plantation workers or outside people. Hunting may occur for bushmeat consumption or wildlife trade, or to reduce crop damage from wild boar (*Sus scrofa* Linnaeus) and Malayan porcupine (*Hystrix brachyuran* Linnaeus) (Corley and Tinker, 2003; Azhar et al., 2013a; Luskin et al., 2014). Estate managers often encourage hunting within the plantation area and even pay hunters to kill pests. As from our opportunistic observations during field survey and interviews among plantation staffs and surrounding communities (see section III.2.1.), hunting is much more common in Bangka plantations than in Riau plantations, and occurs mainly at night. Hunting with dogs is frequent, especially in Bangka.
In brief (Part II.1.):
Agricultural practices (excluding rodent pest control developed in another section) and environmental/abiotic conditions within the oil palm habitat are quite similar in the four plantations, except an older aged stand in Riau_1 (with higher palm trees as a consequence), as well as a younger aged stand and a more dense drainage network in Riau_2. This last characteristic, as with the presence of a busy tarmac road in Riau_1, might influence small carnivore movements within the given plantation.
Vegetation cover (hence supposedly refuge opportunities and food supply for *Rattus* population) are about similar in the four plantations and are not *a priori* candidates for explaining differences in rat population levels between Bangka and Riau. Similarly, within the oil palm habitat, there are no major differences in habitat features that may more or less favor abundance of small carnivores, except human disturbance that might be higher in Bangka than in Riau, due to a greater hunting pressure.
Though all four plantations are quite close in their physical characteristics and design, the landscape within and around plantations is much different, especially between Riau and Bangka, but also Riau_1 compared to Riau_2. The landscape mosaic is quite diverse around both Bangka plantations, including 12 to 15% of forest or forest like habitat patches; whereas oil palm habitat is largely dominating around Riau plantations (the surrounding of Riau_2 plantation being a bit more diverse than the one of Riau_1). Numerous tiny enclaves of rubber agroforestry (forest like habitat) occur within both Bangka plantations, whereas Riau_2 does not retain any patch of natural vegetation inside the planted area, and a large swamp forest is present inside Riau_1 plantation.

The main differences in habitat and landscape characteristics of each plantation studied within the two agroecosystems Bangka and Riau are synthetized in Table 8 presented in section II.4.
Figure 29: Some photos of oil palm habitat within our study sites (Source: A. Verwilghen)
II.2. RODENTS AND SMALL MAMMALS WITHIN AND SURROUNDING OIL PALM PLANTATIONS

Life-history traits of the dominant rat species in oil palm plantations, such as size, age structure, etc., might lead to differential predation, tolerance to chemical treatments or others factors possibly influencing both rats and rat predator population levels. In addition, prey-predator dynamics may depend on the diversity of alternate prey that may keep predator populations more stable during the periods of their main prey population decrease.

In this section, we will give an overview of small mammal diversity (non-volant small mammals) within and surrounding our study sites, focusing on the differences between the regions and on the cline from the interior of the plantation to the fringes of the neighboring habitats. We will also point out major characteristics of the dominant rat species in oil palm plantations. Finally, we will present general figures on rodent damage, as putative indicators of relative rat population level and trends in and between Bangka and Riau.

II.2.1. Species diversity and abundance within and around oil palm plantation

Introduction

As pointed out in the general introduction, one species of rat is usually dominant in mature oil palm plantations in Indonesia, either *R. tiomanicus* or *R. tanezumi*. But what about our study sites? We aim to identify what is/are the dominant small mammal species within the oil palm cultivated area, and to point out what are the main characteristics of those species that may affect, directly or indirectly, population density or estimation of population density. We will also investigate a potential cline of species on the fringes of the oil palm habitat.

Material and methods

We carried out various trapping sessions both within and around some of the plantations, with different objectives. Most of them were only preliminary trapping (aiming to explore how trapping methods may affect population/community estimates) and though they were not specifically framed to assess small mammals diversity, the result of those trappings gives some information about the dominant species in the plantation, species diversity in surrounding habitats, and the cline of species diversity from the interior to the limit of the plantation. Due to time constraints, a) no trapping was carried out in Bangka_2 (the habitats within and around this plantation being very similar to these of Bangka_1), and b) no trapping was carried out within the oil palm habitat in Bangka plantations (data from Andru (2012) being available for this habitat).

Details about each trapping session are detailed in Box 3. More details for R1T2 trapping session is available section III.1.3. Traps lines were checked early every morning and traps re-baited and reset if necessary. Trap-nights were calculated as the number of traps set per line multiplied by the number of lines multiplied by the number of nights. Trapping success was calculated as the total number of captures divided by the total number of traps nights.

For lives traps: squirrels were immediately released after identification; other small mammals were euthanized, weighed, sexed and classical external body measurements were collected (Herbreteau *et
al., 2011). For session B1T1: only few individuals of each different species were sacrificed for confirmation of identification, the others were released after field identification. For break back traps: most animals were severely damaged by ants during the night, which made body measurements impossible; however, tissue samples were preserved and, when possible, the skull also.

Heads were separated from main body and cleaned for further identification based on skull measurements and teeth. Tissue samples (foot or liver) were preserved for later DNA analysis in 95° ethanol. Skulls were prepared at Smartri, Libo (Indonesia), and identified partly at LIPI Indonesian Research Institute, Bogor (Indonesia) and partly at CBGP (Centre de Biologie et de Gestion des Populations), Montferrier (France). Species identification based on morphometrics and external morphology was made using the following references: Musser et al. (1979), Musser and Newcomb (1983), Corbet and Hill (1992), Aplin et al. (2003), Wilson and Reeder (2005), Chaval (2011). Some species were identified in collaboration with CBGP, using DNA analysis of tissue (molecular barcoding method, with species assignation using the RodentSEA reference database available at http/www.ceropath.org/barecoding_tool/rodentsea; (Clairon et al., 2010)). Nomenclature follows Wilson and Reeder (2005).

**Results and discussion**

**Table 5: Small mammal trapping results in and around Riau and Bangka plantations**

<table>
<thead>
<tr>
<th>Code</th>
<th>Plantation</th>
<th>Habitat</th>
<th>Number of individual trapped</th>
<th>Proportion of taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1T1</td>
<td>Riau_1</td>
<td>Oil palm (≈ 300 m from human settlement)</td>
<td>3</td>
<td>Rattus spp.* : 100%</td>
</tr>
<tr>
<td>R1T2</td>
<td>Riau_1</td>
<td>Central oil palm</td>
<td>110</td>
<td>R. tiomanicus: 100%</td>
</tr>
<tr>
<td>R2T1</td>
<td>Riau_2</td>
<td>Oil palm and surrounding habitats</td>
<td>0</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Central oil palm</td>
<td>2</td>
<td>Maxomys whiteheadi: 100%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Secondary forest</td>
<td>2</td>
<td>R. tiomanicus : 50%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Savannah</td>
<td>2</td>
<td>R. exulens: 50%</td>
</tr>
<tr>
<td>R2T2</td>
<td>Riau_2</td>
<td>Ecotone oil palm / forest</td>
<td>30</td>
<td>R. tiomanicus: 93.3%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oil palm fringe</td>
<td>0</td>
<td>Rattus sp.(unknown) : 6.7%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Secondary forest fringe</td>
<td>19</td>
<td>Maxomys spp.: 68.42% (including M. rajah and M. whiteheadi)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Rattus spp.*: 10.5%</td>
</tr>
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<td></td>
<td></td>
<td>Tupaia glis: 10.5%</td>
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<td></td>
<td></td>
<td></td>
<td>Sundamys muelleri: 5.3%</td>
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<td></td>
<td></td>
<td></td>
<td>Callosciurus notatus: 5.3%</td>
</tr>
<tr>
<td>B1T1</td>
<td>Bangka_1</td>
<td>Secondary forest (degraded) surrounding the oil palm plantation</td>
<td>53</td>
<td>Sundamys muelleri: 54.7%</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>Callosciurus notatus: 13.2%</td>
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<td></td>
<td>Niviventer spp.(including Niviventer cremoriventer): 11.3%</td>
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<td></td>
<td>Maxomys spp.*: 9.4%</td>
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<td></td>
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<td>Tupaia glis: 7.5%</td>
</tr>
</tbody>
</table>

*: Genus was identified but species was not confirmed (no barecoding for those individuals); individuals trapped may be from one or different species.
<table>
<thead>
<tr>
<th>Code</th>
<th>Plantation</th>
<th>Habitat</th>
<th>Date</th>
<th>Bait type***</th>
<th>Traps type</th>
<th>Trapping effort</th>
<th>Distance between traps on trap line</th>
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<tbody>
<tr>
<td>R1T1</td>
<td>Riau_1</td>
<td>Oil palm (about 300 m from human settlement)</td>
<td>June 2009</td>
<td>Oil palm fruit</td>
<td>ct</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Peanut butter</td>
<td>ct</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Peanut butter</td>
<td>sbbt</td>
<td>1</td>
<td>1</td>
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<td></td>
<td></td>
<td></td>
<td>Peanut butter</td>
<td>sbbt</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
<td>pt</td>
<td>7</td>
<td>1</td>
</tr>
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<td>R1T2</td>
<td>Riau_1</td>
<td>Central oil palm</td>
<td>May 2011</td>
<td>Oil palm</td>
<td>ct</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>Mix 1</td>
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<td>Mix 1</td>
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<td>sbbt</td>
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<tr>
<td>R2T1</td>
<td>Riau_2</td>
<td>Oil palm and surrounding habitats</td>
<td>June 2009</td>
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<td>Riau_2</td>
<td>Ecotone oil palm / forest</td>
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</tr>
<tr>
<td>B1T1</td>
<td>Bangka_1</td>
<td>Secondary forest (degraded) surrounding the oil palm plantation</td>
<td>August 2011</td>
<td>Oil palm fruit</td>
<td>ct</td>
<td>3</td>
<td>2</td>
</tr>
</tbody>
</table>

*bibt: big break-back trap (iron and snapping bar 9 x 16 cm); ct: cage-trap (locally-made wire-mesh live cage trap; in Riau = L:32cm; l:15cm; h:12cm ; in Bangka = L:23cm; l:12cm; h:12cm); sbbt: small break-back trap (wood and snapping bar 4.5 x 9 cm); sh: Sherman trap; pt=pitfall trap (bucket 25cm in depth and 40 cm diameter sunk into the ground, with vegetation placed in the bottom to provide protection; trap line in a L shaped configuration; a 30 m plastic drift line of about 20 cm in height run perpendicular to the ground directly over the buckets). **Number of consecutive nights. ***: Mix 1 = mix of peanut butter and mashed dry fish ; Mix 2: mix of peanut butter, shrimps paste, banana and oil palm fruit
What is/are the dominant species within the oil palm cultivated area?

Table 5 shows that *R. tiomanicus* is by far the predominant species in the oil palm habitat in Riau plantations.

Trapping results R1T2 (see details in section III.1.3) clearly indicate the dominance of *R. tiomanicus* in Riau_1, at least in the central area of the plantation: among the 110 individuals trapped and successfully sequenced, 100% were confirmed as *R. tiomanicus*.

We carried out additional trapping in Riau_2 plantations (using various baits and traps in order to maximize trapping success of the diversity of potential species, see R2T2 in Box 3), which confirmed the predominance of this species within the oil palm habitat: of 30 individuals trapped, 28 were identified as *R. tiomanicus* and 2 as *Rattus sp.* (unknown species) based on external identification (with Aplin *et al.* (2003); Corbet and Hill (1992), Herbreteau *et al.* (2011)). Although species delimitation based only on morphology is particularly difficult within the genus *Rattus* (Chaval *et al.*, 2010), we may be confident about our identification given that, for R1T2 trapping session, molecular biology had confirmed our preliminary identification for all specimens.

In the framework of her PhD, Andru (2012) also carried out trapping in Riau_1 and Riau_2 oil palm habitat. On 40 individuals trapped and identified through molecular biology, 82.5% were *R. tiomanicus* and the others *R. tanezumi*.

We did not carry out any trapping within Bangka_1 and Bangka_2 oil palm habitats. However, previous trapping carried out by PTSmart indicated that *R. tanezumi* was largely dominant in both plantations, and *Sundamys muelleri* Jentink, the Müller’s rat or giant rat, was also trapped from time to time30 (Naim M. pers.com.). Andru (2012) has demonstrated the dominance of *R. tanezumi* in oil palm plantations of Bangka island: within four plantations sampled (including Bangka_1), *R. tanezumi* represented 97.6% of all individuals trapped (n=167) in the oil palm habitat; the other species trapped were *R. tiomanicus* (1.2%), *R. argentiventer* (0.6%) and *Sundamys muelleri* (0.6%), as identified by molecular barcoding methods. *Sundamys muelleri* was also reported as an oil palm pest in Malaysia (Hoong and Hoh, 1992).

The dominance of *R. tiomanicus* in Riau plantations and of *R. tanezumi* in Bangka plantations is consistent with literature review on the distribution of rat species within Southeast Asia (Aplin *et al.*, 2003; Andru, 2012) (see section I.3.1.).

Even if the reason of replacement of *R. tiomanicus* by *R. tanezumi* remains unclear, some authors (Corley and Tinker, 2003; Wood and Chung, 2003) as well as very recent field work carried out in Riau and Bangka (Andru *et al.*, 2013) put forward the selective role of anticoagulant use, with *R. tanezumi* being more resistant and adaptive (see Box 4 in section II.3.1.). Under this hypothesis, considering that both Riau plantations are old established oil palms estates where the use of rodenticide was minimized, and even stopped for more than 10 years, it is not surprising that *R. tiomanicus* appears as the dominant species. Whereas, in Bangka plantations, which have been heavily treated for a long time, *R. tanezumi* is predominant.

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30 No more information is available on frequency of trapping. Species were identified based on external morphology as well as skull and body morphometrics, as detailed in material and methods section.
The plantain squirrel, *Callosciurus notatus* Boddaert, is also a common rodent in oil palm plantations (Koh and Gan, 2007), especially as palms get taller (Wood, 1984), and *R. exulans* Peale, the Pacific rat, have been reported to damage oil palm (Chung, 2013). Some other small rodent species were recorded within the cultivated area in Indonesian or Malaysian oil palm plantations: the Prevost's squirrel *Callosciurus prevostii* Desmarest, the Indomalayan leopoldamys or long-tailed giant rat *Leopoldamys sabanus* Thomas, the Indomalayan maxomys *Maxomys surifer* Miller, the Rajah spiny rat *Maxomys rajah* Thomas, the Whitehead's spiny rat *Maxomys whiteheadi* Thomas, the dark-tailed tree rat *Niviventer cremoriventer* Miller, and some other small mammals such as the moon rat *Echinosorex gymnurus* Raffles, the Asian house shrew *Suncus Murinus* Linnaeus, and the common tree shrew *Tupaia glis* Diard and Duvaucel (Wood, 1984; Liau et al., 1993; Scott and Gemita, 2004; Koh and Gan, 2007; Maddox et al., 2007; Rajaratnam et al., 2007); however they were only occasionally observed (or of low abundance for *M. whiteheadi*). In addition, (Wood, 1984) reported their trapping (*R. exulans, M. whiteheadi, M. rajah*) only where and when *R. tiomanicus* was at low numbers after control.

- **What about the cline on the fringes of the oil palm habitat?**

Table 5 suggests an abrupt cline from the edge of the oil palm cultivated area to the neighboring habitats. Trapping in the forest habitats adjacent to the plantations in Riau_2 (R2T1) and Bangka_1 (B1T1) show higher species richness compared to the oil palm cultivated area. In Riau_2, of 19 individuals captured in adjacent forest habitat, there was at least 6 species: the majority being *Maxomys* spp. (68.4%; *M. rajah* and *M. whiteheadi*), followed by *Rattus* spp. (10.5%), *Tupaia* sp. (10.5%), *Callosciurus* sp. (5.3%) and *Sundamys muelleri* (5.2%); whereas of 30 individuals trapped inside the oil palm cultivated area but at the fringes, a few meters from the forest, all were *Rattus* spp. Around Bangka_1, the diversity of the neighboring forest was even higher: of 53 individuals captured, about half were *S. muelleri* (54.7%), and the other half was composed of *Callosciurus* spp. (13.2%), *Niviventer* spp. (11.3% including *N. cremoriventer*), *Maxomys* spp. (9.4%), *Tupaia* sp. (7.5%), and undetermined small rodents (3.8%).

Andru (2012) also carried out trapping in Bangka_1 at the ecotone of oil palm plantation and forest, and confirmed the abrupt cline of species diversity from the adjacent forest to the oil palm habitat: of 15 individuals trapped in the fringes of the oil palm, all were *R. tanezumi*, and of 17 individuals trapped in the fringes of the forest, she found at least three species of which *S. muelleri* (47.1%), *Tupaia* spp. (35.3%) and *Niviventer cremoriventer* (17.6%).

Except Rajaratnam et al. (2007) Rajaratnam et al. (2007), who observed a comparable species richness of murids trapped in logged forest and in an oil palm plantation, most authors have highlighted the low small mammal species diversity within the oil palm compared to neighboring forest or shrub habitats (Bernard et al., 2009; Danielsen and Heegaard, 1995; Scott and Gemita, 2004).

Generally, as pointed out by Liau et al. (1993), Maddox et al. (2007) and Wood (1984), the small mammals species other than *Rattus* spp. that were observed in the oil palm habitat were recorded only on the fringes of this habitat (except the moon rat, which was detected in the center of the oil palm habitat and was probably more common); and those species have never become established in the oil palm habitat, due to high competition with *Rattus* spp.
What are the main characteristics of the dominant species that may affect, directly or indirectly, population density or estimation of population density?

The main characteristics of the dominant rodent species, such as morphology, ranging behavior and habitat utilization, or resistance to rodenticide, may impact their ability to become a pest of oil palm and may also lead to differential predation, and may thus, in turn, play a role in favoring rodent outbreaks.

According to Wood and Liau (1984b): *R. tiomanicus* breeds all year round; the mean litter size is at 4.4; the average female pregnancy rate is 17.6 %, or 27.9 % if restricted to sexually mature individuals. We found no data available for *R. tanezumi*.

Table 6: Mean adult weight of the two dominant rodent species in oil palm plantations

<table>
<thead>
<tr>
<th></th>
<th>Mean weight</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>R. tiomanicus</strong></td>
<td>91+/−34 g</td>
<td>Aplin et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>males: 101 g; females: 102 g</td>
<td>Wood and Chung (1990) (for Malaysia)</td>
</tr>
<tr>
<td><strong>R. tanezumi (R. R. complex)</strong></td>
<td>150-230 g</td>
<td>Aplin et al. (2003) (for Malaysia and Indonesia)</td>
</tr>
<tr>
<td></td>
<td>males: 139 g; females: 143 g</td>
<td>Wood and Chung (1990) (for Malaysia)</td>
</tr>
</tbody>
</table>

As reported in Table 6, *R. tanezumi* is comparatively heavier than *R. tiomanicus*. According to Wood and Chung (1990), *R. tanezumi* consumes about twice the amount of oil palm mesocarp as *R. tiomanicus* (in laboratory: a mean 9.9 g/day against 4.29 g/day), which shows its potential to be a more serious pest of oil palm than *R. tiomanicus*.

The greater body size of *R. tanezumi* compared to *R. tiomanicus* may also lead to differential predation: in Bangka, where the *Rattus* species is of greater size, barn owl may feed on smaller and younger (juvenile and subadult) individuals than in Riau. A study in an oil palm plantation in Malaysia (Puan et al., 2011b) demonstrated no clear selection of *R. tanezumi* by barn owls in relation to size of prey. However, we postulate that an adult *R. tanezumi* is large and does not correspond to the common prey size taken by barn owls in oil palm plantations, which is around 90 g (Duckett and Karuppiah, 1990; Small, 1990), which would rather correspond to an adult *R. tiomanicus*. Therefore the barn owl may preferentially select young individuals of *R. tanezumi* or adult individuals of *R. tiomanicus*. This potential selective predation, whether on reproductive (adult) or non-reproductive (juvenile and subadult) individuals may in turn influence the impact that the barn owl has on rat population dynamics (Dickman et al., 1991) in Riau and Bangka respectively. This should be explored in complement to our research, with the tool we provided for relative age prediction in *R. tiomanicus* prey from barn owl pellet macroremains (see section III.1.3.)

Both *R. tiomanicus* and *R. tanezumi* have similar home range (Wood et al., 1988). Puan et al. (2011) demonstrated that the overall occurrence of rats in an oil palm plantation was positively correlated with ground cover variables (vegetation cover, vegetation height and frond pile thickness). *Rattus* spp. are also utilizing palm crowns as a habitat, in addition to ground vegetation, inter-row frond piles and burrows (Buckle et al., 1997). Those habitats are quite similar in Riau and Bangka plantations, given the similarity of agricultural practices concerning
ground cover or trimming (see section II.1.2); therefore their characteristics may equally affect rodent populations of the same species. However, *R. tiomanicus*, known as the “canopy rat” or “wood rat”, seems to be a better climber than *R. tanezumi*. Puan et al. (2011c) reported that the relative abundance of *R. tanezumi* was more negatively correlated with palm age than of *R. tiomanicus*. And Liau (1990) suggested that the slight decline in the amount of damage as the palm get older in an oil palm plantation where *R. r. diardii* (*R. tanezumi*) was dominant might be due to the lower propensity of this species to feed on the fruit bunches still on palms (probably due to its lower ability to climb tall palm tree compared to *R. tiomanicus*). As a consequence, rat damage rate, when assessed only on fruit bunches rather than on detached fruits on the ground (see further), may be underestimated in plantations where *R. tanezumi* is dominant, such as in Bangka_1 and Bangka_2.

Resistance to warfarin in *R. tanezumi* (*R. R. diardii*) was reported by Lam (1984), and was higher and detected earlier than in *R. tiomanicus* (Lee and Kamarudin, 1987; Chia, 2005). Andru et al. (2013) has also demonstrated that *R. tanezumi* shows a much higher degree of tolerance to strong coumatetralyl exposure than *R. tiomanicus*. This may have two consequences: first a relative less efficiency of coumatetralyl rodenticide in plantations where *R. tanezumi* is present, which is the case in Bangka. Secondly, a side-effect on non-targeted wildlife: predators such as barn owl and small carnivores being secondary poisoned by ingestion of resistant live rats that had repetitively consumed the poisoned bait (Naim, 2011).

**II.2.2. Estimation of rat population levels and trends between oil palm plantations, via damage census**

**Introduction**

Though the diversity is less, a higher density of some rodent species might be found in oil palm compared to forest or shrub habitats (Scott and Gemita, 2004; Rajaratnam *et al.*, 2007). According to Wood (1984, 2001), in the absence of control, population of several hundred individuals of *R. tiomanicus* per hectare will occur in oil palm plantation (ranging from 200 to 600 rats / ha). *R. tanezumi* (referred to as *R. r. diardii* by the authors) tends to occur in smaller numbers than *R. tiomanicus* (Wood and Chung, 2003). Trapping success within Riau_1 plantation in 2011 (R1T2) confirmed the relatively high density of rats in the oil palm habitat: the mean trapping success across all lines was 46.3 % the first night (with a maximum of 60.8% and a minimum of 20%), 39.5% the second night (maximum 48%, minimum 32%), and 27.3% the third night (maximum 48%, minimum 12%). Therefore, we presume that rat population level in the four plantations might be high, but differences among plantations are yet to be investigated. According to plantation managers, rats are more abundant in Bangka than in Riau, thereby causing more damage to oil palm fruits. Our objective is to confirm differences between Riau and Bangka, by comparing rat population level and trends between plantations.

**Material and methods**

We don’t have any direct data to compare the level of rat populations between the four plantations. However, rodent damage may be used as a broad indicator of rat population abundance. Indeed, although the relation between fresh damage (percentage of palms showing
signs of recent damage on fruit bunches –i.e. infructescences- on the palm) and absolute rat population size is not well established for oil palm (Khoprasert et al., 2008), some authors such as (Wood, 1976) demonstrated a close correlation between rat population size (estimated by catch, mark, release and recapture technique) and amount of fresh damage. Puan et al. (2011c), also showed that the relative abundance of rats was significantly correlated to the levels of damage to bunches. Therefore, we will use the percentage of palms with fresh damage for a broad comparison of the relative levels of rat abundance between plantations, and to monitor changes over time.

For analysis, we used field data of rodent damage available from PTSmart plantation management. In Riau and Bangka plantations, rodent damage is assessed as the percentage of palm with fresh damage on the ripe fruit bunches still on the palm. Freshness of damage is recognizable by color (damage fads in color after few days). The census is conducted previously to harvesting rounds, before removal of mature bunches. Damage is assessed by eye from the height of the surveyor (no use of mirror to reduce potential bias mentioned previously). A sample of five percent of the trees of each block is inspected (one row every 20 rows, each census the same row, every tree in the selected row is inspected). Damage is recorded as present or not, resulting in the percentage of palms affected per block. In Riau, there are four rounds of inspection per year: in January, April, July and October; whereas in Bangka census is carried out once every month. Data from 2006 till 2012 are available for Bangka and Riau_2 plantations, though for Riau_1 data are available only as from 2008. Data are missing for some blocks, for one or two months at Riau_2 in 2006 and 2007, but it represents a small part of the yearly data (2.8 % for 2007 and 5.8 % for 2006).

As a first step, we assessed, by cross-correlation, if the temporal series of rodent damage in the two plantations from the same region had the same pattern, i.e. were correlated: for each region, we measured the similarity in rodent damage between the two plantations (the cross-correlation, as estimated based on sample covariance) as a function of the time lag (time difference) of one relatively to the other. We found temporal autocorrelation of data for all plantations, thus, to check the validity of our results, we also tested cross-correlation by permutation test (1000 repetitions), as to avoid an overestimation of the degrees of freedom potentially due to temporal autocorrelation. Analyses were conducted using R version 3.0.3. (R Core Team, 2014), with the function “ccf” (package stats) to compute cross-correlation of two univariate series, and the function “acf” to estimate auto-correlation.

In addition, we compared levels of rodent damage in the four plantations from visual analysis of their respective curves.

Results and discussion

• About potential biases

Sumantri and Wood (2012), based on a study in an oil palm plantation in South Sumatra, argued that percentage of palm with fresh damage only loosely correlated to rat population size, making it an imprecise indicator. Many causes may explain the bias, as tentatively investigated below. A minor issue is whether rats are indeed causing the damage observed. Indeed, squirrels may also damage palm fruits and differentiation between rat damage and squirrel damage is usually

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31 5% for blocks of mature palms and 10% for immature.
not done in the field. However squirrel damage is not great and is said to be insignificant compared to damage related to *Rattus* (Wood, 1976; Luskin et al., 2014).

A possible major source of bias of the fresh damage indicator is the palm height (either linked to the age of the palm or to the nature of the soil substrate -e.g. leaning trees in peat soil areas) and pruning operations, which can influence the amount of fresh damage seen on the bunch up the palm tree (Wood and Chung, 2003). Liau (1990) observed that damage score for equivalent rat population levels of the same species were lower as the palms get older and taller. This bias may be overcome if damage is assessed by using a mirror to observe above the eye level, or if damage is assessed on the bunch once harvested and not when still on the tree; however these alternatives are not yet implemented at PTSmart. Moreover, detached and fallen ripe fruits (so called detached fruits) are usually not taken into account in damage assessment, but rodents may feed more or less on detached fruits on the ground rather than on fruit bunches still on the palms. Indeed, rodents may adapt their behavior for one reason or another, including as a functional response 1) to predation (rodents have been shown to change their habitat use and foraging habits when predators such as barn owls are present (Kotler et al., 1994; Abramsky et al., 1996), 2) or as palms grow taller (variable climbing ability according to rodent species). As an example, according to Liau (1990), *R. tanezumi* may feed more on the detached fruits rather than on bunches on the palm, due to his lower ability to climb tall palm trees compared to *R. tiomanicus*. We should keep in mind these limitations, notably the probable bias due to the younger age of the oil palm trees in Rama and the lower climbing ability of the dominant rat species in Bangka, when using the percentage of palms with fresh damage for broad comparison of relative levels of rat abundance between plantations.

- **Does the two plantations from the same region have similar patterns of rodent damage?**

![Cross-correlation graphs](image)

**Figure 30:** Estimated cross-correlation between rodent damage from both plantations of the same region, as a function of the time lag. A time lag of 0 represents no time difference, a time lag of 1 represents one year difference (for Bangka, the interval between two vertical lines represents one month, whether for Riau it represents 3 months). Significance level for cross-correlation is indicated by the dash horizontal line.

As shown in Figure 30, rodent damage patterns within the same region appeared similar, may it be for Bangka or for Riau: for a time lag of zero, i.e. considering both plantations at the same time period, we found a significant positive correlation between both series. In Bangka, the time-
lag window at which correlations are evidenced is much longer than in Riau: in Riau series are correlated only at the same time period (0 month time lag), whereas in Bangka series are correlated for time-lag between -11 months to +3 months.

However, when using permutation test, we found a significant positive correlation between rodent damage series in Bangka plantations at the same time period ($p<0.0001$), but we failed to detect such correlation for Riau plantations ($p=0.113$).

- **Comparison of rodent damage global level among plantations**

  ![Figure 31: Monthly evolution of rodent damage in Bangka and Riau plantations, from 2006 till 2012.](image)

Figure 29 shows level and trends of the observed rodent damage in the four plantations. From visual analysis of this figure, Riau_1 seems different from the others plantations with lower rodent damage (rate below 2% almost all years) and less dispersion of monthly data (Figure 31). Whatever the month, both Bangka plantations had a higher mean damage rate than Riau_1 (around 3% or more), the rate being generally less in Bangka_1 than in Bangka_2. In Riau_2 plantation, the damage level was quite high compared to the one of Riau_1 and laid slightly below Bangka, though sometimes higher.

From Figure 29, and if we consider potential bias in rodent damage assessment, we may infer that the average rat population is higher in Bangka than in Riau. Indeed, the damage level in Riau_1 should be adjusted in order to compensate for the bias due to the overall older and taller palm trees (see previously), leading to relative underestimation of damage on fruit bunches in this plantation compared to other plantations where palm tree are generally lower. In contrast, due to the younger age of palm trees in Riau_2, rodent damage level in Riau_2, and consequently rat population size, might be lower and possibly more similar to Riau_1 than to Bangka. In addition, the higher propensity of *R. tanezumi* to feed on the detached fruits rather than on bunches on the palm (due to his lower ability to climb tall palm trees compared to *R. tiomanicus*) as highlighted by Liau (1990), may lead the damage to be underestimated in Bangka compared to Riau. Consequently, all this would confirm that the rat population would probably be more abundant in Bangka than in Riau plantations.
Figure 32: Rodent damage in Bangka and Riau plantations: annual mean and dispersion of data from 2006 to 2012. Boxes contain the middle 50% of the data. Horizontal solid lines in boxes represent the median value, and the white diamond the mean. End of vertical lines represent the minimum and maximum value, and small circles are outliers.

- **What about the rodent damage peak recorded in Riau_2?**

An outstanding rodent damage rate of around 7.5% was recorded in Riau_2 in January and April 2010 (compared to a rate between 2-2.5% just before and after) (Figures 29 and 32). Various elements demonstrates that it is probably not an aberrant data:

- verification on hard data (field registration document) and oral confirmation by plantation staff;
- investigation of spatial distribution of the damage rate: the high rate is largely distributed in a large number of blocks, with a gradient in the values (see Figure 32). If it was limited to very high rate in one or two blocks, with “normal” rate all around, it could have lead us to hypothesize an error of transcription.

This peak in rodent damage is presumably the consequence of a rat population outbreak. Figure 29 shows a similar though much lower peak at the same period in Riau_1.

Figure 33: Spatial distribution of rodent damage in Riau_2 plantation before -(a) October 2009-, during -(b) January 2010 and (c) April 2010-, and after -(d) July 2010- the peak of 2010.

- **Does the rat population remained stable or showed seasonal cycle?**

Figure 29 shows no clear pattern indicating any seasonal cycle of rodent damage. In the tropics, due to relatively stable environmental conditions, the effect of cycling in vertebrate population is commonly reduced compared to European regions, but some authors suggest that rodents may generally be more common in the latter part of the dry season than...
during the wet season (Singleton and Petch, 1994). Extreme and unusual climatic conditions such as flooding during the wet season (Wood and Liau, 1984b; Madsen and Shine, 1999) or very severe drought (see section II.1.2.) might also affect rat population dynamics.

Trapping results from Scott and Gemita (2004) in oil palm and surrounding habitats indicated no statistically significant difference in overall density of small mammals between wet and dry seasons. In a long-term (10 years) study in a mature oil palm plantation in Malaysia without control measures, Wood (1984) demonstrated that the population of *R. tiomanicus* fluctuates slowly, between about 200 and 500 rats/ha, with no marked seasonal effects, although he noted that exceptionally heavy and prolonged rainfall might possibly influence negatively the survival rate. The absence of seasonal variation in rat populations in oil palm plantation is probably due to a relatively constant temperature and to a constant food supply, thanks to continuous oil palm fruiting throughout the year, as suggested by Lenton (1984). Wood (1984) study was extended for 10 more years, over the period of replanting, and population trends shows cycle of about 7 years (Wood and Chung, 2003). According to Corley and Tinker (2003), the reason why, in the absence of control measures, the population remains quite stable over a long period and rarely exceeds 500 rats/ha, seems to be due to some intraspecific mechanisms (such as population pressure affecting breeding success or survival of young rats) rather than to external environmental variables. The existence of some form of self-regulation for rat population in oil palm plantations was suggested by Wood and Liau (1984b), and acknowledged by Wood and Chung (2003).

In brief:

- Species richness of non-volant small mammals within the oil palm habitat was very low compared to surrounding habitats; it was basically restricted to *Rattus* spp., even in the fringes of the oil palm plantation (abrupt cline at the ecotone of the oil palm habitat).
- Rodent damage within Bangka plantations showed similar temporal patterns, and rodent damage levels in both Bangka plantations were higher than in Riau plantations. Using rodent damage as a broad indicator of rat population relative size and considering the probable bias due to the assessment method, we may infer that *Rattus* were more abundant in Bangka than in Riau, and that the rat population level was quite similar within each region.
- *Rattus* population in oil palm habitat was relatively high (compared to neighboring habitats) and fluctuates slowly (except the very punctual and unusual outbreak in Riau_2 early 2010), with no obvious seasonal cycle. In the conditions of our study sites, food availability and climate conditions are not limiting factors of rat population growth and cannot explain the difference of abundance from Bangka to Riau plantations.
- *R. tiomanicus* was largely dominant in Riau plantations, whereas *R. tanezumi* was predominant in Bangka plantations. According to the literature, *R. tanezumi* has a greater tolerance to rodenticide than *R. tiomanicus*, which very probably favor rat outbreak in plantations where this first species is dominant, such as in Bangka. In addition, *R. tanezumi* has a larger size than *R. tiomanicus*; this may induce differences in the functional responses of the predator community (rat intake), which might in turn influence rat population dynamics.
II.3. RODENT PEST MANAGEMENT PRACTICES AND THEIR RELATIVE SUCCESS

We found previously that rodent damage was more important in Bangka plantations than in Riau plantations, from which we may infer that the rat population was more abundant in Bangka than in Riau.

In this part, we will investigate rodent control practices and their variability between both regions. We will start by investigating rodenticide use, based on data provided by PTSmart. We will notably show the evolution of rodenticide application in Bangka, compared to the evolution of rodent damage. We will then focus on barn owls, trying to answer to the question: are they really as well established in Bangka as they are in Riau? Indeed, even if it is well known that barn owls are unable to control rat population on their own during outbreak (Blonadel, 1967; Chia et al., 1995), a low barn owl density in Bangka would explain, at least partly, a lower prey intake (other factors possibly influencing prey intake will be investigated in the next section) and consequently the impact of the barn owl on rat population would possibly be reduced.

II.3.1. Rodenticide use

Both Riau plantations have not been treated with rodenticide for more than 10 years, while both Bangka plantations have been treated with rodenticides for a long time (at least since 2003) and constantly. From 2006 to 2012, quantities of rodenticides applied in each Bangka plantation vary from 3 to 40 grammes of active ingredient/ha/year, with a mean monthly application per block constantly decreasing (Figure 33 and 34). By comparison, in Franche-Comté (France) Giraudoux et al. (2012) reported a range of about 0.075 to 0.375 g of active ingredient/ha/year between 2000 and 2011. In this area, vole outbreaks are problematic and extensive grassland areas are treated with bromadiolone rodenticide in the framework of integrated pest management, with the quantity of active ingredient which could be used restricted by law to a maximum of 1 g/ha/year (Delattre and Giraudoux, 2009; Coeurdassier et al., 2014).

Figure 34: Rodenticide application in Bangka plantations: annual mean and dispersion of data, from 2006 to 2012. Boxes contain the middle 50% of the data. Horizontal solid lines in boxes represent the median value, and the white diamond the mean. End of vertical lines represent the minimum and maximum value; small circles are outliers.
The rodenticide used in Bangka plantations is coumatetralyl. It is a first generation warfarin derivative anticoagulant (anti-vitamin K), which is known to be less damaging to barn owls than the second generation rodenticides (see Box 4). Considering that barn owls have been introduced in Bangka plantations for integrated pest management, this product is being used preferably over other molecules since 2002; before 2002, brodifacoum was used (Sudartho Ps, com.pers.).

Box 4: Trials carried out in the 70s (Wood, 1976; Wood and Liau, 1977) suggested no resistance to warfarin from R. tiomanicus and R. argentiventer, although occasionally a behavioral resistance arose. In the 80s, increased warfarin resistance in R. tiomanicus was found as a problem in regularly exposed populations in Malaysian oil palm plantations, in parallel to a build-up of R. tanezumi\(^{32}\) (Wood and Chung, 1990; Wood et al., 1990). R. tanezumi was known to have a higher degree of natural tolerance to warfarin and a potential to develop resistance in a shorter period (Greaves, 1994; Chia, 2005), which might give this species a higher relative competitive ability and be one cause of its rise and the replacement of R. tiomanicus in heavily treated areas (Liau, 1995; Wood and Chung, 2003). More recently, Andru et al. (2013) have also demonstrated strong resistance in coumatetralyl exposure in R. tanezumi/R3 clade. This general resistance phenomenon to “first generation” anticoagulants (warfarin, coumatetralyl) motivated the shift to using “second generation” compounds (including brodifacoum, bromadiolone and flocoumafen). However, although barn owls appear relatively tolerant to warfarin and coumatetralyl secondary poisoning (Duckett, 1984; Fisher et al., 2003a), second-generation rodenticide have serious effects on them (Mendenhall and Pank, 1980; Newton et al., 1999; Naim et al., 2011; Salim et al., 2014b), and it should therefore be avoided in plantations where barn owls are used for biological control, as recommended by Duckett (1984).

- **Baiting procedure: difference between theory and practices**

The recommended baiting procedure in PTSmart plantations is the following. Rodenticide application decision is based on the incidence of fresh damage observed on ripe fruit bunches (FD\%):
- for oil palm >3 years in age: treatment when FD\% >= 5\%;
- for oil palm 2 to 3 years in age: treatment when FD\% >= 1\%;
- for < 2 years old plantation: no threshold, treatment if any rat damage is observed.

The critical level of 5\%, widely used in the industry, corresponds to an economic threshold (treatment cost/benefit) (Chia, 2005).

In the four studied plantations, palm trees are older than 10 years, therefore the 5\% threshold applies. Rat damage census is generally carried out early in the month, and rodenticide application is carried out just after, if needed. Poison bait is offered to rats in wax-bound cubes formulated with 1.125 ppm active ingredient (coumatetralyl), at up to one bait per palm, with replacement of missing bait at 3-day intervals until acceptance declined below 20\%. For Bangka, acceptance threshold for replacement of missing bait have been reduced to 15\% instead of 20\%.

In practice, plantation managers in Bangka and Riau react differently from each other: in Bangka recommendations are followed and rodenticide is systematically applied as soon as the 5\% threshold is reached; whereas in Riau, rodenticide is never applied, even though the 5\% threshold is reached, which is not uncommon, notably in Riau_2 (Figure 34). Even after the

\(^{32}\) named by the authors as R. R. diardii
outstanding rodent damage peak in 2010 in Riau_2, no rodenticide was applied. Thus, in Riau plantations, rodent damage is better tolerated and, traditionally, successful barn owls introduction is associated with no perceived need for rat control with chemicals.

**Figure 35:** Proportion of blocks with rodent damage >5%, in Bangka and Riau plantations

- **Comparative evolution of rodent damage and rodenticide application**

The following figures show the evolution of rodenticide applications from 2006 to 2012 compared to evolution of rodent damage, whether the monthly mean per year (Figure 35a) or detailed per month (Figure 35b).

Results indicated an overall reduction, for each plantation, of both quantity of rodenticide applied per ha and proportion of the plantation treated area, while overall rodent damage shows a diminution in Bangka_1 but remains quite stable in Bangka_2. If we compare the temporal evolution of rodent damage in Bangka, where rodenticide is used, with its evolution in Riau, where no rodenticide is applied (Figure 29), one cannot detect a clear pattern of rodent damage reduction which might be related to the use of rodenticide, or on the contrary a clear pattern of rodent damage increase which might be related to the non-use of rodenticide.
Figure 36: Rodent damage versus rodenticide application, yearly (a) and monthly (b) evolution from 2006 to 2012. In (a), vertical lines ended by horinzonal lines represent error bars.

Some authors such as Wood (1976) or Wood and Liau (1984a) have shown that in treated areas with initial high infestation rate, rat population declined to negligible level just after rodenticide treatment (punctual treatment), remained low for 6 months and may take over one year to recover at the initial level; with reinfestation coming from survivors or by immigration from nearby still-infected blocks or plantations. But these are quite old studies, when rat population were not so resistant to rodenticide as they are nowadays.
As pointed out by Puan 2013, chemical control often results in a decline of pest numbers immediately after treatment. However, their continued use may lead to resistance arising in the rat population. The curve of rodent damage trends from 2006 to 2012, notably in Bangka_2, seems to confirm that the rat population is not very much impacted by long term rodenticide treatments, as it remains high. Presumably, the rat population in Bangka is quite tolerant to rodenticide treatment, whatever the reason (behavioral, genetical, etc.). Andru et al. (2013) have demonstrated physiological tolerance to the rodenticide (coumatetralyl) in *R. tanezumi* in Bangka, and hypothesize that this high level of phenotype resistance in the rat population in Bangka was probably maintained by the intensive and continued rodenticide treatment. According to Wood (2001), “some planters suggest that rats actually became more of a problem after systematic [chemical] control began”.

As shown in Figure 34, the proportion of blocks with rodent damage over 5% tended to be progressively reduced from 2006 to 2012. However, Figure 29 indicates that the percentage of rodent damage per block did not reduce in the same proportions, and was even quite stable for Bangka_2. This could mean that rodent damage is concentrated within fewer blocks.

- **About spatial distribution of rodenticide treatment**

It is interesting to explore the spatial distribution of rodenticide use, in order to further discuss:
- The potential of reinfestation coming by immigration from nearby still-infected blocks or plantations
- The potential food supply for predators just after rodenticide treatment.

Spatial scale of treatment is the block (about 30 ha). Per block data for rodenticide applications is not available; however, per block data for rodent damage is available. Considering that rodenticide is systematically applied in each block where rodent damage reaches or exceeds 5% in Bangka, we investigated spatial distribution of the damage rate ≥5%, which is representative of spatial distribution of rodenticide treatment. Results for year 2011 are shown as example.

Figure 36 illustrates that, for each monthly treatment, treated blocks are usually surrounded by non-treated blocks. For example, in Bangka_1, in 2011, monthly treated area ranged from 1.9% to 7.9% of the plantation, with an average of 4.2%. This means that blocks with (potentially) lower rat density after treatment are surrounded by non-treated blocks with (potentially) higher rat density, and therefore, even if rodenticide has an immediate and local effect on rodent population size, treated blocks might be quite rapidly reinfested by rat populations migrating from surrounding blocks.

This has consequences in terms of food availability for barn owl just after treatment. Indeed, the nesting boxes are distributed throughout the oil palm habitat in a regular grid of at least one per block (see next section), and the nesting place constitutes a point source for the barn owl’s hunting activity (Kan *et al.*, 2014), but barn owls may range far away from the block where they are nesting, quite paradoxically especially during breeding season. Lenton (1980, cited by Hafidzi *et al.* (2003)) recorded a home range of males in oil palm plantation of 20-78 ha during the non-breeding season and of 142 ha during the breeding season. Therefore, when the rat population reduced in the block where barn owls are nesting (consequently to rodenticide
treatment in this block), if not poisoned (by feeding on the intoxicated rats around), barn owls may forage for food in surrounding blocks where rats are affected by the treatment. Thus, food availability might not be a limiting factor for barn owl survival in Bangka plantations. Though, indirect intoxication might affect population growth, as discussed in section III.1.2 about barn owl reproduction patterns in Bangka comparatively to Riau.

Similarly, small carnivores may not be affected by a local rat population decrease (at block scale), given that they may forage for food over very large areas (see section II.1.1.B: from 200 to 1,400 ha for the leopard cat, depending on resource availability). However, they would presumably be affected by indirect intoxication as a result of the rodenticide treatment.

Figure 37: Monthly spatial distribution of rodenticide treatment occurrence in 2011, for Bangka_1 and Bangka_2 plantations, based on rodent damage threshold data (>=5 %).
In brief:
- Both Riau plantations have not been treated with rodenticide for more than 10 years; while both Bangka plantations have been treated with coumatetralyl for a long time and frequently, though with decreasing quantities applied.
- The high rodent damage level in Bangka plantations induced intensive rodenticide use, following PTSmart management procedures. However, plantation management showed a higher “tolerance” to rodent damage in Riau than in Bangka: rodenticide was never applied in Riau even though the 5% threshold was occasionally reached.
- Over a six year period:
  - in Riau plantations, without rodenticide treatment, there was no marked increase of rodent damage: rodent damage in Riau_1 remained relatively stable while rodent damage in Riau_2 decreased;
  - in Bangka plantations, where rodenticide was constantly used, rodent damage slightly decreased but remains globally high.

II.3.2. Barn owl introduction and nest boxes occupancy

Introduction

Barn owls were introduced for rodent pest control in Riau and Bangka plantations in the 1990s. They are provided with nest boxes, whether made of cement, wood or plastic, which design proved to be successful in attracting barn owls for breeding (Sudarso Ps, pers. com.)\(^3\). Nest boxes occur at the rate of one box per block of 30 ha in both Riau plantations and about three boxes per block of 30 ha in both Bangka plantations. In oil palm plantations in Southeast Asia, nest box density reported in the literature commonly range from one to three boxes per 30 ha (Small, 1990; Ho and Teh, 1997; Heru et al., 2000; Duckett, 2008; Noor Hisham and Cik Mohd Rizuan, 2013), with a high initial number of nest boxes usually progressively reduced to a lower density following visible success of rat control. In Bangka, continued rat outbreaks have led to the establishment of a relatively high density of nest boxes.

According to plantation managers, the barn owl population has established well in all of the four plantations, meaning that almost all nest boxes are occupied, both in Riau and in Bangka, and that no unusual mortality has been recorded. This would mean that, in Bangka, barn owls are about three times more abundant that in Riau.

Our objective here is to investigate whether barn owl population levels in Bangka might or not be as high as perceived by local managers.

Material and methods

In our study sites, the success of barn owl introductions and their population growth are theoretically controlled by monitoring the occupancy rates of each nest box, in addition to the

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\(^3\) However, nest boxes constructed out of plastic drum are expected to provide hotter nesting conditions which are less attractive for the barn owl, as suggested by Charter et al. (2010). Naim et al. have just initiated an experiment in order to assess the influence of box type (wood or plastic) on breeding performance in Riau_1 plantation.
numbers of eggs laid, chicks and fledgings. This monthly census of nest boxes, carried out by PTSmart plantation staff, is still going on in the four plantations, but more as a routine, the data not being really used. Moreover, these data are not very reliable as demonstrated by our data mining and field verification; it is therefore not possible to use those nest box occupancy rates to compare relative barn owl abundance in Riau and Bangka.

However, other data might be used as source of information. Indeed, we have collected pellets in nest boxes for dietary analysis (see section III.1.1), and, indirectly, the presence/absence of pellets in nest boxes may be used as an indicator of nest box occupancy, which may indirectly give some information about the relative abundance of barn owls. However, only one of the three nest boxes per block has been monitored in Bangka plantations, against every nest box per block in Riau, and, in Bangka, the nest box monitored was not chosen at random\textsuperscript{34}. Therefore, this data might only be used as an indicator of the occupancy rate of nest boxes visited in each site, and cannot be used to compare relative abundance of barn owls in Bangka and Riau by assessing the overall occupancy rate in each plantation.

All fresh and intact pellets from one box per block were collected in all the blocks both in Riau and Bangka plantations, three times a year (three collection sessions: A, B, C), from 2011 to 2012. The timings of pellets collection are detailed in Table 9 section III.1.1.; the three periods were chosen to be representative over the year, reflecting the variability of barn owl breeding (peak breeding season, lean breeding season) and the variability of climate (rainy season, dry season). For this analysis, we retained data for one session only per year, choosing the session which maximized, for each plantation each year, the percentage of nest boxes with presence of pellets, which would theoretically maximize the occupancy rate and would thus be more representative of barn owl abundance. A total of 1206 visits were made (603 nest boxes visited each year); sampling effort per plantation is detailed in Table 7.

\textbf{Table 7:} Sampling effort to assess barn owl nest box occupancy in Riau and Bangka plantations: number of nest boxes visited

<table>
<thead>
<tr>
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<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_1</th>
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<tr>
<td>Year 2011</td>
<td>166</td>
<td>159</td>
<td>141</td>
<td>137</td>
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<td>Year 2012</td>
<td>166</td>
<td>159</td>
<td>141</td>
<td>137</td>
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The percentage of nest boxes with presence of pellets was calculated as the number of nest boxes with one or more fresh pellets divided by the total number of nest boxes visited for the given plantation in the given year. This percentage might be used as an indicator of the occupancy rate of nest boxes visited.

Probability of presence of pellets in nest boxes in relation to the region and the year were investigated using a generalized linear mixed-effects model (GLMM) of the binomial family, with plantation as random effect (to account for pseudo-replication within plantations).

\textsuperscript{34} The nest box monitored was the one with presumably the highest number of pellets. Indeed, the main objective of pellet collection was dietary analysis, thus, in order to maximize the strength of statistical analysis for dietary analysis (sample size), we chose, for each block, the nest box with presumably the highest number of pellets. This choice was made based on data previously collected on a routine basis by PTSmart plantation staff, and the indicator use was the number of chicks (as we presume that the nest box with the highest number of chicks would have the highest number of pellets). Unfortunately, we demonstrated that these data previously collected on a routine basis by PTSmart plantation staff were not very reliable (see first paragraph of material and methods). Therefore, we cannot be sure that the nest box chosen was the one with the highest number of pellets, but, on the other side, we cannot say that the choice was done at random. Consequently, the bias induce by the nest box selection process on results related to barn owl occupancy rate can hardly be assessed.
Likelihood ratio tests were used to test for the effect of each variable (i.e. p-values were obtained by comparing, via anova, the model with the variable in question and the reduced model without the given variable). To test for difference in probability of pellets being present in nest boxes among plantations, we used another generalized linear model of the binomial family, with no random effect and excluding the variable region (to be as conservative as possible). Analysis of variance was performed on these models to test for the effect of variables; coefficients associated with the models selected enabled us to compare plantations two by two.

Model assumptions about homoscedasticity and normality were checked by visual inspection of the plots of the residuals against the fitted value; normality was formally confirmed by One-sample Kolmogorov-Smirnov test. When model assumptions were not upheld for non-mixed effect models, permutation test (1000 permutations) enabled us to confirm the effect of variables.

As pointed out in section III.1.2., R² definition and calculation for mixed-effect models is under debate (Xu, 2003; Edwards et al., 2008; Nakagawa and Schielzeth, 2013). For generalized linear mixed-effects models, we calculated two pseudo R²: marginal R², which describes the proportion of variance explained by the fixed effect alone, and conditional R², which describes the proportion of variance explained by both the fixed and random effects (Nakagawa and Schielzeth, 2013). For non-mixed generalized linear models, we used McFadden approach, calculating pseudo R² as 1-residual deviance/null deviance (Faraway, 2006). These pseudo R² of models selected are given for information purposes only, in Appendix 4, as they cannot be interpreted independently or compared across datasets: they are valid and useful in evaluating multiple models predicting the same outcome on the same dataset, with R² of the same type (in this situation, the higher pseudo R² indicates which model better predicts the outcome).

All analyses were conducted using R version 3.0.3. (R Core Team, 2014). Packages lme4 version 1.1-7 and nlme version 3.1-117 were used for modelling. The package pgirmess version 1.5.9 was used for permutation tests and One-sample Kolmogorov-Smirnov tests. The package Ggplot2 version 1.0.0 was used for most graphics.

The condition of the nest box might be a limiting factor affecting its occupancy, as barn owls are reluctant to nest in boxes in bad condition, for example missing part of the roof or where the perch is not stable. Therefore, it seems necessary to discuss our results about occupancy rate in relation with the proportion of nest boxes in “good condition” (vs in “bad condition”). Thus, we calculated the percentage of nest boxes in “good condition” over the total nest boxes visited to assess the occupancy rate; a nest box was considered as in “good condition” as far as its condition would not be a critical limiting factor for a barn owl to nest in it. When a nest box was missing, it was however considered as “visited”, and thus included in the total number of nest boxes visited, but it was qualified as in “bad condition”.

**Results and discussion**

In Bangka, 100% of the nest boxes were in good condition. In Riau_1, in 2011 and 2012 respectively, 4.8% and 12.1% were in bad condition or missing. In Riau_2, in 2011 and 2012 respectively, 2.5% and 0% were in bad condition or missing.

The highest occupancy rates reported in Bangka_1, Bangka_2, Riau_1 and Riau_2 were 84.4%, 77.4%, 81.9% and 91.2% respectively (see Figure 37), suggesting that barn owls are well established in both Riau and Bangka plantations. If we had considered only nest boxes in good
condition for the calculation (and not all nest boxes visited), the occupancy rate in Riau would have been even higher (with highest rate for Riau_1 and Riau_2 of 86.1% and 93.5% respectively).

Some authors have reported results of barn owl nest box occupancy rates in mature oil palm plantations, mainly in Malaysia. Heru et al. (2000) reported an occupancy rate reaching up to 91% in plantations in Riau province, about three years after the erection of the nest boxes, with a density of one box per block of 30 ha, and no more rat baiting since barn owls were introduced; his criterion for “occupation” was the presence of eggs, chicks or young, indicating that the nest box was used as a breeding site. In Bangka province, Duckett (2008) reported occupancy rates of 83.5% and 91.7% with about 24 ha per box and without use of rodenticide. A seasonal variation was observed by Small (1990) in Malaysian plantations using warfarin rodenticide, with occupancy rates (presence of adults, youngs or eggs) of nest boxes (one/2 ha) ranging from 30-40% to a peak of 80-90% during the breeding season, indicating that barn owls might not frequently use the nest box during the non-breeding season. High occupancy rates, 77.6% and 92% were also reported more recently by Noor Hisham and Cik Mohd Rizuan (2013) in Malaysia, two years after establishment and with a density of one box/20 ha.

**Figure 38**: Percentage of nest boxes with presence of pellets: detailed per year and per plantation (a), with yearly mean for each plantation (b), with mean for each region (c). In figure (b) and (c), mean is represented by a white-filled diamond. All nest boxes were visited in Riau plantations (one per block), whereas only one in three nest boxes per block was visited in Bangka plantations. Data represent one collection session per year, chosen to maximize the occupancy rate.

The mean percentage of nest boxes with presence of fresh pellets was 70.1% in Bangka plantations and 79.8% in Riau plantations (Figure 37c). We failed to detect an effect of either region (p=0.064) or year (p=0.063) on presence/absence of pellets. However, focusing at the plantation level, a difference among plantations was detected (p<0.00001): except for Riau_1 and Bangka_1, for which we failed to detect a difference (p=0250), every plantation was different from each other (Riau_2 value was greater than each other plantation value, and Bangka_1 value was greater than Bangka_2 one; p<0.00001). Model selected and results (p-
values and R²) are detailed in Appendix 4. Normality of error was not upheld for the generalized linear mixed-effect model when investigating difference between regions, however, in that case, the null hypothesis was accepted, and the risk to accept H0 wrongly due to absence of normality is unlikely.

We considered that the occupancy rate of the nest box visited was representative of this same nest box from one year to another, as barn owls are very attached to their nest site once selected and will usually not move from one to another, unless the nest box condition deteriorates (Duckett and Karuppih, 1990; Lee and Ho, 1999).

If we hypothesize that the nest boxes visited in Bangka was the only nest boxes occupied among the three nest boxes available, then barn owls in Bangka would probably be slightly less abundant than in Riau. If on the contrary we hypothesize that the nest box visited is not the only nest box occupied, then we cannot infer anything about population relative abundance as we don’t know about occupancy rate in the two others nest boxes in Bangka. There was definitely a bias in nest box selection in Bangka (not at random), but its effect on results was not investigated.

If barns owls would appear not to be colonizing all the available nest boxes, we may wonder what could be the cause. According to Taylor (1994), in natural situation, it seems likely that the availability of suitable nest site in suitable foraging habitat is responsible ultimately for limiting barn owl density. Food supply in oil palm estate is not a limiting factor, probably even in Bangka were rodenticide is used but may cause only limited decline of rat population both numerically and spatially (see previously). Biophysical conditions within the oil palm habitat, notably related to vegetation cover, are quite similar and would not limit considerably detection rate and foraging efficiency by owls. All nest boxes taken in consideration at Bangka were in good conditions and suitable for barn owl nesting. Therefore, the only possible limiting factor of barn owls population growth in Bangka, and therefore on barn owls not colonizing all the available nest boxes, would be rodenticide use. Indeed, even if barn owls appeared to relatively tolerate coumatetralyl (Fisher et al., 2003a), a continued or repeated use of this rodenticide may have an impact on population growth as hypothesized in section III.1.2.

To conclude, our analysis suggests that barn owls are well established in Bangka. We have no evidence to suggest that barn owl population in Bangka is lower than in Riau and not optimized for rodent control.

In section III, we will explore others potential constraints to rat control by barn owls, notably in relation to breeding and prey intake.

- **In brief:**
  - Nest boxes density is of about one per 30 ha (1/block) in Riau plantations and one per 10 ha (3/block) in Bangka plantations. Barn owl nest boxes density in Bangka is a priori considered as optimum, while in Riau it is among the lowest reported in the literature.
  - Our analysis of nest boxes occupancy suggests that barn owls were well established in both Riau and Bangka plantations, although the occupancy rate of nest boxes monitored in Bangka was slightly lower than those visited in Riau (but only one third of all nest boxes were monitored in Bangka, whereas in Riau all nest boxes were monitored).
II.4. CONCLUSION

In this section, we have documented the oil palm plantation agroecosystem and its surrounding landscape, focusing on rodent pest management. The main characteristics of each plantation studied are detailed in Table 8. Two main systems emerged from the comparison:

Riau plantations, with
- rodent population more or less controlled, resulting in economically bearable rodent damage;
- rodent population within the oil palm habitat dominated by *R. tiomanicus*;
- no rodenticide treatment (for more than 10 years);
- well established barn owls, in a low density of barn owl nest boxes (about 1 box/30 ha);
- landscape dominated by oil palm plantations;

and Bangka plantations, with
- high of rodent damage linked to rodent outbreaks;
- rodent population within the oil palm habitat dominated by *R. tanezumi*;
- intensive rodenticide treatment (for at least the last 8 years);
- well established barn owls, in a high density of barn owl nest boxes (about 1 box/10 ha);
- relatively diverse landscape, in a matrix of agroforestry and forest like habitat.

In Riau plantations, rodent damage was maintained at an acceptable level without any rodenticide treatment, whereas in Bangka plantations, the use of rodenticide, even in association with barn owl introduction, did not prevent rodent damage.

Due to similar management and agricultural practices (excepted for rodent pest control), all four plantations are quite close in their physical characteristics and design. However, their landscape context is markedly different, especially between Riau and Bangka.

Another major difference between Bangka and Riau is related to the dominant *Rattus* species within the plantation. The fact that the dominance rat species in Bangka plantations was *R. tanezumi* might at least partly explain rodent outbreak/damage in this system, indeed, this species showed great resistance to rodenticide. Moreover it is of larger size than *R. tiomanicus*. This may induce differences in prey intake for the barn owl community and might in turn infer on rat population dynamics. Those hypotheses call for further focused studies.

Others factors might contribute to explain rodent outbreaks at Bangka. In the next section, we will explore other potential constraints to rat control by barn owls, notably in relation to breeding and prey intake. We will also investigate the abundance, diversity and diet of another predator community: the small carnivores.
Table 8: Main characteristics of each plantation studied within the two agroecosystems Bangka and Riau

<table>
<thead>
<tr>
<th>System</th>
<th>Biogeography</th>
<th>Plantation</th>
<th>Area planted</th>
<th>Planting year</th>
<th>Intra plantation: forest or forest like habitat *</th>
<th>Landscape</th>
<th>Rodent dominant species</th>
<th>Rodenticide use</th>
<th>Barn owl</th>
<th>Mean nest box occupancy rate</th>
<th>Rodent damage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Plantation and surroundings (15 km buffer)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>forest or forest like habitat *</td>
<td>oil palm habitat*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riau</td>
<td>Sumatra island</td>
<td>Riau_1</td>
<td>4386 ha</td>
<td>1986 - 1990</td>
<td>2.34 %</td>
<td>2 %</td>
<td>85.3%</td>
<td>R. tiomanicus</td>
<td>None</td>
<td>1 / 30 ha</td>
<td>79.8%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Riau_2</td>
<td>4124 ha</td>
<td>1991 - 2002</td>
<td>0.11 %</td>
<td>3.2 %</td>
<td>80.6%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bangka</td>
<td>11 910 km²</td>
<td>Bangka_1</td>
<td>3680 ha</td>
<td>1993 - 1996</td>
<td>1.9 %</td>
<td>12 %</td>
<td>13.8 %</td>
<td>R. tanezumi</td>
<td>Intensive</td>
<td>1 / 10 ha</td>
<td>&gt;= 70.1 %</td>
</tr>
<tr>
<td></td>
<td>Bangka island</td>
<td>Bangka_2</td>
<td>3658 ha</td>
<td>1991 - 1996</td>
<td>1 %</td>
<td>15 %</td>
<td>18 %</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* cumulative area of habitat within the plantation, in percent of the total plantation area.
As reported in the general introduction, predation patterns (intensity, selectivity) of barn owls and small carnivore communities may affect prey community structure and population dynamics. In assessing the potential predation pressure of a predator on a prey community, one factor to take into account is the density of the predator: in a given system, for a given high prey density (the number of prey is not a limiting factor for predation) and for predators showing constant consumption of prey with no satiation, a higher number of predators will kill a higher number of prey (Holling, 1959). Prey preference, which is reflected by the diet, as well as physiological parameters such as reproduction, will also influence rat kill rates. “Knowing how many rodent prey a predator kills does not tell us if that predator determines the growth rate of the prey population” (Krebs, 2013); however it may provide clues on a potential differential predation impact on the rat population. Selective predation on rat population in relation to size or age may also influence rat population dynamics. Thus, the objective of this section is to explore some population parameters, such as the abundance, diversity, diet, and/or reproduction of two predators (barn owls and the small carnivores), in Bangka and Riau. This could become part of a multifactor hypothesis explaining difference in rat population levels between Bangka and Riau agroecosystems.

The first part of our study will focus on barn owl populations. From the previous section (II.3.), it is likely that barn owl population density in both Bangka and Riau plantations are stable and correspond to the density range reported in the grey literature related to rat control by barn owls in oil palm plantations (see section I.3.2.). However, the rat offtake by the barn owl may be different in Bangka and Riau, and this may be partly explained, among other factors, by parameters related to barn owl reproduction (e.g. barn owls with an extended breeding season may consume more prey as reproduction increases their food requirement) or diet, which both influence prey intake. Therefore, we will investigate potential differences in barn owl rat intake between Riau and Bangka plantations, both from a prey type point of view - how much of the diet of the barn owl is constituted by rats? - and from predation intensity point of view – are there differences in barn owl breeding season patterns (frequency and duration) and/or brood numbers, that might have consequences in term of prey intake intensity? -.

To investigate the issue of selective predation in relation to size or age, which may also influence rat population dynamics, one must be able to determine the age structure of the prey items, and to compare this to the age structure of the prey population in the field. In Riau and Bangka plantations, the dominant rodent species are respectively R. tiomanicus and R. tanezumi (see section II.2.1.), and, they are presumably the main prey of the barn owl (see further: III.1.3 and III.2.2.). However, so far, no tool is available for reconstructing barn owl prey population age structure for those two species. We will thus investigate statistical models using allometric measurements on macroremains from their pellets, in order to further assess the relative age determination of R. tiomanicus preyed on by the barn owl.

We will then turn to consider the small carnivore community. Our main hypothesis is that rat predation (offtake) by the small carnivore community is less intense in Bangka than in Riau. Rat offtake depends, among other factors, on the abundance and composition of the small carnivore community. Small carnivore species recorded in Sumatra and
Bangka islands -and thereby potentially present in our study sites- were reported previously (see section I.3.3. and Appendix 1), however knowledge about their occurrence and abundance within our study sites is lacking. Similarly, we have no clue about the diet of the small carnivore community in our study sites, which should partly reflect small carnivore species composition. Therefore, in a comparative approach among study sites, we first investigate small carnivore community abundance and richness within Riau and Bangka plantations. In addition, we will assess the overall importance of small mammals in the diet of small carnivores at the community level.

### III.1. VARIATIONS IN PREY INTAKE FROM BARN OWL: REPRODUCTION AND DIET

Our previous analysis on nest boxes occupancy rate (part II.3.2.) suggested that barn owls were well established in both Riau and Bangka plantations, and we had no evidence to suggest that barn owl population in Bangka is lower than in Riau and not optimized for rat control. However, differences in Bangka and Riau systems such as parameters related to barn owl diet (based on prey availability and vulnerability, and on barn owl prey preference) and reproduction, may affect number of rats killed per barn owl per year in Bangka compared to Riau.

Studies above (part II.1.2. and II.2.1.) lead to the assumption that 1) the similarity of the prey behavior (*R. tanezumi, R. tiomanicus*) and of the oil palm habitat in both systems may not induce a higher prey vulnerability in one or the other system, 2) but that the greater average body mass of *R. tanezumi* (139-230 g, main rodent species in Bangka) compared to *R. tiomanicus* (57-125 g, main rodent species in Riau) may influence prey selection and intake, and thus possibly influence the prey population.

In this section, we will explore potential variations in prey intake between Bangka and Riau related to other parameters:
- barn owl diet (prey preference): do rat proportions in the barn owl diet differ between Bangka and Riau? Different frequency of occurrence of rat prey items in barn owl pellets would reflect differences in rat intake.
- barn owl reproduction (predation intensity): are there differences in breeding seasons (frequency, duration, etc.) and/or brood numbers between Bangka and Riau? Considering that food requirements of the barn owl increases during the breeding season, a more or less extended breeding season may induce more or less prey intake per barn owl.

Our main hypothesis is that rat prey intake, i.e. predation on rats, by barn owls is lower in Bangka than in Riau. Demonstrating that, 1) the proportion of rats in barn owl diet is lower in Bangka than in Riau, and that 2) barn owl breeding performance, and consequently food requirement, is less in Bangka than in Riau, may provide clues to support this hypothesis.

To further investigate barn owl selective predation in relation to size or age of rat, we will develop a model based on the correlation between osteometric measurements and crystalline lens weight of caught specimens, in order to determine the age structure of prey macroremains found in pellets.
III.1.1. Proportion of rodents and rats in the barn owl diet

Introduction

Our objective is to investigate if there are differences in the proportion of rodents, especially rats, in barn owl diet between Bangka and Riau plantations. Differences in the proportion of rodents/rats in the barn owl diet would reflect differences in rodents/rats prey intake. Our hypothesis and prediction is that, in Bangka plantations, the proportion of rodents, and notably of rats, in barn owl diet is lower than in Riau plantations.

Material and methods

Barn owls have been present in the four oil palm plantations for more than 20 years. In each plantation, barn owls are provided with nest boxes: on average one nest box per block in Riau plantations and three nest boxes per block in Bangka plantations.

In every block, we collected all the intact fresh barn owl pellets inside one nest box. Pellets were usually collected three times per year, in 2011 and 2012. The period of pellet collections are detailed in Table 9. The three yearly periods were chosen as to be representative, over the year, of the variability of barn owl breeding (peak breeding season, low breeding season) and the variability of climate (rainy season, dry season). One pellet collection session occurred during breeding seasons, thereby maximizing the number of pellets collected, as we know that barn owls do not frequently use the box when not breeding (Small, 1990). In addition, given that seasonal variations such as climate or barn owl reproduction may lead to changes in predation behavior and thus differential prey content in pellets, two other periods were chosen in low breeding period but under different climatic conditions. Sometimes, the period of pellet collection was extended a bit later that originally intended, due to field constraints.

Table 9: Periods of pellet collection sessions in each plantation

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>Session A</td>
<td>01/04 - 22/05</td>
<td>18/04 - 13/06</td>
<td>21/02 - 16/03</td>
</tr>
<tr>
<td>2011</td>
<td>Session B</td>
<td>19/07 - 15/08</td>
<td>27/07 - 26/08</td>
<td>10 - 24/08</td>
</tr>
<tr>
<td>2011</td>
<td>Session C</td>
<td>25/10 - 14/11</td>
<td>02/10 - 14/12</td>
<td>21/10 - 04/11</td>
</tr>
<tr>
<td>2012</td>
<td>Session A</td>
<td>06 - 29/04</td>
<td>11/04 - 24/05</td>
<td>29/02 - 15/03</td>
</tr>
<tr>
<td>2012</td>
<td>Session B</td>
<td>06 - 26/07</td>
<td>11 - 30/07</td>
<td>26/07 - 09/08</td>
</tr>
<tr>
<td>2012</td>
<td>Session C</td>
<td>03 - 28/10</td>
<td>31/10 - 03/11</td>
<td>21/10 - 08/11</td>
</tr>
</tbody>
</table>

Table 10: Variations in climate and barn owl breeding seasons for chosen period of pellet collection

<table>
<thead>
<tr>
<th>Barn owl breeding season</th>
<th>Riau</th>
<th>Bangka</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Session A (April-May)</td>
<td>Session B (July-August)</td>
</tr>
<tr>
<td>Low</td>
<td>Peak</td>
<td>Low</td>
</tr>
<tr>
<td>Peak</td>
<td>Low</td>
<td>Low</td>
</tr>
<tr>
<td>Low</td>
<td>Low</td>
<td>Low</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Climate</th>
<th>Riau</th>
<th>Bangka</th>
</tr>
</thead>
<tbody>
<tr>
<td>Begin dry season</td>
<td>Session A (February-March)</td>
<td>Session B (July-August)</td>
</tr>
<tr>
<td>End rainy season</td>
<td>Dry season</td>
<td>Rainy season</td>
</tr>
</tbody>
</table>
In each plantation, pellets were collected in every blocks, but only a subsample of these blocks were retained for the analysis (i.e. only pellets collected in this subsample of blocks were dissected for diet analysis): subsampling (choice of blocks) was based on their representativeness of the various landscape situations in the oil palm plantation (some blocks located in the center of the plantation was retained, as well as some blocks located in the periphery and surrounded by various habitats). For each time period, we retained a number of blocks in each plantation which would lead to a similar sample size (number of pellets) in both regions, and to keep the same proportion of “central” and “peripherals” blocks. In Bangka_2, all blocks were retained, given that, in the first year, the number of pellets collected was relatively low compared to the other plantations. Figure 38 shows the location of the blocks selected from which pellets were dissected.

As soon as they were collected, pellets were dried in a greenhouse (or simply sun-dried) for two or three days, and then stored in plastic bags for further dissection.

Figure 39: Location of oil palm plantation blocks (subsampling) from which barn owl pellets were dissected.
Barn owls pellets were dissected and macroremains were segregated using tweezers. Prey items were classified in the following main categories: small mammal, amphibian, reptile, bird, insect, indeterminate. For each pellet, the occurrence of each prey category was recorded. Presence of vegetal or other material such as plastic was also recorded but this information has not been taken into account here, neither was some insects at larva or pupa stage which were obviously not prey, but necrophagous. Prey were identified using bones, skulls or teeth morphology, hair and feather or any other recognizable remains (FCPN, 2010). All amphibians were frogs, so they appear as a ‘frog’ category in the graphics. All reptiles were identified as lizards, snakes or indetermined. In most pellets, small mammal remains were headless because of prey decapitation before bringing it to the nest, as reported by others authors (Lim et al., 1993; Puan et al., 2011b), so identification as a more precise taxon may not be possible. However, whenever possible, distinction between “rodent” and “non-rodent” was made within the main category ‘small mammal’. When head parts (skull or jaw) were present, rodents were identified based on their dental pattern: a pair of incisors on each jaw, separated from molars by a long gap-the diastema- without canines (Corbet and Hill, 1992; FCPN, 2010). When head parts were absent or not in good enough condition to allow identification as “rodent or “non-rodent”, it was listed as “undetermined”.

We calculated:
- the frequency of occurrence (in percent) of small mammals: number of small mammal items analyzed for the given estate or region X 100 / total number of items of main categories, in all the pellets analyzed for the given estate or region;
- the percentage of pellets containing small mammals: number of pellets with small mammals for a given estate or region X 100 / total number of pellets analyzed for the given estate or region;
- the percentage of small mammal items for which identification as “rodent” or “non-rodent” is possible: number of small mammal items for which identification as “rodent” or “non-rodent” is possible, for a given estate or region x100/ total number small mammal items analyzed for the given estate or region; number of small mammal items for which identification as “rodent” or “non-rodent” is possible was named as subsample A;
- the frequency of occurrence (in percent) of rodent items among the small mammal items which may be identified as “rodent” or “non-rodent”: number of rodent items X 100 / size of subsample A.

Among the pellets containing rodent macroremains from subsample A, we selected a subsample of 425 pellets (subsample B) for which identification to genus was possible thanks to good condition of head parts. Identification of rodent genus was based on skull and teeth patterns (Musser, 1981; Musser and Califia, 1982; Musser and Newcomb, 1983; Lekagul and McNeely, 1988; Corbet and Hill, 1992). We calculated the frequency of occurrence (in percent) of Rattus genus within rodent prey items from this subsample B.

A Chi-Square test was performed to investigate significant differences between percentages among estate or region. When Cochran rule was not validated (i.e. when less than 80% of expected counts greater than 5, and at least one expected value null), Permutation Chi-Square test was used instead. A p-value of 0.05 was taken as the threshold for significance.

In the framework of a comparative approach among plantations, we assume that our sampling design greatly reduced potential bias related to collection period (year, season) or distribution within the plantation. Indeed, for each plantation, our sample is representative 1) of the diversity of the environment (oil palm habitat and landscape), 2) and, along the year, of the variability of
climate and breeding season. In addition, we have no reason to suspect a variation in diet during our study period, given that our sample is representative of seasons throughout the year, and previous research has not reported any seasonal change in barn owl diet on oil palm plantations (Lenton, 1984). Moreover, same areas were sampled each year, at approximately the same periods. Therefore, due to time constraints, for each plantation, data of all years and all seasons and from all blocks were pooled, and we did not investigate the effect of year or season, nor the effect of the location in the diet of the barn owls.

Diversity indices were calculated to compare diversity of the diet among plantations and regions. Because all prey items could not be identified to species or even genus level (only some rodent item samples may be identified up to genus), the categories used correspond to the lower taxonomic level identified before the genus (rodent, bat, indetermined small mammals, bird, lizard, snake, indetermined reptile, insect). Undetermined species were excluded from the calculation. The following indices were calculated:

- Simpson’s index of diversity (1 - D), which represents the probability that two individuals randomly selected from a sample belong to different categories. The greater the value, the greater the sample diversity.
- Pielou evenness index (J), which represents species evenness of the community.

Formulæ for calculation of the two indices are, respectively:

\[
1-D = 1 - \left( \sum \frac{n_i (n_i - 1)}{N(N-1)} \right)
\]

\[
J = \frac{- \sum (P_i \log_2(P_i))/\log_2 S}{S}
\]

Where:
- \(n_i\) = number of individuals in species “i”
- \(N\) = total number of individuals in all species
- \(P_i\) = relative abundance of species \(i = n_i / N\)
- \(S\) = the total number of species, with \(i\) going from 1 to \(S\)

All analyses were conducted using R version 3.0.3. Graphics were plotted using Excel version 2010. To calculate diversity indices, we used pgirmess package for Pielou index, and vegan version 2.0-10 package for the Simpson’s index.

Results

Over the study period, a total of 3,196 barn owl pellets were analyzed (1,745 for Riau and 1,451 for Bangka), and 3,272 prey items were identified (1,751 for Riau and 1,521 for Bangka).

As reported in Table 11 and Figure 39, small mammals represented almost all prey items found in barn owl pellets: 99.7% in Riau plantations and 94.9% in Bangka plantations. The percentage of small mammal items in barn owl pellets was significantly greater (\(p > 0.0001\)) in Riau than in Bangka. We failed to detect a statistically significant difference in occurrence between plantations of the same region, either in Riau (\(p = 0.537\)) or in Bangka (\(p = 0.404\)). In Riau, whether Riau_1 or Riau_2, 100% of barn owl pellets contained small mammals. In Bangka, the amount dropped to 99.2% (see Table 11). The difference between Bangka and Riau was statistically significant (\(p =0.0008\)). We did not find statistical difference in term of percentage of barn owl pellets containing small mammals between plantations in Bangka (\(p = 0.434\)).
Figure 40 Frequency of occurrence (in %) of prey items from main categories in barn owl pellets collected in Riau and Bangka plantations in 2011 and 2012; n represents the total number of prey items identified.

Identification as “rodent” or “not rodent” was possible for 30.2% of small mammal items (subsample A); among these, 99.8% of items were rodents in Riau plantations and 98.8% in Bangka plantations; all “not rodent” remains were identified as bats. See Table 11 for details per plantation. We failed to detect difference among plantations or regions (p>5%).

Table 11: Percentage of pellets containing small mammals and frequency of occurrence (in %) of rodents in the diet of barn owls in Riau and Bangka plantations in 2011 and 2012 (N represents the number of pellets analyzed; n represents the number of items analyzed).

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Total Riau</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
<th>Total Bangka</th>
</tr>
</thead>
<tbody>
<tr>
<td>% of pellets containing small mammals</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>99.59%</td>
<td>99.1%</td>
<td>99.2%</td>
</tr>
<tr>
<td></td>
<td>(N=1,106)</td>
<td>(N=639)</td>
<td>(N=1,745)</td>
<td>(N=491)</td>
<td>(N=960)</td>
<td>(N=1,451)</td>
</tr>
<tr>
<td>% of small mammals items for which identification as “rodent” or “non rodent” is possible = subsample A</td>
<td>27.2%</td>
<td>24.2%</td>
<td>26.1%</td>
<td>30.5%</td>
<td>37.5%</td>
<td>35.1%</td>
</tr>
<tr>
<td>% of rodents prey items within subsample A</td>
<td>100%</td>
<td>99.3%</td>
<td>99.8%</td>
<td>100%</td>
<td>98.3%</td>
<td>98.8%</td>
</tr>
<tr>
<td></td>
<td>(n=301)</td>
<td>(n=155)</td>
<td>(n=456)</td>
<td>(n=149)</td>
<td>(n=358)</td>
<td>(n=507)</td>
</tr>
</tbody>
</table>
In addition to small mammals, insects and birds were occasionally found in barn owl pellets in Riau plantations. In Bangka plantations, prey items were more diverse: they included reptiles and frogs, in addition to insects and birds. These non mammal prey items were rarely found and their contribution to the barn owl diet ranged from 0.1 to 2% (Figure 39). Diversity indices calculated, as reported in Table 12, were lower in Riau than in Bangka, indicating that the diet of the barn owl was more diverse and evenly distributed on the latter.

Table 12: Diversity indices for the diet of barn owls in Bangka and Riau plantations

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bankga_1</th>
<th>Bankga_2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simpson index</td>
<td>0.3983</td>
<td>0.3737</td>
<td>0.4717</td>
<td>0.5284</td>
</tr>
<tr>
<td>Pielou index</td>
<td>0.2595</td>
<td>0.2575</td>
<td>0.3587</td>
<td>0.4155</td>
</tr>
</tbody>
</table>

In a subsample of 425 barn owl pellets containing rodent small mammal items that may be identified to genus level, the proportion of *Rattus* were 100% in Riau plantations and 96.2% in Bangka (p_value=0.017). No significant difference of *Rattus* frequency of occurrence in barn owl pellets were found between Bangka_1 and Bangka_2 plantations (p_value=0.727). Other genera found in pellets in Bangka plantations are *Sundamys* (2.1%) and *Calloscirus* (0.4%); see Table 13.

Table 13: Contribution of each genus of rodent (percentage among rodent prey items) in a subsample of 425 barn owl pellets collected in Riau and Bangka plantations in 2011 and 2012 (N represents the number of pellets analyzed, named as subsample B; this subsample B is part of subsample A rodent macroremains for which identification of genus was possible).

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Total Riau</th>
<th>Bankga_1</th>
<th>Bankga_2</th>
<th>Total Bangka</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>(N=116)</em></td>
<td><em>(N=74)</em></td>
<td><em>(N=190)</em></td>
<td><em>(N=54)</em></td>
<td><em>(N=181)</em></td>
<td><em>(N=235)</em></td>
<td></td>
</tr>
<tr>
<td><em>Rattus</em></td>
<td>100 %</td>
<td>100 %</td>
<td>100 %</td>
<td>94.4 %</td>
<td>96.7 %</td>
<td>96.2 %</td>
</tr>
<tr>
<td><em>Sundamys</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.7 %</td>
<td>1.7 %</td>
<td>2.1 %</td>
</tr>
<tr>
<td><em>Calloscirus</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.6 %</td>
<td>0.4 %</td>
</tr>
<tr>
<td>Undetermined</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.9 %</td>
<td>1.1 %</td>
<td>1.3 %</td>
</tr>
</tbody>
</table>

**Discussion**

The general patterns of our results are consistent with previous studies on barn owl diet, including those carried out in oil palm plantations.

In both Riau and Bangka plantations, the barn owl diet was dominated by non-volant small mammals. Other prey such as frogs, insects, birds, bats and reptiles were only occasionally taken as food: non-volant small mammals were present in almost everyone of the 3,196 pellets (in 100 % in Riau and in about 99 % in Bangka), and this category represented from 94% to 99.8 % of all prey items in each plantation. Our results, based on a subsample of 425 pellets, suggested that non-volant small mammals consumed by barn owl are confined entirely to rodents. As reported by Taylor (1994), terrestrial small mammals and in particular rodents are by far the most important prey in almost all areas, and in productive habitat where small mammals are abundant, barn owls feed almost exclusively on them. In oil palm plantations in Malaysia, Puan *et al.* (2011b) found rodent bones in 95.1% of the 203 pellets they analyzed; and Lenton (1984) reported that small mammals represented 99.2% of all prey items based on the analysis of 2,389 pellets, over 98% being rodents.
Our results suggested the predominance of *Rattus* in barn owl diet in both regions: this genus contributed from between 96.2% (in Bangka) to 100% (in Riau) of all non-volant small mammals prey items on a subsample of 425 pellets. Though this has been discussed by Bernard *et al.* (2010), the barn owl diet usually reflects the abundance of prey species within the hunting territories (Bunn *et al.*, 1982; Figueroa *et al.*, 2009). In our study, the narrow prey spectrum was probably because of *Rattus* predominance in the oil palm habitat, as demonstrated by others authors in Malaysian oil palm plantations. From a sample of 2,839 pellets, Lenton (1984) found that 98.16% of prey items were rats, notably *R. tiomanicus* (89.7%) which was the most common species found in the field. Puan *et al.* (2011b), analyzing 203 pellets, reported that 67.4% of skeletons were identified as *R. tanezumi* (named as *R. r. diardii* by the authors), which was the species they most frequently trapped (64.2%) in the area; another 27.4% were two Rattus species also captured in the area in the same rank order as their frequency in the diet. Small (1990), based on the analysis of 22,496 prey items, reported that 99.4% of the diet of the barn owl consisted of *Rattus*, the other small mammals found being shrews, bats and a squirrel. In the present study, *Sundamys* also contributed to the diet of the barn owl in Bangka plantations, up to 3.7% in Bangka_1 and 1.7% in Bangka_2; this is consistent with previous field trapping of *Sundamys muelleri* in Bangka oil palm plantation (see II.2.).

As mentioned previously, we have no reason to suspect a variation in diet during our study period. Indeed, our sample is representative of various seasons along the year, and other research also did not report any seasonal change in barn owl diet on oil palm plantations (Lenton, 1984).

Our results showed a slight but significant difference in dietary composition between Riau and Bangka, whereas results did not vary from plantation to plantation within the same region. Though rodents make up the bulk of the diet in all our study sites, the percentage occurrence of small mammal items in barn owls pellets was greater in Riau than in Bangka, and the diet of the barn owl tends to be slightly richer in Bangka than in Riau: prey items others than non-volant small mammals contribute to 0.3% of the diet in Riau plantations, against 5.5% in Bangka plantations. Moreover prey taken as food by the barn owl were more diverse in Bangka: they include reptiles and frogs in addition to insects, birds and bats as found in Riau.

Our results thus suggest differences between the two agroecosystems in term of food resources used by the barn owl community. But we don’t know whether this is linked to prey availability (in relation to prey abundance and vulnerability) or to barn owl preference. Prey vulnerability is presumed to be similar in all plantations, because of similar microhabitat within the oil palm blocks. Rat abundance is seemingly not a limiting factor for barn owl predation in our study sites (see arguments in section III.1.2); yet, we cannot totally exclude that there could be a prey shift from rats to other prey types in case of punctual and very localized (block scale) decrease in rat population consecutive to rodenticide use. The difference in food resource used by the barn owl may also occur because of alternative prey resources being more attractive in Bangka than in Riau plantations (even if the main prey, i.e. rats, is not limiting). Indeed, though the barn owl is assumed to be mainly opportunistic, i.e. its diet generally reflects prey availability (Taylor, 1994), some studies showed that barn owls may exhibit complex patterns of prey selection. For example, Bernard *et al.* (2010), studying dietary response of barn owls to large variations in population of voles in the Jura mountains, showed that prey selection of a focal species can be affected by the density or availability of other prey species. Another hypothesis might be put forward to explain differences in diet in Bangka plantations comparatively to Riau, in connection with to the greater size of the
dominant rat species in Bangka (R. tanezumi) comparatively to Riau (R. tiomanicus): an adult R. tanezumi might be a prey too large for the barn owl, compared to R. tiomanicus, thus barn owls may preferably prey on young individuals and complement with other smaller non-mammals prey (such as batrachians, insects, birds and reptiles), given that in Bangka alternate small mammal species such as Sundamys muelleri are of even larger size than R. tanezumi. So, definitely, more research is needed to investigate if the differential in food resource used by the barn owl is either explained by prey availability or by barn owl preference. In section III.1.3., we will provide a tool to further investigate one aspect linked to selective predation in relation to rat size/age.

Our results suggest a greater importance of rats in the diet of the barn owl in Riau plantations comparatively to Bangka, but it says nothing about the impact of barn owls on the rat population. In a very simplistic model, where barn owls are the only rat predators, if rat recruitment rate is higher than barn owl predation combined with other mortality sources, whatever the level of barn owl predation, barn owls may not have much influence on rat population level. With more complex models taking into account predators interactions (facilitation or competition), the impact of barn owl predation on rat population is even more difficult to assess.

To conclude, our results support the hypothesis that, on a yearly basis, one barn owl may in average consume slightly less rats in Bangka plantations than in Riau plantations. Our next step is to investigate potential variation in food requirement, and consequently predation pressure, between Riau and Bangka plantations.

III.1.2. Barn owl reproduction and food requirement

Introduction

Our objective is to investigate differences in breeding season numbers and/or length, and/or brood numbers between Bangka and Riau plantations. Breeding of young considerably increases food requirements up to two to four times according to Small (1990) or (Lenton, 1980)-, therefore predation should increase during the breeding season. We predict that barn owl breeding season in Bangka plantations is less extended than in Riau plantations, and/or that the barn owl reproduction in Bangka plantations is less intense than in Riau plantations; which both may induce a lower annual prey intake in Bangka compared to Riau.

Material and methods

We used some of the data collected by PTSmart plantation management on a routine basis since barn owl introduction: monthly census of number of eggs laid by barn owls in each nest box, in the four plantations. Based on data mining and field verification, we found that the level of reliability varies from one plantation to another. This will be discussed below. Data from year 2008 and 2009 were analyzed; but for Riau_2 only data from 2009 were used (data exploration showed too many inconsistences or discrepancies for Riau_2 in 2008). We calculated, for each month in each plantation, the number of eggs per nest box as the total number of eggs in all nest boxes divided by the number of nest boxes reported as “in good condition” (a nest box was considered as in “good condition” when its condition would not be a critical limiting factor for a barn owl to nest in it; see section II.3.2.). Histograms were displayed to assess differences in the number and extent of breeding season(s). We also calculated the mean
number of eggs per nest box for each plantation and then for each region, each year, which may be indicative of barn owl reproduction intensity.

Difference in numbers of eggs per nest boxes between Riau and Bangka regions were investigated using linear mixed-effects models, with plantation as random effect (to account for pseudo-replication within plantations). Likelihood ratio tests were used to test for the effect of year and region (i.e. p-values were obtained by comparing, via anova, the model with the variable in question and the reduced model without the given variable). To test for difference in eggs per nest box among plantations, we used another linear model, with no random effect and excluding the variable region (to be as conservative as possible). Analysis of variance was performed, and coefficient associated with the model selected enables us to compare plantations two by two. Model assumptions about homoscedasticity and normality were checked by visual inspection of the plots of the residuals against the fitted value; normality was formally confirmed by One-sample Kolmogorov-Smirnov test, and homogeneity of variance by Bartlett test (when sufficient observations in each group). When model assumptions were not upheld for non-mixed effect models, permutation test (1000 permutations) enabled us to confirm the effect of variables. The $R^2$ measure of explained variation is well known for linear regression, however, for mixed-effect models, $R^2$ can be defined in a number of ways and their use may be hindered by theoretical or practical issues (Xu, 2003; Edwards et al., 2008; Nakagawa and Schielzeth, 2013). To assess the overall goodness-of-fit of linear mixed-effects models, we used, as pseudo $R^2$, the $R^2$ of the correlation between the fitted and observed values, as suggested by Byrnes (2008). For non-mixed linear models, we used the adjusted $R^2$ as commonly reported. Adjusted $R^2$ or pseudo $R^2$ of models selected are given for information purposes only, as they cannot be interpreted independently or compared across datasets: they are valid and useful in evaluating multiple models predicting the same outcome on the same dataset, with $R^2$ of the same type (in this situation, the higher pseudo $R^2$ or adjusted $R^2$ indicates which model better predicts the outcome).

Our analyses were conducted using R version 3.0.3. (R Core Team, 2014). Package lme4 version 1.1-7 was used for modelling. The package pgirmess version 1.5.9 was used for permutation test and One-sample Kolmogorov-Smirnov test. The package Ggplot2 version 1.0.0 was used for most graphics.

**Results**

Figure 40 shows that yearly reproduction pattern of barn owls, represented by distribution of egg laying, differed among Bangka and Riau. There were two peaks in egg laying in Riau against only one peak in Bangka: though barn owls laid eggs in all months of the year, meaning that breeding occurs throughout the year, egg laying, and thus the incidence of breeding, considerably increased twice a year for Riau (generally in January/February and June to August) and once a year for Bangka (generally around January, February and/or March). Egg laying was lowest around April in Riau, and around October in Bangka.

Figure 41 and statistical analysis show that the mean number of eggs per nest box was higher ($p =0.014 \leq 5\%$; pseudo $R^2=0.87$) in Riau (mean$=0.66$; standard error$=0.049$; 95% confidence interval$=0.56-0.76$) than on Bankga (mean$=0.39$; standard error$=0.056$; 95% confidence interval$=0.28-0.5$). No difference was found between years ($p =0.379 >5\%)$ nor between plantations ($p =0.092 >5\%$; Adjusted $R^2=0.78$).
Figure 41: Egg laying pattern in Riau and Bangka plantations: number of eggs per nest box in 2008 and 2009. Red dashed line shows yearly mean level for each plantation. Standard deviation is figured in blue (except for Bangka_1 because no detailed data available to calculate it).

Figure 42: Number of eggs per nest box (a) per plantation and (b) per region. Boxes contain the middle 50% of the data. Horizontal solid lines in boxes represent the median value, and the white diamond the mean. End of vertical lines represent the minimum and maximum value, and small circles are outliers.
Discussion

- **Does the breeding season patterns observed seemed normal or unusual?**

According to Taylor (1994) “all [barn owl] populations that have been studied, including those within the tropics, show at least some seasonality of breeding”. The barn owl breeding seasonality found in Riau plantations is consistent with a literature review on barn owl breeding in South East Asia. Surveying 18 barn owl nest sites within oil palm landscapes in Malaysia, Lenton (1984) recorded that breeding occurs in all months of the year but shows a broad seasonality: most barn owl pair produce two broods a year, and the incidence of breeding increased in January/February and August/September each year and was lowest between April and June. Small (1990) counted monthly all adults, young or eggs present in nest boxes installed in some oil palm plantations in Malaysia. The majority of barn owls concentrate their breeding in two broods over the period of June to February, with low occupancy rate between April and May each year; the principal breeding season was found from June/July till September/October, and second clutches were laid soon after showing another peak around January. Results of others authors such as Duckett and Karuppiah (1990) support this pattern, which is quite similar to the one found in Riau plantations.

In contrast, barn owl breeding pattern in Bangka plantations is unusual: the breeding season is less extended than in Riau plantations and show only one peak, early in the year (January-March), reflecting only one annual brood.

- **How could the lowest breeding performance in Bangka be explained?**

One can easily discard differences in data collection: though we found that reliability of data reporting (monthly census of number of barn owl eggs laid in each nest boxes) varies from one plantation to another, we never found a time or spatial pattern in those discrepancies. Biases being equal in all plantations, one can assume that trend comparisons between time series are reliable and independent from biases due to data collection.

Taylor (1994) reported evidence that barn owl clutch size, was positively related to the density of suitable foraging habitat around the nests and that its annual variation was closely correlated to cyclic variations in food supply. Difference in breeding performance between Bangka and Riau is likely not linked to biophysical factors, as climate, foraging habitat, and nesting conditions (appropriateness of nest boxes for breeding are similar).

The first hypothesis is linked to prey availability which could be a limiting factor for barn owls reproduction in Bangka, and notably clutch size. We postulate in section II.2 that *Rattus* population in studied oil palm habitat is relatively high (compared to neighboring habitats) and fluctuates slowly, with no obvious seasonal cycle, providing abundant prey for barn owls. However, rodenticide usage, may causes local decline of rat population immediately after treatment (spatial scale of treatment is the block, not all blocks are treated; treatment is carried out monthly, the same block is generally not treated all the year long; see section II.3.1), which in turn may result in a shortage of food resource for barn owls and therefore less energy will be invested in reproduction. Nevertheless, this hypothesis is unlikely, knowing that 1) *Rattus* population may recover rapidly (partly due to immigration from nearby blocks), 2) barn owl may forage for food in surrounding...
blocks where rat populations were not affected by treatment, 3) and that, in Bangka, the predominant *Rattus* species (*R. tanezumi*) has a greater tolerance to rodenticide. Therefore, prey availability is probably not a limiting factor for barn owl reproduction in Bangka plantations.

The most probable explanation of a restricted breeding season in Bangka is related to the effects of secondary intoxication from coumatetralyl rodenticide on barn owls. Rat tolerant to rodenticide may not die, but the anticoagulant will persist in organs and tissue for some time (Fisher *et al.*, 2003b). Parmar *et al.* (1987) reported a value of 55 days for coumatetralyl elimination half-life in the rat liver. Barn owls are highly likely to consume live poisoned rats. Some results shown that coumatetralyl presents a relatively low hazard of acute secondary poisoning for barn owls (Duckett, 1984; Fisher *et al.*, 2003a). However, accumulation of rodenticide residues by repeated ingestion of poisoned rats may have a harmful effect on barn owls, and finally affect its reproduction (egg laying and clutch size) or chick survival negatively. We found no reference indicating that coumatetralyl ingestion has physiological effects on reproduction capacity itself for the barn owl. However, Taylor (1994) pointed out evidence that pesticides cause egg breakage and embryo deaths in many raptor species including barn owls, resulting in a reduction of breeding performance. In oil palm plantations in the 80s, Duckett (1984) postulated a possible effect on clutches and Small (1990) mention that warfarin may have some negative effects on egg and chick survival. Naim *et al.* (2011) compared breeding performance of barn owls in immature oil palm plantations in Malaysia, on plots baited with rodenticides (respectively warfarin and brodifacoum), and a non-baited control plot. They found no significant difference in mean clutch size for all treatments, and the mean clutch size was not significantly correlated to mean rat damage. However, their study showed that the mean hatching success as well as the mean fledging success were significantly higher on the non-baited control plot compared to rodenticide treated plots, and that fledging success was positively correlated to mean rat damage. In their discussion, the authors mentioned the risk of secondary poisoning death of chicks and breeding pairs by feeding on rats which have ingested the bait, but they suggested that the hatching and fledging success was rather influenced by the availability of rat preys (decrease of rat numbers after rodenticide treatment will reduce hunting success, leading to fewer prey delivered to females and chicks, which may die from starvation). We might also suspect that reduced hunting success and food intake could be caused by sublethal effects of rodenticide interfering with locomotion (Stone *et al.*, 2003). More recently, Salim *et al.* (2014a) studied the relationship between reproductive performance of barn owls in Malaysian oil palm plantations and anticoagulant rodenticide residues (bromadiolone and chlorophacinone) in their pellets. They found a strong negative correlation with the mean concentration of residues detected in the pellets and either the mean clutch size, brood size or fledging success of the barn owls. The authors also took interest in the occupancy rate of nest boxes in the treated versus non-treated areas. Their results showed that, in the first breeding season, the occupancy rate was comparable in all areas, but that the treated areas showed a decreasing trend of occupancy for the second or third breeding seasons (with a lowest rate of 28.6% recorded in the fourth breeding season), whereas a 100% occupancy rate was achieved in the third and fourth breeding seasons in the non-treated areas.

For our sites, if food availability is not a limiting factor for breeding performance, such as we previously postulated, the most probable explanation would be that, as a consequence of secondary poisoning by feeding on poisoned rats, barn owls breeding pairs are less healthy in Bangka than in Riau and therefore, in Bangka, they don’t have enough energy to produce two broods each year.
What may be the consequence of a lower breeding performance in Bangka?

As a consequence of a lowest breeding performance, barn owl prey intake in Bangka is supposedly less than in Riau. Indeed, as reported by Duckett and Karuppiah (1990) as well as by Small (1990), an adult barn owl consumes on average one rat per day, but the feeding of young considerably increases requirements: one breeding pair with their young will consume on average 1,200 to 1,500 rats per year. Lenton (1980) even reported estimation up to 3,000 rats as the annual consumption for one breeding barn owl pair. We found that breeding season in Bangka is less extended than in Riau and only had one peak, reflecting only one annual brood. This result suggests that barn owl feeding requirements would be less in Bangka and, consequently, prey killed per barn owl in one year would be less in Bangka than in Riau. To some extent, only one brood a year in Bangka may reduce the ability of the barn owl to respond numerically to rat density.

To conclude, our results, both in terms of barn owl food requirements and proportion of rats in their diet (see previous point), support the hypothesis that, on a yearly basis, barn owls may consume fewer rats in Bangka plantations than in Riau plantations, that is barn owl predation on rats is lower in Bangka than in Riau. Though it is well known (see section I.3.2.) that barn owls are unable to control rat population when rat infestation is high, this may have consequences in terms of impacts on rat populations: barn owl predation impact could be one of multiple factors that contribute to explain the difference of rat population level between Bangka and Riau.

III.1.3. Barn owl prey selection in relation to size-age of rats: an assessment tool for further investigations

Does the barn owl community prey upon different rat age classes in Riau and Bangka plantations? If yes, it could affect rat community structure and thus lead to a differential impact on rat population dynamics between Riau and Bangka.

In the next pages, we will provide a tool to investigate this issue further for R. tiomanicus, the main prey of the barn owl in Riau plantations. We will explore the correlations between the eye lens weight and a range of osteometrics measurements of caught specimens of this rat species, as well as the frequency and physical integrity of different types of bones in barn owl pellets, in order to predict the relative age structure of R. tiomanicus population in prey pellets. The research was conducted in Riau_1 plantation (Libo Estate).
Aude Verwilghen*, Marie-Agnès Rabillard, Yannick Chaval, Dominique Rieffel, Martua Hashiholan Sinaga, Mohd Naim, Jean-Pierre Caliman, Patrick Giraudoux and Francis Raoul

Relative age determination of *Rattus tiomanicus* using allometric measurements

**Abstract:** For sustainable oil palm production, barn owl (*Tyto alba*) predation should be enhanced and monitored to better understand its impact on rodent population dynamics, notably for selective predation based on age or size. Our aim was to assess the best combination of osteometric variables that predict eye lens weight and thus the relative age of an individual *Rattus tiomanicus* based on pellet remains. We captured 161 individuals in an oil palm plantation in Indonesia and measured 15 osteometric variables for the jaw, skull, and femur. We investigated the variables’ correlations with eye lens weight and estimated the measurement errors. In addition, 120 pellets were collected to assess the frequency of different types of bones. Predictive modelling was then used. We suggest that the model using the femur length would be more appropriate, even if it is slightly less precise than the models that consider the skull and jaw variables. The femur was well represented in the pellet sample, its length highly correlated with the eye lens weight, with a low measurement error. Our study demonstrates the utility of femur length for age prediction in prey from macromammals in oil palm plantations, wherein most pellets are headless and *R. tiomanicus* is the dominant prey.

**Keywords:** allometry; barn owl pellet; eye lens weight; oil palm plantation; rodent.

**Introduction**

Oil palm is one of the world’s most rapidly expanding crops; the main producer countries are Indonesia and Malaysia (Oil World 2012). Expanding oil palm plantations (OPPs) over large areas support rodent population outbreaks, and certain rodents are considered invasive pests that cause significant damage to production (Liao 1990, Turner and Gilbanks 2003). Pest control typically includes treating a field using anticoagulant rodenticides and/or reinforcing barn owl predation (*Tyto alba*, Scopoli) in the plantation by providing nest boxes (Wood and Fee 2003). For more sustainable oil palm production, natural predation by barn owls should be enhanced, which requires that we better understand its impact on rodent population dynamics (Hafidzi 1994), notably for selective predation based on rodent age or size (Saint Girons 1973, Kittleyn 1997).

In Southeast Asian OPPs, barn owls primarily feed on rats (Lenton 1984, Small 1990, Puan et al. 2011); their prey spectrum is almost entirely confined to the three species, which are the major pests for oil palm crop: *Rattus tiomanicus* Miller, the Malaysian field rat; *Rattus argentiventer* Robinson and Kloss, the ricefield rat; and *Rattus tanezumi* Temminck (synonym: *Rattus rattus diardi* Lentink), the oriental house rat (Liao et al. 1993, Corley and Tinker 2003, Wood and Fee 2003). In most mature estates, *R. tiomanicus* predominates (Hafidzi and Saayon 2001, Wood and Fee 2003, Chia 2005), wherein it comprises most of the barn owl prey (Lenton 1984). Although barn owl predation on
rats on oil palm estates is widely used and has been primarily studied in Malaysia for a long time (Duckett 1976, 2008, Lentor 1980, Small 1990), the real effect of barn owl predation on the rat population is inconclusive (Chia et al. 1995, Wood and Fee 2003). In addition, there is no clear pattern for selective predation based on size, weight, or age (Small 1990, Lim et al. 1993, Hafidz and Naîm 2003, Puan et al. 2011), and certain authors suggest that differential barn owl predation may be site specific (Trejo and Guthmann 2003, Leveau et al. 2006). Therefore, predation must be locally investigated to adapt pest control strategies to each plantation/site.

Thus, as suggested by Sherfy et al. (2006), prediction models based on morphometrics are valuable for reconstructing the prey population age structure, which is a useful tool for monitoring the demographic consequences of population control. Eye lens weight (ELW) is considered to be the most accurate age indicator for mammals because it varies much less with environmental conditions than other body measurements (Lord 1959, Friend 1967, Morris 1972, Pucek and Lowe 1975, Lehrs 1994, Gliwicz and Janczewicz 2001, Lalás et al. 2006, Augusteyn 2008). ELW is widely used to estimate rodents’ exact or relative age (Le Louarn 1971, Poulet 1980, Barnett and Dutton 1995, Burlet et al. 2010). Eye lens growth patterns from known-age individuals bred in a laboratory have primarily been investigated using voles and mice (Rowe et al. 1985, Yabe and Arakawa 2009). A few Rattus species also exhibit a quantitative relationship between age and ELW (Williams 1976, Hardly et al. 1983, Tanikawa 1993, Shrestha et al. 2002); however, Rattus tiomanicus has not been studied. The eye lens cannot be retrieved from raptor pellets; however, other macroremains can be collected, such as skulls and bones. Therefore, models have been developed to predict the ELW from osteometric measurements. Variables related to skull and jaw dimensions are typically considered most appropriate for small-mammal age estimations using macroremains (Quéré et al. 1994, Granjon and Traoré 2007). However, because of prey decapitation, the absence of skull was frequently reported for barn owl pellets from Southeast Asian OPPs (Medway and Yong 1970 in Lentor 1984, Lim et al. 1993, Hafidz and Naîm 2003, Puan et al. 2011); thus, it was necessary to use variables other than cranial and dental variables. Very few authors have investigated the allometric relationships between osteometric measurements and age or size/body weight for R. tiomanicus (Small 1990, Lim et al. 1991, 1993), although this species is the most studied rodent pest in OPPs (Wood 1984, Wood and Liu 1984a,b, Buckle et al. 1997, Chia 2005). Moreover, only two authors, Lim et al. (1993) and Puan et al. (2011), have explored the relationship between femur length and relative age, respectively, for R. tiomanicus and Rattus tanezumi, to overcome the absence of skull elements in pellets.

In this study, we investigated the correlations between ELW and a range of osteometric measurements for Rattus tiomanicus trapped in a Sumatran (Indonesia) OPP. Our objectives were to assess the following: (i) the frequency of different types of bones and their physical integrity in barn owl pellets and (ii) the best combination of osteometric variables to predict R. tiomanicus lens weights theoretically (i.e., considering all variables) and practically (i.e., considering the bones most often observed in owl pellets).

Materials and methods

Study site and sampling design

The research was conducted at the Libo Estate, which is a large-scale OPP (approximately 4370 ha) in the Riau Province, Sumatra. The climate is typically humid equatorial, with an average temperature of 28°C, a mean annual rainfall of 2500 mm, and two dry seasons in February and June through August. The palm plantation is old (it was planted between 1986 and 1990) and has not been treated using rodenticide for >10 years after the introduction of barn owls for rodent pest control in the 1990s. The rodents were trapped in May 2011. Nine trap lines with 25 cage traps were set up approximately every 9 m at the base of palm trees. The traps were set for two or three consecutive nights (seven trap lines were only set for two consecutive nights) and controlled each morning. We used locally constructed cage traps (32×12×15 cm) that were baited with freshly cut half of a palm fruit. The traps were located in the plantation core at a minimum distance of 600 m from human settlements to minimise trapping species other than Rattus tiomanicus.

Species identification and osteometric measurements

The rats were euthanised using chloroform (outdoors with safety precautions for the operator’s health) and then sexed, and classic external body measurements were collected (weight, head/body, and tail lengths; see Herbretou et al. 2011). The head and left leg were severed for further dissection, boiled in an autoclave at 121°C for 30 min, and then submerged in water for 1 week to ease bone and flesh separation. For eye lens processing, various similar
techniques are described in the literature (Poulet 1980, Rowe et al. 1985, Shrestha et al. 2002, Jánowa et al. 2007), and as noted by Lalis et al. (2006), the accuracy is rarely assessed. We adapted the protocol to tropical conditions. The eyeballs were removed and fixed in 4% formalin for at least 2 weeks in a refrigerator. The lenses were then excised, washed with distilled water, and oven dried at 40°C in two batches for 9 and 7 days (given the humid conditions, a preliminary trial was used for the first batch to estimate the drying duration necessary for weight stabilisation). Once out of the oven, the eyeballs were immediately weighed in pairs to the nearest 0.1 mg. The mean weight of each pair was used for analysis.

One hundred and sixty-one presumably Rattus tiomanicus individuals (identified according to external morphology; Corbett and Hill 1992, Aplin et al. 2003) were used as the reference collection for our measurements. A subsample composed of 120 individuals was selected using the following process. A principal component analysis with log-transformed osteometric measurements (see below) was used to select three variables that were least correlated between each other and least correlated for animal size (BP, CLM1-3, and Jaw1; see Figure 1). The animals were then selected at the periphery and centre of the data cloud from a triangular graph, wherein the axes were the three variables. The animals were then identified using a molecular barcoding method, with species assignment using the RodentSEA reference database available at http://www.ceropath.org/barcoding_tool/rodentsea (Clairon et al. 2010).

The following 15 osteometric variables (Figure 1) were measured to the nearest 0.1 mm for each specimen by the same person using digital calipers: (i) in accordance with Dickman et al. (1991) and Quéré et al. (1994), 11 variables for the skull and jaw that relate well to age and are typically collected intact from bones and easily found in pellets; (ii) two femur variables, one composing the entire length of the bone, and the other excluding the distal epiphysis cartilage that is often absent (hereafter, the "short length"); (iii) the femur was used because certain authors note that heads are frequently absent from the pellets in OPPs, likely because barn owls decapitate their prey before carrying them to the nest (Lenton 1984, Lim et al. 1991); and (iii) two incisor variables were measured to use small-carnivore scat in the model because incisors are typically the only intact rat remnant in a scat (Bonnaud et al. 2008).

Material used for measurement (skull, femur, and eye lenses of each of the 161 specimens) is available at the Centre de coopération internationale en recherche agronomique pour le développement (CIRAD), Montpellier, France. Specimens are labelled LH105XXXX (xx being the number of the individual trapped on the line XX; trappers are labelled AA, AB, AC, AD, AE, AR, AS, AT, AU).

The final aim of this study was to propose a model with a combination of variables (osteometric measurements) that best predicts the ELW and thus the relative rat age based on pellet remains. Therefore, concurrent with trapping, we collected the intact barn owl pellets inside nest boxes in our study area and the vicinity. One hundred pellets were collected in 57 nest boxes, covering an area of approximately 1600 ha (typically, one nest box in each block of 30 ha). It has been suggested that the presence or absence of skulls in pellets is associated with an owl’s breeding cycle (Lenton 1984, Hafidzi and Naim 2003). Subsequently, 20 additional pellets were retrieved in August 2010, during the barn owl breeding peak, to encompass a potential behavioural change in prey consumption. We examined the occurrence and integrity of the rodent skull, jaw, and femur in pellets to assess which of the 15 variables were most likely to be collected from the pellets. We also estimated the imprecision for measurements from the same observer over two measurement sessions; the 15 variables from a sample composed of 30 rats were measured twice by the same person.
Statistical analysis

The percentage of measurement error (\%ME; i.e., the percentage of sample variation due to measurer imprecision) can be defined as "the ratio of the within-measurement component of variance to the sum of the within- and among-measurement component" (Bailey and Byrnes 1990):

\[ \%\text{ME} = \frac{\left( s_{\text{within}}^2 / s_{\text{within}}^2 + s_{\text{among}}^2 \right)}{} \times 100. \]

The mean squares of the one-way ANOVA were calculated to determine the components of variance:

\[ s_{\text{within}}^2 = \frac{\text{MSS}_{\text{within}}}{m} \]

and

\[ s_{\text{among}}^2 = \frac{\text{MSS}_{\text{among}}}{m} \]

where \( m \) is the number of repeated measurements (Yzerinac et al. 1992, Claude 2008).

Two sets of models were computed based on two sets of variables: (i) all osteometric variables without considering whether they can be frequently collected from the pellets ("theoretical" model) and (ii) variables most commonly found in pellets due to high bone integrity (i.e., likely to be most useful for researchers and practitioners working with pellets; "practical" models). The practical models were constructed using the osteometric variables selected on the basis of three criteria: (i) the frequency in pellets is >10%; (ii) the Pearson correlation coefficient for the given variable with an ELW is \( r > 0.5 \); and (iii) the ME percentage is <10%. Because we did not have a biological \textit{a priori} for the order of variables in the model, a stepwise procedure (backward and forward) was used to select the best set of predictors based on the Akaike information criterion (AIC) (Burnham and Anderson 2002). Visual analyses of bivariate graphs among the ELW and osteometric measurements suggested that linear modelling was an acceptable option. The normality of model residuals was determined using the Kolmogorov-Smirnov goodness of fit test. We used a 10-fold cross-validation procedure to estimate the coefficient of determination (R²) and the root mean squared error (RMSE), which is a good measure of model fit and accuracy.

The prey's sex cannot be defined in pellets using our measurements. However, we investigated a potential difference in ELW between sexes from our trapped sample using a linear model. In addition, we also investigated the performance of models, including the variable sex as a covariate, to assess whether a bias was induced by using only one equation for both sexes.

The data were statistically analysed using the R software (version 2.15.0); R Foundation for Statistical Computing, Vienna, Austria) and the packages ade4, bootstrap, DAAG, epicalc, lattice, pgirmess, plotrix, and ipred.

Results

\textbf{Rattus tiomanicus} characteristics

Among the 120 individuals that were subsampled for molecular identification, 110 were successfully sequenced, 100% of which were confirmed as \textit{Rattus tiomanicus}. Summary statistics on the body and bone measurements (Table 1) as well as ELW distribution (Figure 2) suggest that both juvenile and adult specimens were sampled with minimum and maximum body weights at 17 and 139 g, respectively. The sex ratio of our sample was 1.36 males per female. We did not detect a significant difference in ELW between males and females (P-value = 0.0723, p = 0.7883; Kolmogorov-Smirnov test of

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean±standard deviation</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight (g)</td>
<td>72.73±32.27</td>
<td>17.00</td>
<td>139.00</td>
</tr>
<tr>
<td>Body length (mm)</td>
<td>139.9±15.1</td>
<td>90.00</td>
<td>183.00</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>144.4±14.6</td>
<td>85.00</td>
<td>189.00</td>
</tr>
<tr>
<td>Eye lens weight (mg)</td>
<td>35.98±7.02</td>
<td>13.20</td>
<td>64.00</td>
</tr>
<tr>
<td>Jaw (mm)</td>
<td>16.82±0.24</td>
<td>11.77</td>
<td>21.02</td>
</tr>
<tr>
<td>L1</td>
<td>8.87±0.87</td>
<td>4.77</td>
<td>12.18</td>
</tr>
<tr>
<td>L2</td>
<td>5.27±0.43</td>
<td>3.51</td>
<td>7.08</td>
</tr>
<tr>
<td>L3</td>
<td>5.19±0.55</td>
<td>3.21</td>
<td>7.52</td>
</tr>
<tr>
<td>L5</td>
<td>6.16±0.15</td>
<td>4.23</td>
<td>6.86</td>
</tr>
<tr>
<td>Lower incisor</td>
<td>1.62±0.20</td>
<td>0.87</td>
<td>2.35</td>
</tr>
<tr>
<td>Skull (mm)</td>
<td>36.27±2.62</td>
<td>25.67</td>
<td>41.92</td>
</tr>
<tr>
<td>GSI</td>
<td>5.68±0.45</td>
<td>4.30</td>
<td>7.10</td>
</tr>
<tr>
<td>LR</td>
<td>12.74±1.24</td>
<td>8.21</td>
<td>17.30</td>
</tr>
<tr>
<td>CLM1–3</td>
<td>6.40±0.19</td>
<td>5.21</td>
<td>7.12</td>
</tr>
<tr>
<td>LD</td>
<td>9.87±1.01</td>
<td>6.51</td>
<td>12.92</td>
</tr>
<tr>
<td>BP</td>
<td>4.49±0.40</td>
<td>2.60</td>
<td>6.49</td>
</tr>
<tr>
<td>Upper incisor</td>
<td>1.97±0.20</td>
<td>1.18</td>
<td>2.71</td>
</tr>
<tr>
<td>Femur (mm)</td>
<td>23.57±3.00</td>
<td>12.62</td>
<td>30.40</td>
</tr>
<tr>
<td>Long femur</td>
<td>20.20±2.63</td>
<td>10.97</td>
<td>26.45</td>
</tr>
</tbody>
</table>

L1, mandible length; L2, mandible height; L3, diastema length; L4, jaw height; L5, molar row length; GSI, greater skull length; IB, interorbital breadth; LR, length of rostrum; CLM1–3, molar row length; LD, length of diastema; and BP, breadth of palate.
residuals normality: p=0.9747; Bartlett test of homogeneity of residuals variance: p=0.2532).

Bone frequency in pellets and measurement errors

As reported in Table 2, full osteometric measurements were impossible in at least 70% of pellets because of the low integrity of the skull and jaw bones in barn owl pellets. However, we measured the short femur in 80.8% of pellets. Between the two different sessions of measurements (by the same person), the percentage of measurement errors was low for the short femur (%ME=0.23). The L1 and L2 values were also among the lowest at 1.8% and 1.4%, respectively. Seven variables, L3, L4, L5, Lower incisor, IB, CLM1–3, and Upper incisor, were >10% ME.

Predictive models for the relative age estimation

The Pearson correlation coefficients (r) between the ELW and the variables CLM1–3 and L5 were <0.4 (Table 2).

Other variables were strongly correlated with lens weight; r ranged from 0.79 to 0.92, and the most correlated variables were the short and long femur. Using criteria based on frequency in pellets (>10%), the measurement errors (<10%) and correlation with lens weight (≥0.8), only six variables, namely, L1, L2, LD, and BP, as well as the short and long femur, were selected for the first predictive model (see Table 2). The model that best predicted the ELW was the model that included L2, LD, BP, and the short femur with an AIC=435.62 and $R^2=0.847$ (model 1, Table 3). Because most pellets are headless, we investigated a model based on the short femur measurement only; the AIC for this model (model 2, Table 3) was greater than model 1 (458.04 vs. 435.62). The accuracy evaluation for the two “practical” models through cross validation showed that model 1 was slightly more accurate at estimating ELW than the model that only included the femur (Rmse=3.86 vs. Rmse=4.14, only considering the femur). A “theoretical” model was constructed on

<table>
<thead>
<tr>
<th>Osteometric variable</th>
<th>Frequency in pellets (%)</th>
<th>Measurement error (%)</th>
<th>Correlation with eye lens weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jaw</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L1***</td>
<td>30.0*</td>
<td>1.8*</td>
<td>0.85* &lt;0.001</td>
</tr>
<tr>
<td>L2***</td>
<td>30.8*</td>
<td>1.4*</td>
<td>0.89* &lt;0.001</td>
</tr>
<tr>
<td>L3</td>
<td>32.5*</td>
<td>11</td>
<td>0.83* &lt;0.001</td>
</tr>
<tr>
<td>L4</td>
<td>32.5*</td>
<td>10.8</td>
<td>0.87* &lt;0.001</td>
</tr>
<tr>
<td>L5</td>
<td>32.5*</td>
<td>10.6</td>
<td>0.37* &lt;0.001</td>
</tr>
<tr>
<td>Lower incisor</td>
<td>32.5*</td>
<td>14.5</td>
<td>0.86* &lt;0.001</td>
</tr>
<tr>
<td>Skull</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GSL</td>
<td>2.5</td>
<td>0.2*</td>
<td>0.87* &lt;0.001</td>
</tr>
<tr>
<td>IB</td>
<td>21.7*</td>
<td>26.4</td>
<td>0.79* &lt;0.001</td>
</tr>
<tr>
<td>LR</td>
<td>8.3</td>
<td>4.9*</td>
<td>0.89* &lt;0.001</td>
</tr>
<tr>
<td>CLM1–3</td>
<td>25.8*</td>
<td>26.8</td>
<td>0.27 &lt;0.001</td>
</tr>
<tr>
<td>LD***</td>
<td>23.3*</td>
<td>1.9*</td>
<td>0.86* &lt;0.001</td>
</tr>
<tr>
<td>BP***</td>
<td>23.3*</td>
<td>4*</td>
<td>0.83* &lt;0.001</td>
</tr>
<tr>
<td>Upper incisor</td>
<td>22.5*</td>
<td>12.7</td>
<td>0.83* &lt;0.001</td>
</tr>
<tr>
<td>Femur</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long femur***</td>
<td>25.0*</td>
<td>1.2*</td>
<td>0.92* &lt;0.001</td>
</tr>
<tr>
<td>Short femur***</td>
<td>80.8*</td>
<td>0.2*</td>
<td>0.92* &lt;0.001</td>
</tr>
</tbody>
</table>

L1, mandible length; L2, mandible height; L3, diastema length; L4, jaw height; L5, molar row length; GSL, greater skull length; IB, interorbital breadth; LR, length of rostrum; CLM1–3, molar row length; LD, length of diastema; and BP, breadth of palate. The values that fit with the pre-selection criteria (see Material and methods) are marked with an asterisk; the variables pre-selected for “practical” predictive modelling are indicated with three asterisks.
Table 3  Comparison of predictive model fitness and accuracy for *Rattus tiomanicus* eye lens weight estimation using a stepwise procedure and cross validation.

<table>
<thead>
<tr>
<th>Pre-selection of variables</th>
<th>Model</th>
<th>Best combination of variables and associated equation</th>
<th>AIC</th>
<th>$R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1, L2, LD, BP, short and long femur</td>
<td>1</td>
<td>ELW=-(1.5060 L2+0.8163 LD+2.7511 BP+1.4777 Short femur)-28.0396</td>
<td>435.62</td>
<td>0.847</td>
<td>3.86</td>
</tr>
<tr>
<td>L1, L2, LD, BP, short and long femur, sex</td>
<td>1 sex</td>
<td>ELW=-(1.5420 Sex+1.6010 L2+0.9090 LD+2.560 BP+1.2760 Long femur)-28.278</td>
<td>431</td>
<td>0.851</td>
<td>3.83</td>
</tr>
<tr>
<td>Short femur</td>
<td>2</td>
<td>ELW=-(2.8060 Short femur)-20.705</td>
<td>458.04</td>
<td>0.859</td>
<td>4.14</td>
</tr>
<tr>
<td>Short femur, sex</td>
<td>2 sex</td>
<td>ELW=-(1.1860 Sex+2.8130 Short femur)-20.3405</td>
<td>456.72</td>
<td>0.851</td>
<td>4.16</td>
</tr>
<tr>
<td>All variables</td>
<td>3</td>
<td>ELW=-(0.8263 L2+2.4834 L5+0.7125 LD+2.6186 BP+4.4933 Upper incisor+5.5058 Lower incisor+1.2114 Short femur)-17.1739</td>
<td>422.05</td>
<td>0.865</td>
<td>3.78</td>
</tr>
<tr>
<td>All variables, including sex</td>
<td>3 sex</td>
<td>ELW=-(1.2600 Sex+1.1010 L2+1.6030 L3+2.425 L5+1.0300 LD+2.5020 BP+4.1460 Upper incisor+6.1260 Lower incisor+1.2450 Short femur)-16.637</td>
<td>419.1</td>
<td>0.851</td>
<td>3.71</td>
</tr>
</tbody>
</table>

Models 1 and 2 are “practical” models, and model 3 is the “theoretical” model. ELW, eye lens weight; L1, mandible length; L2, mandible height; L3, diastema length; L5, molar row length; LD, length of diastema; and BP, breadth of palate.

Table 4  Parameter estimates and associated standard error (SE) for the *Rattus tiomanicus* eye lens weight prediction models.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model 1</th>
<th>Estimate</th>
<th>SE</th>
<th>Model 2</th>
<th>Estimate</th>
<th>SE</th>
<th>Model 3</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td></td>
<td>-28.0396</td>
<td>2.4500</td>
<td></td>
<td>1.5060</td>
<td>0.5760</td>
<td></td>
<td>0.8263</td>
<td>0.5763</td>
</tr>
<tr>
<td>L2</td>
<td></td>
<td>1.5060</td>
<td>0.3613</td>
<td></td>
<td>8.413</td>
<td>0.5351</td>
<td></td>
<td>2.7511</td>
<td>0.9358</td>
</tr>
<tr>
<td>BP</td>
<td></td>
<td>2.7511</td>
<td>0.9358</td>
<td></td>
<td>0.413</td>
<td>0.2697</td>
<td></td>
<td>1.4777</td>
<td>0.2697</td>
</tr>
<tr>
<td>Short femur</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td></td>
<td>-20.705</td>
<td>1.9790</td>
<td></td>
<td></td>
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<td>Short femur</td>
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<td>Model 3</td>
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<td>LD</td>
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<td>Upper incisor</td>
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<td>4.4933</td>
<td>2.3100</td>
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<tr>
<td>Lower incisor</td>
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<td>5.5058</td>
<td>2.3749</td>
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<td>0.2710</td>
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L1, mandible length; L2, mandible height; L3, diastema length; L5, molar row length; LD, length of diastema; and BP, breadth of palate.

the basis of all of the jaw, skull, and femur variables. The seven-variable combination that best predicted the ELW is shown in Table 3 (model 3). This model performed better than both of the best “practical” models (AIC=422.05 and $R^2=0.865$); however, we only detected a slight improvement in the prediction precision ($RMSE=3.78$). The standard errors for the parameter estimates in the three models are presented in Table 4. Including the variable sex as a covariate slightly improved the performance of the models (models 1 sex, 2 sex, and 3 sex; Table 3). Our assumptions on the homogeneity of variance, independence, linearity, and normality of error were examined for each model. The normality of residuals was confirmed for each model (Kolmogorov-Smirnov test, $p=0.843$ for model 3, $p=0.426$ for model 1, and $p=0.331$ for model 2).

**Discussion**

We presented a set of best equations for the prediction of *Rattus tiomanicus’* ELW, based on various skull, jaw, and femur measurements. We demonstrate here that, because rodent heads are frequently absent from barn owl pellets in Malaysian and Indonesian OPs, the predictive model based only on the femur was the most useful, although slightly less precise than the models based on skull and jaw variables. We also argue that we can confidently attribute most, if not all, femurs in the pellets studied herein to *R. tiomanicus*.

**Species Identification**

As has been reported since the 1970s, *Rattus tiomanicus* is still the dominant species in mature OPs in Southeast Asia; however, it has progressively been replaced by *Rattus tanezumi* (previously *Rattus rattus diardi*) in several localities, notably the Malaysian peninsula (Wood and Fce 2003). The *R. tiomanicus* predominance in our study area was confirmed through our trapping experiments. The specimens successfully sequenced herein ($n=110$)
were confirmed as *R. tiomanicus*. Additional investigations at the same estate confirmed that *R. tiomanicus* was predominant; the 19 specimens identified using the same molecular barcoding method were *R. tiomanicus* (Andru et al. 2013). Therefore, although we cannot completely exclude sibling species (Wilson and Reeder 2005, Pagés et al. 2010), we can assume that virtually all of the 161 specimens were *R. tiomanicus*.

Predictive modelling, a compromise between parsimony, accuracy, and practicability

Except for the upper and lower molar row length (CLM1–3 and L5), the monovariate correlations (r > 0.80) between the jaw or skull variables and ELW were strong; length of rostrum (LR) and L2 yielded the best correlations (both r > 0.89). We could not find similar investigations on *Rattus* species in the international literature, which precludes a comparison. Our results differ from the *Microtus* results. Shi et al. (2006) found that the length of the *Microtus altaicus* Thomas upper molar row correlated best with age, and Quéré et al. (1994) found that the *Microtus arvalis* Pallas great skull length, LR, and molar row length (CLM1–3) correlated best with age. Moreover, the breadth of palate yielded one of the lowest correlations for *M. arvalis*, whereas in our results, it correlated well with ELW and was included in the final equation. We found a high measurement error for certain variables, such as CLM1–3 (26.9%), which may be due to the difficulty in finding precise landmarks on bones; therefore, these measurements were discarded from “practical” modelling.

We did not detect a significant difference in ELW between males and females. These data are consistent with Williams (1976) and Shrestha et al. (2002), who did not detect a difference in ELW based on sex for other *Rattus* species, such as *Rattus exulans* Peale and *Rattus brunnneus* Hodg, respectively. The latter species is currently regarded as a *Rattus tanezumi* synonym (Wilson and Reeder 2005). Certain authors have reported that males have slightly heavier lenses than females, such as for *Rattus norvegicus* Berkenhout (Hardy et al. 1983) and other rodents (Rowe et al. 1985, Yabe and Arakawa 2009). Our results indicate that the models perform only slightly better when the variable sex is used as a covariate. Therefore, using models 1–3 to predict age may produce a minor sex-related bias. However, Hardy et al. (1983) noted that considering the sex variable in modelling may not be justified because the improvement therefrom is slight.

Many studies aimed at estimating the age, size, or body mass of prey from pellets prefer only lower jaw variables because this organ is highly frequent and well preserved in macroremains (Morris 1979, Trejo and Guthmann 2002, Granjon and Traoré 2007, Bueno and Motta-Junior 2008). However, we found that approximately 70% of pellets were headless. This result is consistent with other reports (Medway and Yong 1970 in Lenton 1984, Lim et al. 1993, Halidži and Naim 2003, Puan et al. 2011). Considering the frequent absence of heads in barn owl pellets on OPPs, we focused on elements other than the skull, jaw, and teeth for modelling. In addition, the tendency of the barn owl to decapitate larger prey may yield a bias if the skull or jaw is used to estimate the age or size distribution and further assess the impact of barn owl predation (Lim et al. 1993). The femur was a good candidate for ELW prediction because it was well represented in our pellet sample, and the variable short femur highly correlated with the ELW. Moreover, the femur measurement error was the lowest compared with the other variables used in the final equations. Thus, the final equation with only the short femur would be more accurate, even if the prediction precision was not greatly improved by considering all the variables.

Model limits and extrapolation

Age prediction is more accurate in younger animals (Tanikawa 1993, Shrestha et al. 2002). William (1976) found that the ELW was only a useful indicator of *Rattus exulans* age for up to 3 or 4 months. Myers et al. (1977, in Hardy et al. 1983) studied indigenous rats in Australia and found a similar lack of precision at this threshold, which clearly limits age determination using the ELW.

Our measurements are consistent with the maximum weight of adult rats reported in the literature (Corbett and Hill 1992, Aplin et al. 2003). However, according to Wood (1984), young rats up to approximately 10 g cannot be trapped by the cage traps used in our study. As the body weight of our specimens ranged from 14 to 139 g, we may not have included certain juvenile individuals in our models.

Because the rats’ food supply does not vary greatly month to month owing to a relatively constant temperature and continuous oil palm fruiting throughout the year (Lenton 1984), an effect from rat nutritional status or season on ELW and, thus, age estimations is unlikely.

The equations proposed here are theoretically only applicable for comparing the population structure in the same area during the same period (Quéré et al. 1994). However, even if the rats were trapped in May, extrapolating to another season or year should not be a problem in the tropics and specifically in OPPs without
chemical control. Indeed, the rat population dynamics do not change markedly with the seasons (due to continuous oil palm tree fruiting; Lenton 1984), the population demography fluctuates slowly, and the weight spectrum is approximately constant (Wood 1984, Wood and Liu 1984b). In contrast, the location is important because population-based genetic variations cannot be excluded.

Owing to the lack of skulls or presence of broken skulls, it is difficult to identify prey species in pellets, which may be an issue for attributing the femur to the correct species. However, the barn owl diet generally reflects the abundance of prey species in the hunting territories (Bunn et al. 1982, Figueras et al. 2009), as demonstrated for OPPs by Lenton (1984) and Puan et al. (2011). Therefore, because Rattus tiomanicus is the predominant species in our study area, we confidently assume that this species is the major, if not the only, prey in the barn owl pellets studied. In areas where several rat species are sympatric and abundant, new-generation molecular methods can be used to ensure that femurs from the pellets are from R. tiomanicus (Galan et al. 2012).

**Conclusion**

Our study demonstrates that the femur length is relevant to ELW predictions for prey from macromammals, specifically in OPPs, wherein most pellets are headless. Our models represent a preliminary step to establish a relative age structure for Rattus tiomanicus consumed by the barn owl and to compare it to the population structure in the field, with a view to further assessing the impact of barn owl predation and improving ecologically based pest control.

**Acknowledgments:** We thank the technicians from SMARTRI who helped with the fieldwork as well as PTSmart Tbk for their accommodation and for providing access to the facilities and plantation. We are grateful to the State Ministry of Research and Technology of Indonesia, which supported this research (0131/SIP-FRP/SM/V/2011).

Received July 18, 2013; accepted January 30, 2014; previously published online March 5, 2014.

**References**


In brief:
Our result suggested difference in food requirement of the barn owl population in Bangka and Riau plantations. The mean number of eggs yearly laid by barn owls is less in Bangka than in Riau. In Riau, there are two peaks of egg laying, against only one in Bangka. The limited breeding season in Bangka (only one annual brood in Bangka compared to two in Riau) would lead to a lower food requirement for the breeding pairs and their chicks; and consequently prey intake from barn owl community each year would be less in Bangka compared to Riau. We suggest that secondary intoxication from coumatretalyl rodenticide may affect barn owl reproduction, and explain their lower breeding performance in Bangka compared to Riau.

Our results also showed differences in dietary composition among Riau and Bangka: the proportion of rats in barn owl diet is slightly less in Bangka plantations than in Riau plantations; and prey taken as food by the barn owl were more diverse in Bangka (including reptiles and frogs in addition to insects, birds and bats as found in Riau).

Our hypothesis was that rat prey intake from barn owl population each year would be less in Bangka compared to Riau. Our results on barn owl food requirements and on barn owl diet, reflecting predation pressure, support this prediction. If barn owl predation on rats is lower in Bangka than in Riau, this could, to some extent, be one of a multifactor explanation for differences in rat population levels between Bangka and Riau.

Barn owl selective predation based on rodent age or size may also affect community structure and in turn have an impact on rat population dynamic. We provided a tool to further assess relative age of *R. tiomanicus* (the main barn owl prey in Riau plantations) from barn owl pellets macroremains.
Our previous results and analysis (III.1.) suggested that, though barn owls are well established in both Riau and Bangka plantations, predation pressure (barn owl food requirement) and diet (proportion of rats in barn owl diet) are different between Bangka and Riau, supporting our hypothesis that yearly rat prey intake from the barn owl community would be less in Bangka than in Riau.

After barn owls, we will now focus in small carnivores, which are another potential rat predator. We predict that the contribution of the small carnivore community to rat offtake is less in Bangka than in Riau. As depicted in the general introduction, the predation rate of the small carnivore community on the rat population should be mediated, among others, by the abundance of each predator species and the relative importance of the rat in the diet of each species. Therefore, we aimed to test our general prediction by estimating if the lower rat damage observed in Riau plantations is associated with 1) the predominance of highly carnivorous predator species, 2) a higher proportion of rodent prey in the small carnivore community diet. In this view, we first aimed to investigate small carnivore community in terms of richness and species relative abundance within Riau and Bangka plantations. Feral/domestic cats being small carnivores and potential rat predators, they were included in the assessment; hereinafter, the term “small carnivores” will be used when domestic/feral cats are included, and “wild small carnivores” when they are excluded. In addition to abundance comparisons, we will then compare food habits of the small carnivore community encountered within each plantation.

When taking an interest in the persistence of wild small carnivores in oil palm landscapes, it is valuable to estimate the relative abundance of domestic/feral dogs in the oil palm plantations, because they may have a negative impact on wild small carnivores, through direct predation, competition and/or diseases transmission (Vanak and Gompper, 2009; Azhar et al., 2013a; Hughes and Macdonald, 2013), like domestic/feral cats may also do (Izawa et al., 2009; Medina et al., 2014). Therefore, we also compared relative abundance of dogs among our study sites.

### III.2.1. Small carnivore abundance and community composition

**Introduction**

Our objective is to compare small carnivore abundance and species richness in Riau and Bangka plantations. We predict that small carnivores are less abundant in Bangka plantations than in Riau plantations; and that rodent specialists are more abundant in the small carnivore community of Riau comparatively to Bangka.

Our approach focuses on differences between regions, i.e. Riau versus Bangka, but also on differences among plantations, in order to estimate variability within regions. Abundance indices of small carnivores over the whole sampling period were compared, both at community level and at species level (identification at species level was only possible for spotlight counts). Complementary to abundance index, diversity indices were also calculated. Then we investigated variations in annual kilometric abundance index (KAI) of the whole small carnivore community to assess potential trends.
We predict that small carnivore abundance is negatively correlated with rodent damage. To investigate this issue we examined the relationship between KAI from spotlight counts and rodent damage.

In addition to assessing small carnivore abundance, we compared relative abundance of dogs among our study sites. We predict that small carnivores are less abundant in plantations where dogs are more abundant.

**Material and methods**

**Field signs and direct observations**

Our intention was not to estimate absolute population density, which was out of reach for methodological and logistical reasons, but to compare relative abundance levels between regions and plantations. Therefore we used indices (kilometric abundance indices: KAI) that provided estimates of relative abundance. The use of KAI was preferred over estimates of actual density or true abundance because the former have been shown to allow robust assessment of population trends and the latter requires a number of prerequisites and assumptions to be valid (Linnell et al., 1998; Wilson and Delahay, 2001; Engeman, 2003; Long et al., 2008; Funston et al., 2010) that make their use not realistic within the context of this study. Abundance indices were calculated in the four plantations (Riau_1, Riau_2, Bangka_1, Bangka_2) from the frequency of field signs (faeces counts) and direct observations (spotlight counts) per kilometer of sampling effort. These methods, noninvasive and cost-effective, are commonly used to assess the relative abundance of carnivores, specifically when comparing abundance between areas or to monitor trends over time (Wilson and Delahay, 2001; Forsyth et al., 2005; Mitchell and Baloch, 2007; Long et al., 2008), including in tropical countries (Thorn et al., 2010). Surveys were conducted on roads. Indeed, the probability of detecting carnivores can be increased by surveying along roads, as most of them, notably felids, prefer travelling and defecating along these features (Macdonald, 1980; Jenny, 1996; Austin et al., 2007b; Gordon and Stewart, 2007; Long et al., 2008; Mohamed et al., 2013; Nakabayashi et al., 2014). Surveys were conducted in the dry season during three consecutive years, from 2010 to 2012. Surveys were conducted at the same period each year (June/July for Riau and July/August for Bangka) because counts may be affected by seasonal shifts in activity patterns of some species, as reported for foxes by Forsyth et al. (2005).

Kilometric abundance indices (KAI) (number of observations per kilometer) were obtained to compare relative abundance and species richness of the small carnivore community between plantations. KAI from faeces counts (KAI\textsubscript{FAE}) is less representative of abundance than KAI from spotlight counts (KAI\textsubscript{SPL}), because faeces is also used as a scent mark by small carnivores, notably felids, therefore faeces are usually not left at random but strategically placed, and the same place may be frequently revisited and remarked (Wilson and Delahay, 2001; Sunquist and Sunquist, 2009). Consequently, KAI\textsubscript{FAE} is rather a proxy of the cumulative number of visits to a site than of the abundance in a given habitat. Though faeces count is a cost effective method, many studies did not find a clear correlation between KAI\textsubscript{FAE} and other methods, either in an agricultural landscape in France (Giraudoux, 1991), in North American forests (Gompper et al., 2006) or in a grassland dominated landscape in South Africa (Thorn et al., 2010). However, Güthlin et al. (2014), taking landscape characteristics into account, have proved that KAI\textsubscript{FAE} was highly correlated with abundance estimated by camera trapping, in a study on red fox in Germany. For some species, faeces counts may provide an efficient method to evaluate relative abundance, as demonstrated by...
Harrison et al. (2002), who compared this survey techniques to others (tracks, spotlight and calling) for estimating fox abundance in grasslands in New Mexico. Cavallini (1994) also found that, in some conditions such as similar rainfall, faeces count may be a reliable index of fox abundance in mixed wood and grassland (mainly cultivated) landscape. Moreover, Gompper et al. (2006), comparing noninvasive survey techniques to survey carnivore communities in temperate forests, showed that trail-based fecal surveys revealed the presence of foxes at sites where other techniques failed to discern this species. This technique might therefore be more representative of the species diversity within the whole carnivore community than spotlight counts. To conclude, given that both density and activity of small carnivores affect KAI for spotlight counts and faeces counts, they can be used with caution to compare relative abundance of small carnivores in space and time, within limits that will be discussed below.

**Faeces counts**

Faeces of small carnivores were counted on fixed transects along plantation dirt roads, totaling 30.86 km, 44.55 km, 37.82 km and 46.25 km each year in Riau_1, Riau_2, Bangka_1 and Bangka_2. Survey effort was higher in both Bangka plantations because of fewer signs detected during preliminary exploratory surveys in 2009. Transect locations were chosen on roads within the plantation and along its border, making these representative of the diversity of landscapes and habitats in each plantation (see Figure 42). Survey was performed along main roads and collection roads around oil palm blocks, but not along collecting trails within oil palm blocks. Indeed, though roads are relatively homogenous and ensure a substantial visibility, visibility along trails was much reduced and highly variable due to fluctuating width and ground vegetation cover; thus surveying along these paths in addition to roads would have introduced bias.

Surveys were conducted once a year, during the dry season, because during the rainy season heavier and faster faeces degradation occurs due to rainfall (Cavallini, 1994). Two observers walked along road transects at a slow pace (about 3 hours/km), each one scanning one side of the road. All small carnivore faeces encountered were counted, and collected for further diet analysis (see next section). As depicted in the general introduction, several wild small carnivores may coexist in an oil palm plantation, in addition to the presence of domestic or feral dogs and cats. Many authors (Ray and Sunquist, 2001; Davison et al., 2002; Long et al., 2008) have pointed out the difficulty of consistently distinguishing the faeces of different carnivores species based only on faeces size and morphology. Some families have characteristic faeces as described below, however, according to Chame (2003), even visual assignment to family level is problematic, and the diagnosis at the generic level is of no value. Reliable species identification techniques using molecular methods are available and represent a promising development (Farrell et al., 2000; Deyoung and Honeycutt, 2005; Galan et al., 2010; Mukherjee et al., 2010; Dinkel et al., 2011; Michalski et al., 2011; Goossens and Salgado-Lynn, 2013), but due to time and financial constraints, we were not able to carry out DNA analysis in this study. Therefore, given the potential for confusing faeces of sympatric small carnivore’s species, we pooled all faeces collected within a “small carnivore” category and considered the community level, including faeces of domestic/feral cats (which may be confused with leopard cats, as reported by Lee et al. (2014c)).

Small carnivore faeces were discriminated from non-small carnivore faeces by size, shape and broad content (Walker, 1996; Chame, 2003). Occasionally, presence of other signs nearby such as footprints helped with identification. Footprints were identified using a collection of mammals.
footprint identification guides (van Strien, 1983; Payne et al., 1985; Walker, 1996; Sidorovich, 1999; White and Edwards, 2001; Francis, 2008). Faeces size varies less among carnivores than for other groups (Stuart and Stuart (1998), cited by Chame, 2003), and a maximum diameter of about 2.5 cm seems reasonable to encompass all species of small carnivores. Therefore we selected only faeces with a maximum diameter of about 2.5 cm. Cylindrical faeces of sausage-shape, with sub divisions, tapered at one of the extremities is characteristic of the carnivore order (Chame, 2003). Some small carnivore families or sub-families have a distinctive and typical shape and may be more easily recognizable. Faeces of compact form with well-defined segments and one of the extremities especially tapered and hairy can be identified to Felidae family, while narrower, flattened, generally more single unit and twisty patterns can be assign to Mustelids (Tabeni et al., 2012; Bashir et al., 2014). To complement this, the content of faeces can also used for diagnosis (Chame, 2003): felids faeces reflect a strictly carnivorous diet, while presence of fish, crustacean and mollusk remains distinguish aquatic mustelids such as Lutrinae (the otter faeces usually smell fish or cod oil, unlike the mongoose one; Duplaix N., pers. com.); and fruit, seed, insect, crustacean, plant tissue and shell fragments are commonly found in omnivorous Canidea, Mustelidea and Viveridea. Dog faeces where easily identified and excluded based on their very large size and/or to some characteristic diet remains such as rice (domestic dogs) and/or whole oil palm fruit(s) (according to our observations, small carnivores do not ingest the whole fruit but consume only mesocarp, while dogs frequently ingest the entire palm fruit). Civet faeces can come in different shapes and colors and may have typically fruits/seeds content for frugivorous ones; they might sometimes be confused with primate faeces, but primate faeces are usually single and amorphous or somewhat cylindrical or rounded shape. Color may be a criterion of inclusion; for example faeces of carnivores can sometimes be totally white, as a result of a high calcium content as a consequence of bone ingestion (Chame, 2003).

Based on these inclusion or exclusion criteria, all faeces presumably from small carnivores were counted, georeferenced using GPS (Garmin GPSmap 60CSx) and photographed, and identification of their family or other taxonomic level was reported whenever possible. A degree of certainty of the identification was assigned both at the “small carnivore” level and at a lower taxonomic level: degree 2 for high confidence (sure), degree 1 for medium confidence (highly probable) and degree 0 being a guess (uncertain). The degree of certainty was first assigned in the field during pedestrian transects and was later checked by expert knowledge from two small carnivores specialists (A. Jennings and G. Veron) based on photographs. In the field, freshness of the faeces was also recorded (degree 2=fresh=surface of the faeces still humid; degree 1=uncertain=surface dried but still in good conditions of preservation; degree 0= old faeces, more or less degraded).

Only faeces with a high or medium confidence level of identification for small carnivore level were selected for the analysis. We calculated a kilometric abundance index (KAI\textsubscript{FAEC}) for the whole small carnivore community, as the total number of faeces observed per kilometer walked each year in each plantation. Arithmetic means of the three years were calculated to obtain an index for the overall survey period in each plantation and in each region.

\footnote{According to Chame (2003), in Brazilian Northeast, great felid faeces may be discriminated from small felids faeces by a diameter larger than 2.1 cm. Rabinowitz and Walker (1991) surveying carnivores in Thailand also consider a diameter of 2 cm to groupe faeces either as from large or small carnivores. However, faeces of some species of otters or mongooses may have a greater diameter, reaching 2.5 cm or even more. This critical level of 2.5 cm was used by Farrell et al. (2000) to distinguish large from small carnivores in Venezuela.}
Spotlight counts

Spotlight counts consisted of direct sightings along plantation dirt roads during night time, from a vehicle. Most carnivores, particularly nocturnal species, have a particular reflecting eye feature, the *tapetum lucidum*, producing “eyeshine” when a bright light is shone in the eye (Wilson and Mittermeier, 2009); this feature eases detection of individuals during night time. Moreover the major period of activity for most small carnivore species is at night, and night survey therefore increases the encounter rate.

A vehicle was used rather than pedestrian transects, since tropical carnivores typically occur at a low density (Belant *et al.*, 2013) and large distances are needed to obtain more sightings, thereby increasing the power of the statistics (Linnel *et al.*, 1998). Moreover, small carnivores are frequently less concerned by vehicles compared to human on foot. In addition, as soon as eyeshine is detected far away from the vehicle, a high speed eases the reach of the animal for identification.

A non-random design was preferred: routes were chosen along roads within and at the border of the plantations as to be representative of the diversity of landscapes and habitat conditions in each plantation. Distance of the overall routes in Riau_1, Riau_2, Bangka_1 and Bangka_2 were 84.5 km, 109.4 km, 119 km and 115.8 km respectively. Survey effort was higher in Riau_2 and on both Bangka plantations because of fewer sightings during preliminary exploratory surveys in 2009. The overall route for each plantation was divided into two or three individual routes carried out on separate nights. Indeed, observations require a lot of attention, which may decline if the route made each night is too long. Individual route length ranged between 23.2 km and 64.5 km on a single night. Except in 2010 when it was done only once, each individual route was done three times each year. The three sessions on each individual route were carried out on three successive nights, but not necessarily consecutively. In total, 3,003 km were covered (429 km in 2010, then 429 km times three in 2011 and in 2012).

Surveys were conducted after dusk, from about seven o’clock. Individual roadside counts lasted on average about three hours (ranging from one hour and a half to four hours, depending on the number of animals observed). Weather conditions might be important as they may enduce a shift in activity: when rainfall did occur, surveys were stopped and continued or carried out another night. Moonlight level is also known to affect activity of mammals, the majority being “lunarphobic” (Rode-Margono and Nekaris, 2014). Moon phase was reported to have an impact on hunting activity of felids for example (according Sunquist and Sunquist (2009), felids avoid hunting in open areas on moonlit nights), which may influence their probability of detection. Thus, surveys on bright moonlight nights were also avoided.

Counts were made standing from the open-back of a vehicle, which travelled at a constant speed of about 25km/hour, by an observer using a single handled spotlight of one million candle power / 100 Watt bulb (Lightforce SL 240). The observer was assisted by another person to handle the spotlight, and the driver of the vehicle was assisted by a copilot with a GPS in which the route was previously uploaded. When driving, the spotlight was directed straight on the horizon of the road, and occasionally scanned the borders of the roads. Our experience has shown that, thanks to the high power and wide-angle of the spotlight combined with the headlights of the vehicle switched on full beam, the observers may eye scan about 120° on both sides of the vehicle and detect animal on/along the road as well as on the palm trees adjacent to the roads; however, due to quite dense understory vegetation and a “high” speed, ground visibility within the oil palm habitat was usually not exceeding more than 50 m from the edge of the road.
Any observation of small carnivores was recorded, including domestic/feral cats; we also reported domestic or feral dog sightings. For each observation, the vehicle stopped to confirm species identification (and eventually the main observer got off the vehicle). Species were identified with a degree of certainty (sure -degree 2-, highly probable -degree 1-, or uncertain -degree 0-), and time of the sighting and location (GPS Garmin GPSmap 60CSx) were recorded. There is a risk of multiple counts of individuals for highly mobile species, but this was offset in our comparative approach, as bias is likely to be the same each night in each plantation.

To compare relative abundance between plantations, we calculated a kilometric abundance index ($KAI_{SPL}$), as the number of individuals observed per kilometer, for each plantation, each year. $KAI$ was calculated at different taxonomic levels: for the entire small carnivore community (including domestic/feral cats), for wild small carnivores only (excluding domestic/feral cats), for family group (Felidae, i.e. wild cats, and Viveridae, all Viveridae appearing to be civets), and then at species level. $KAI$ for the dog group was also calculated. Only observations qualified as sure (degree 2) were retained. For 2011 and 2012, the highest value of each series of three successive counts was used to compute the yearly abundance indices, representing the minimum number of individuals actually present in the route count in that given year. Arithmetic means of the three years were calculated to obtain an index for the overall survey period in each plantation and in each region.

When examining the relationship between small carnivore $KAI_{SPL}$ and rodent damage, the latter was estimated by the percentage of trees damaged per block per month in the given plantation in the given year (see section II.2).
Figure 43: Sampling design: in white (a) routes used for spotlight counts and (b) transects used for faeces counts
Community composition, richness and diversity indices

Whereas faeces counts did not yield results to species or even family level, visual observation of individuals during spotlight counts enabled us to identify species, and consequently informed us about species richness among plantations and regions, as well as relative abundance and other biodiversity assessment indices.

We first compared the proportion of observations of each species among plantations, based on all observations pooled across sessions and years for each plantation. For each plantation, for each species, we summed up all observations for a given species and divided it by the total number of observations of all species. Results were expressed as a percentage.

In addition to proportional comparisons, the following indices were calculated to compare diversity and evenness among plantations and regions (undetermined species were excluded from the calculation):

- Simpson’s index of diversity (1 - D), which represents the probability that two individuals randomly selected from a sample will belong to different species. The greater the value, the greater the sample diversity.

- Pielou evenness index (J), which represent species evenness of the community, i.e. how close in number each species of the community is.. The greater the value, the more all individuals are evenly distributed on all species. This index is based on Shannon-Wiener index.

Formulae for calculation of the two indices are, respectively:

\[
1-D = 1 - \left[ \sum n_i (n_i - 1)/N(N-1) \right]
\]

\[
J = - \sum (P_i \log_2[P_i]) / \log_2 S
\]

Where:

- \(n_i\) = number of individuals in species “i”
- \(N\) = total number of individuals in all species
- \(P_i\) = relative abundance of species \(i = n_i / N\)
- \(S\) = the total number of species, with \(i\) going from 1 to \(S\)

Statistics

Linear mixed-effect models were used to test for difference between small carnivores KAI accordingly to the category definitions (communities, species; see above) among regions, with plantation as random effect (to account for pseudo-replication within plantation). Likelihood ratio tests were used to test for the effect of each variable: two candidate models were compared via anova, the model with the variable in question and the reduced model with the given variable dropped.

Results were also examined at plantation level to identify variations among plantations that might be obscured at the regional level. For this, we investigated another series of linear models with no random effect and excluding the variable region (a conservative way, as to maximize differences among plantations). Analysis of variance on these models was used to investigate the effect of each variable and choose the best model to test for differences among plantations. Coefficients associated with the model selected enabled us to compare plantations two by two.

Normality of error was checked with One-sample Kolmogorov-Smirnov test; model assumptions about homogeneity of variance were checked by visual inspection of the plots of the residuals against the fitted value; when possible it was formally verified by a Bartlett’s test. When model assumptions were not confirmed for non-mixed effect models, or when Bartlett’s test could not be
performed because of small sample size, a permutation test (with 1000 permutations) enabled us to confirm the effect of variables. As pointed out in section II.3.2., R² definition and calculation for mixed-effect models is under debate (Xu, 2003; Edwards et al., 2008; Nakagawa and Schielzeth, 2013). To assess the overall goodness-of-fit of mixed-effect models, we used the R² of the correlation between the fitted and observed values, as suggested by Byrnes (2008). For non-mixed linear models, we used the Adjusted R-square as commonly reported. Adjusted R² and pseudo R² of models selected are given for information purposes only, in Appendix 5, as they cannot be interpreted independently or compared across datasets: they are valid and useful in evaluating multiple models predicting the same outcome on the same dataset, with pseudo R² of the same type (in this situation, the higher pseudo R-squared indicates which model better predicts the outcome).

The relationship between small carnivore abundance (KAI) and estimated rodent damage (RD) was investigated using linear mixed-effects models with rodent damage as the response variable and plantation as a random effect, in order to take into account pseudo-replications at plantation level. This relationship was investigated respectively at community level, for data yielded from spotlight counts and then from faeces counts, and at species level for the leopard cat, the domestic cat and the common palm civet. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the reduced model without the effect in question. Models assumptions and goodness of fit (R²) were checked the same way as previously described for KAI.

Small carnivore species compositions among plantations or regions were compared using the Likelihood Ratio Chi-Square statistics on contingency table (proportion comparison). After testing for independence (i.e. homogeneity: similar proportions) among all plantations and all species, we proceeded to adequate partitioning of the contingency table to test for independence between regions (or between plantations from the same region) for a given species (or for a group of species, e.g. felids) versus all the other species.

All analyses were performed using R version 3.3.0 (R Core Team, 2014). For linear regression, package lme4 version 1.1-7 or nlme version 3.1-117 were used for modelling, and the package pgirmess version 1.5.9 for permutation test and One-sample Kolmogorov-Smirnov test. To calculate diversity and evenness indices, we used pgirmess package (version 1.5.9) for Pielou index, and vegan package (version 2.0-10) for Simpson index. The loglm function from the MASS package (version 7.3-33) was used to test for the hypothesis of independence related to species composition. The package Ggplot2 (version 1.0.0) was used for most graphics.

**Interviews**

In addition to abundance indices, secondary information (interviews) was used to document the small carnivore community within oil palm plantations through local knowledge. Conducting interviews is a common technique in tropical regions for assessing distribution and trends of wildlife species (Belant et al., 2013; Mohd-Azlan et al., 2013). In this study, interviews were only used as a rapid assessment, preliminary to field surveys, and not as the primary method: the results of interviews served mostly to confirm/infirm results of spotlight counts about dominant species or family.

Interviews among plantations staff/workers, hunters, fishermen and smallholders were conducted in March and September 2010. In each plantation, various levels of employees were interviewed, from...
the local manager and his assistant, to heads of division (each plantation is divided into three to six divisions) and several field workers (harvesters or collectors). Field workers were interviewed in the field during their work time or at home (in villages within the plantation); in the field, we tried to select workers operating in different areas of the plantation which were representative of various ecological conditions (e.g. swamp and non swamp-areas, more or less nearby forest areas). Smallholders, hunters and fishermen were interviewed opportunistically when encountered during field surveys, except for one very old hunter, who was identified as a resource person, and who was interviewed in his house. Small holders had their field(s) around the agro-industrial plantation. Hunters and fishermen were inhabitants from surrounding local communities, fishing and hunting occasionally within the plantation. About 15 to 20 persons were interviewed in each plantation.

The informant was shown pictures (illustrations from Francis (2008) and Payne et al. (1985); photos extracted from Small Carnivores Conservation Journal or Cat News Journal) of each species potentially occurring, and was asked if he/she ever sight this animal within the oil palm plantation. We also asked the informant if he/she saw the animal “recently” (within about five years) or a long time ago, and discussed temporal trends. In Bangka, if the informant reported a zero occurrence of wild felids in the oil palm landscape, we asked him/her if he/she has ever seen or ever heard about occurrence of any wild felids on the island.

In this study, we did not report the results of interviews at species or genus level, but only at family level, in order to minimize bias resulting from misidentification. Indeed, although conducting interviews is a common tool throughout Southeast Asia to gather information on carnivore species abundance and distribution, these records on their own have a high risk of error (Mohd-Azlan et al., 2013). Incorrect identification of the species or taxonomic level under discussion is one source of error. Indeed, we assume that the respondent divides the natural world up into named forms broadly congruent with our western “scientific” classification systems and nomenclature, and that he can recognize such forms from photographs and/or illustration (Mohd-Azlan et al., 2013), but it might not be the case. To reduce this bias, we showed the informant several pictures of the same species coming from different sources (see previous), as some may be more or less recognizable. However, experience gained during these interviews showed that misidentification occurred frequently, as some species indicated by the informant were obviously not occurring in the region. We should have discussed with him more deeply about the description of the animal, the various forms that may occur, and its/their local name(s), to ensure more reliable identification. Nevertheless, this would have not dismissed the possibilities for confusion in identifying species in the field. According to Mohd-Azlan et al. (2013), with some groups, notably otters and mongooses, it is very implausible that credible species-level identification might be obtained, given the difficulties that even experienced surveyors have in identifying species from field sightings. Therefore, considering only family level when reporting the results greatly reduces the risk of error from misidentification in the field or from documents.

Results

* Small carnivores’ abundance

A picture of the data dispersion by group (small carnivore, wild cat, civet, domestic/feral cat) for each plantation on the entire survey period is shown on Figure 43 and Table 14 gives a recap of mean kilometric abundance per taxonomic category.
Figure 44: Kilometric abundance indices (KAI) yielded by (a) spotlight counts and (b) faeces counts in each plantation: data spread over the entire survey period. Each dot represents a different survey period, i.e yearly KAI. For spotlight counts, yearly KAI is the highest value of observations of the given taxon among the three sessions carried out each year. White diamond represents the mean over the whole study period. Horizontal dot lines with asterisk, above dots, represent the significance level of the p-value when testing differences of KAI between plantations; only significance level ≤ 0.05 are figured (* for ≤ 0.05, ** for P ≤ 0.01 and *** for P ≤ 0.001); see Appendix 5 for details.

Table 14: Mean kilometric abundance indices (KAI) of small carnivores and domestic/feral dogs in each plantation, during the overall period from 2010 to 2012, with standard error. Yearly KAI used to calculate the mean consider the highest value of observations of the given taxon among the three sessions carried out each year.

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Riau</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
<th>Bangka</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spotlight counts</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small carnivore</td>
<td>0.312</td>
<td>0.174</td>
<td>0.243</td>
<td>0.075 ±0.020</td>
<td>0.12 ±0.015</td>
<td>0.098</td>
</tr>
<tr>
<td>±0.058</td>
<td>±0.074</td>
<td>±0.052</td>
<td></td>
<td>±0.017</td>
<td>±0.017</td>
<td></td>
</tr>
<tr>
<td>Domestic/feral cat</td>
<td>0.028</td>
<td>0.046</td>
<td>0.037</td>
<td>0.055 ±0.027</td>
<td>0.098 ±0.017</td>
<td>0.076</td>
</tr>
<tr>
<td>±0.01</td>
<td>±0.026</td>
<td>±0.013</td>
<td></td>
<td>±0.017</td>
<td>±0.017</td>
<td></td>
</tr>
<tr>
<td>Wild small carnivore</td>
<td>0.288</td>
<td>0.131</td>
<td>0.209</td>
<td>0.032 ±0.003</td>
<td>0.025 ±0.005</td>
<td>0.028</td>
</tr>
<tr>
<td>±0.052</td>
<td>±0.051</td>
<td>±0.048</td>
<td></td>
<td>±0.003</td>
<td>±0.003</td>
<td></td>
</tr>
<tr>
<td>Felidae</td>
<td>0.193</td>
<td>0.094</td>
<td>0.144</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>±0.03</td>
<td>±0.035</td>
<td>±0.03</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leopard cat</td>
<td>0.189</td>
<td>0.081</td>
<td>0.136</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>±0.034</td>
<td>±0.036</td>
<td>±0.033</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undetermined wild cat</td>
<td>0.004</td>
<td>0.012</td>
<td>0.008</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>±0.004</td>
<td>±0.003</td>
<td>±0.003</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viveridae /Civets</td>
<td>0.118</td>
<td>0.046</td>
<td>0.082</td>
<td>0.032 ±0.003</td>
<td>0.025 ±0.005</td>
<td>0.028</td>
</tr>
<tr>
<td>±0.036</td>
<td>±0.024</td>
<td>±0.025</td>
<td></td>
<td>±0.003</td>
<td>±0.003</td>
<td></td>
</tr>
<tr>
<td>Common palm civet</td>
<td>0.103</td>
<td>0.04</td>
<td>0.071</td>
<td>0.012 ±0.006</td>
<td>0.017 ±0.008</td>
<td>0.014</td>
</tr>
<tr>
<td>±0.034</td>
<td>±0.021</td>
<td>±0.022</td>
<td></td>
<td>±0.005</td>
<td>±0.005</td>
<td></td>
</tr>
<tr>
<td>Small-toothed palm civet</td>
<td>0.004</td>
<td>0</td>
<td>0.002</td>
<td>0.012 ±0.008</td>
<td>0</td>
<td>0.006</td>
</tr>
<tr>
<td>±0.004</td>
<td>±0.002</td>
<td>±0.002</td>
<td></td>
<td>±0.004</td>
<td>±0.004</td>
<td></td>
</tr>
<tr>
<td>Malay civet</td>
<td>0</td>
<td>0.003</td>
<td>0.001</td>
<td>0.003 ±0.003</td>
<td>0.003 ±0.003</td>
<td>0.003</td>
</tr>
<tr>
<td>±0.003</td>
<td>±0.001</td>
<td>±0.001</td>
<td></td>
<td>±0.002</td>
<td>±0.002</td>
<td></td>
</tr>
<tr>
<td>Undetermined civet</td>
<td>0.016</td>
<td>0.012</td>
<td>0.014</td>
<td>0.012 ±0.003</td>
<td>0.006 ±0.006</td>
<td>0.009</td>
</tr>
<tr>
<td>±0.01</td>
<td>±0.006</td>
<td>±0.005</td>
<td></td>
<td>±0.003</td>
<td>±0.003</td>
<td></td>
</tr>
<tr>
<td>Domestic/feral dogs</td>
<td>0.012</td>
<td>0.012</td>
<td>0.012</td>
<td>0.022 ±0.021</td>
<td>0.058 ±0.049</td>
<td>0.040</td>
</tr>
<tr>
<td>±0.020</td>
<td>±0.014</td>
<td>±0.015</td>
<td></td>
<td>±0.037</td>
<td>±0.037</td>
<td></td>
</tr>
<tr>
<td><strong>Faeces count</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small carnivore</td>
<td>1.123</td>
<td>1.781</td>
<td>1.452</td>
<td>0.202 ±0.06</td>
<td>0.159 ±0.04</td>
<td>0.180</td>
</tr>
<tr>
<td>±0.43</td>
<td>±0.62</td>
<td>±0.37</td>
<td></td>
<td>±0.03</td>
<td>±0.03</td>
<td></td>
</tr>
</tbody>
</table>
Both for spotlight and faeces counts, and for all taxonomic categories (at community or species level), analysis of variance for all cases except one (see below), we failed to detect an effect of Year on KAI variability (p>0.05); therefore this variable was removed from the model when testing for differences between regions or plantations. One exception is for the small toothed palm civet, for which we kept the variable Year in the model given that it appeared to significantly affect KAI. For each case, final model selected and results (p-values and R²) are detailed in Appendix 5.

For a regional level of comparison, as shown in Table 14, the mean KAI of the whole small carnivore community on the overall study period as yielded by spotlight counts was more than two times higher in Riau (KAI\(_{SPL}\) =0.243) than in Bangka (KAI\(_{SPL}\) =0.098) (p=0.036). The difference was about ten times greater when considering KAI yielded from faeces counts: KAI\(_{FAE}\) of 1.45 in Riau compared to a KAI\(_{FAE}\) of 0.18 in Bangka (p=0.006). If we excluded domestic/feral cats and consider only wild small carnivores, the mean KAI from spotlight counts was about ten times greater in Riau (KAI\(_{SPL}\) =0.209) than in Bangka (KAI\(_{SPL}\) =0.029) (p=0.022).

We also investigated differences in abundance between regions at species level. All wild small carnivores observed within the oil palm habitat were either felids or civets (Figure 45). Four different species were recorded: the leopard cat (Prionailurus bengalensis), the Malay civet (Vivera tangalunga), the common palm civet (Paradoxurus hermaphroditus), and the small-toothed palm civet (Arctogalidia trivirgata) (see photographs on Figure 44). Some species were undetermined, but all were identified as wild felids or as civets. According to Table 14, the leopard cat occurred only in Riau plantations. The common palm civet index of abundance also appeared greater in Riau compared to Bangka (KAI\(_{SPL}\) = 0.071 in Riau, KAI\(_{SPL}\) = 0.014 in Bangka, p=0.049), but we failed to detect a significant difference between regions for domestic/feral cats (p=0.065). For the small-toothed palm civet and the Malay civet, there were very few observations in both cases, and we failed to detect a significant difference of KAI between Riau and Bangka (p=0.400; p=0.553 respectively).

From Figure 43 and Table 14, Riau_2 small carnivores KAI level yielded from spotlight counts appeared more similar to levels from both Bangka plantations than to Riau_1 level. Therefore we carried out analyses at the plantation level, investigating differences among plantations. Detailed results of each model (p-values and Adjusted R² may be found in Appendix 5)

Our analysis confirmed that, for spotlight counts at community level (small carnivores and wild small carnivores) KAI\(_{SPL}\) in Riau_2 plantation appeared similar to the Bangka plantations (we failed to detect significant differences between these: p>0.05), though it was significantly different from Riau_1 for wild small carnivores (p=0.02). A similar pattern was found for the leopard cat and the common palm civet: KAI in Riau_2 was found to be different from Riau_1 one (p<0.05) but we failed to detect differences with Bangka plantations (p>0.05).

Abundance indices yielded from faeces counts showed different patterns: this time it was Riau_2’s KAI which was found to be significantly different from KAI in each Bangka plantation (p=0.017, p=0.019), while we failed to detect differences between Riau_1 and each Bangka plantation KAI (p=0.111 and p=0.126).

---

36 Among undetermined wild felids observed on Riau, one was identified as potentially being a fishing cat (it was spotted on a tree in the swamps of the conservation area in Riau_1; its coat was more grey than the typical yellowish coat of leopard cats seen in the area, and its tail was shorter), and another one had a coat with cloud-like or marble pattern of dark splotches like a clouded leopard or a marble cat.
Figure 45: Photos of wild small carnivore species encountered during spotlight counts (Source: A. Verwilghen).

Leopard cat (*Prionailurus bengalensis*)

Common palm civet (*Paradoxurus hermaphroditus*)

Small-toothed palm civet (*Arctogalidia trivirgata*)

Malay civet (*Vivera tangalunga*)
We failed to detect any difference of KAI among plantations for the domestic/feral cat (p=0.123), as well as for the Malay civet (p=0.885) or the small-tooth palm civet (p=0.271).

About models assumptions: normality of error was confirmed in every case (One-sample Kolmogorov-Smirnov test; p>0.05), except for the Malay civet when investigating differences among regions; however, in this last case, the null hypothesis was accepted, and the risk to accept H0 wrongly due to absence of normality is unlikely.

In some cases (KAI at community level), non-homogeneity of variance was suspected and Ho was rejected; we therefore could not exclude that differences observed were due to non-compliance to model assumptions.

- **Community composition**

As illustrated in Figure 45, in the Riau plantations, leopard cats represent the most abundant sightings within the small carnivore community, representing 49.8 % of sightings, and common palm civets ranked second with 24.3% of sightings. For each of the two species, our statistical analyses did not detect significant differences in percentage occurrence between Riau_1 and Riau_2 (p=0.90 and 0.85). The small toothed palm civet and the Malay civet were rarely recorded in Riau (respectively 0.3% and 0.5%). In Bangka plantations, no wild felids were observed, but domestic/feral cats represented 78.5% of the small carnivore sightings (no significant difference detected between percentages in Bangka_1 and Bangka_2; p=0.41), followed by common palm civet with 10.4% (no significant difference was detected between percentages in Bangka_1 and Bangka_2; p=0.21), small-toothed palm civet with 3.5% (7% in Bangka_1 and none in Bangka_2) and Malay civet with 2.5% (3.5% in Bangka_1 and 1.5% in Bangka_2). If we consider the felid group, whether wild or domestic, they represented respectively 66.4%, 75.5%, 81.5% and 75.4% of sightings within the small carnivore community in Riau_1, Riau_2, Bangka_1 and Bangka_2 plantations; we failed to detect significant differences in the percentage represented by the felids group, may it be between Riau and Bangka region (p=0.07) or in between plantations from the same region (p=0.12 and 0.41).

Considering all species encountered, our analysis revealed a significant difference in the small carnivore community species composition among all plantations (p<0.00001). However, the species proportions were similar in the community (p=0.17) in Bangka, while in Riau species proportion differed significantly (p=0.0001). This indicated that the diversity of observations was larger in Riau than in Bangka.

![Figure 46: Small carnivore community composition in each plantation, over the whole study period (spotlight survey, 2010 to 2012). Number of observations for each species was calculated based on pooled data of all yearly sessions, and are presented in percent of total occurrence (number of observations all species included) in each plantation, with number annotated when above 5%.

125
Looking at diversity and evenness indices (Table 15): the community of small carnivores appears less diverse (lower Simson index) in Bangka in overall than in Riau, but more or less equitable/evenly distributed (higher and lower Peilou index on Bankga_1 and Bangka_2 respectively compared to Riau).

Table 15: Diversity and evenness indices for the small carnivore community (spotlight survey, 2010 to 2012).

<table>
<thead>
<tr>
<th></th>
<th>Simpson diversity index</th>
<th>Pielou evenness index</th>
<th>Number of species observed</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Riau</strong></td>
<td><strong>0.599</strong></td>
<td><strong>0.643</strong></td>
<td></td>
</tr>
<tr>
<td>Riau_1</td>
<td><strong>0.538</strong></td>
<td><strong>0.522</strong></td>
<td>≥ 4 *</td>
</tr>
<tr>
<td>Riau_2</td>
<td><strong>0.643</strong></td>
<td><strong>0.684</strong></td>
<td>≥ 4 *</td>
</tr>
<tr>
<td><strong>Bangka</strong></td>
<td><strong>0.301</strong></td>
<td><strong>0.380</strong></td>
<td></td>
</tr>
<tr>
<td>Bangka_1</td>
<td><strong>0.329</strong></td>
<td><strong>0.722</strong></td>
<td>4</td>
</tr>
<tr>
<td>Bangka_2</td>
<td><strong>0.271</strong></td>
<td><strong>0.303</strong></td>
<td>3</td>
</tr>
</tbody>
</table>

* Within the undetermined individuals, two were seemingly wild felids of different species than the leopard cat.

The estimated abundance of leopard cats in Riau oil palm plantations, and the supposed absence of wild felids in Bangka were confirmed by interviews (Table 16). In Riau 73.5% of respondents reported the occurrence of wild felids (in majority leopard cats) within or surrounding the plantation; whereas 94.5% of Bangka respondents have never seen any wild felids in the plantations or its surrounds, nor anywhere on the whole island. Viverridae were very frequently reported by respondents in Riau plantations and less in Bangka plantations (respectively 91.2% and 30.5% of respondents), whereas other small carnivore families such as Herpestidae (mongooses) or Prionodontidae (lisangs) were rarely (in Bangka) or never (in Riau) reported.

Table 16: Presence of wild small carnivores (family level) within the oil palm habitat as reported from interviews

<table>
<thead>
<tr>
<th></th>
<th>Percent of respondents (out of a total of 70) who reported the occurrence of a given family</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Felidae</td>
</tr>
<tr>
<td><strong>Riau</strong></td>
<td>73.5%</td>
</tr>
<tr>
<td>Riau_1</td>
<td>64%</td>
</tr>
<tr>
<td>Riau_2</td>
<td>80%</td>
</tr>
<tr>
<td><strong>Bangka</strong></td>
<td>5.5%</td>
</tr>
<tr>
<td>Bangka_1</td>
<td>0%</td>
</tr>
<tr>
<td>Bangka_2</td>
<td>12.5%</td>
</tr>
</tbody>
</table>

- **Interannual trends**

Interannual trends cannot be assessed accurately with only a 3 year study, however our results indicate that temporal pattern in Bangka plantations seemed different from that Riau plantations. From Figure 46 it appears that the annual kilometric abundance indices of small carnivores in Bangka plantations was quite stable over the study period, whereas there was a general increase in Riau plantations.
Figure 47: Annual trends of small carnivore kilometic abundance indices (KAI) observed in each plantation, over the study period (2010 to 2012). KAI from spotlight counts represent wild small carnivores only, while KAI from faeces counts is representative of the entire small carnivore community, including domestic or feral cats.

From interviews results, the only obvious temporal trends concern civets in Bangka, which were reported by all hunters as dramatically decreasing for several years.

- Small carnivore abundance compared to rodent damage

We investigated the relationship between estimated rodent damage (RD), as a response variable, and estimated small carnivore abundance (KAI) with linear mixed effect models, introducing a random effect for Plantation. Be it at community level or species level, we failed to detect an effect of Year and Region, hence these variables were dropped from the model (all p>0.05). Therefore, model selected for the analysis with RD as response variable included only KAI as fixed effect (with Plantation as a random effect). We detected a significant correlation between RD and KAI respectively for the small carnivore community (p=0.003 for data yielded from spotlight counts and p=0.004 for data yielded by faeces counts), for the wild small carnivore community (p=0.003), and at species level for the leopard cat (p=0.009) and for the common palm civet (p=0.002). However, we failed to detected a significant correlation between RD and KAI for the domestic/feral cat (p=0.46). For each case, R² of the correlation between the fitted and observed values ranged between 0.5 and 0.8. For each model selected, normality of residuals was formally confirmed (One-sample Kolmogorov-Smirnov test; p>0.05) and models assumptions about homogeneity of variance were acceptable.

When displaying the relationship between RD and KAI at community level across plantations and years (Figure 47), the scatter plot showed a negative correlation: estimated rodent damage decreased when the estimated abundance of the small carnivores or wild small carnivore community increased. Moreover, comparing plantations from the same region showed similar patterns: in Bangka plantations, estimated rodent damage is higher and wild small carnivores are estimated as less abundant, compared to Riau plantations (if we exclude the outlier point for Riau_2
on 2010, see section II.2.2). Patterns are similar when taking into consideration only the leopard cat: rodent damage decreased with increasing abundance of leopard cats.

![Small carnivore community: Spotlight counts vs. Faeces counts](image1)

![Wild small carnivore community: Spotlight counts](image2)

**Figure 48**: Relationship between estimated rodent damage and estimated small carnivores abundance in Riau and Bangka plantations. One point represent one year (from 2010 to 2012) on one plantation. Small carnivore kilometric abundance indices (KAI) are yielded from spotlight counts or faeces counts. Fitted lines for RD response are yield from linear mixed-effect models with KAI as fixed effect and Plantation as random effect; those lines are only indicative given the low sample size per plantation.

- **About dogs**

We failed to detect statistical difference of domestic/feral dogs abundance between Riau and Bangka (p=0.095) and among plantations (p=0.261).

![Kilometric abundance index (KAI: number of observations / kilometer) for dogs in Riau and Bangka plantations](image3)

**Figure 49**: Kilometric abundance index (KAI: number of observations / kilometer) of domestic or feral dogs in Riau and Bangka plantations over the whole study period. Data yielded from spotlights counts. Each dot represents a different survey period, i.e yearly KAI. Yearly KAI is the highest value of observations of the given taxon among the three sessions carried out each year. White diamond represents the mean over the whole study period.
Discussion

- About methodological biases

Our results are prone to various sources of bias. In particular, detection probabilities may be affected by the limitation of our survey methods in regard to the characteristics of the habitats and the species behavior.

Different species may not be seen with equal probability, introducing bias when assessing species richness. Therefore, differences in species encounter rates during spotlight surveys may not strictly reflect patterns of abundance between species.

For example, lack of records from spotlight count is uninformative about the status of species that are at least partially diurnal, such as some Asian weasels (Rode-Margono et al., 2014) and some mongoose, notably the short-tailed mongoose (Gilchrist et al., 2009; Jennings et al., 2010a; Mathai et al., 2010). Moreover, detection of individuals during spotlight surveys is mainly based on their “eyeshine” ability. This feature is more or less obvious among species, and some diurnal species may even lack it, as reported by Gilchrist et al. (2009) for some mongoose species. Absence of sightings for some species may also reflect their attachment to a specific microhabitat which was greatly under-sampled. This may be the case for otters or short-tailed mongoose, often found in close proximity to water bodies (Veron et al., 2015).

There are possibly other biases linked for example to the choice of roads for sampling, as the use of roads varies among species (Harmsen et al., 2010). The ground-dwelling leopard cat is probably preferentially using roads at night, as reported by Austin et al. (2007b), Rajaratnam et al. (2007) and Mohamed et al. (2013). Data for common palm civets and Malay civet in forest habitat also showed that those species readily use roads at night (Colon, 2002; Wilting et al., 2010; Nakabayashi et al., 2014). Nevertheless, targeting roads very probably increased detection rate for leopard cats to a greater extent than for common palm civets (Sollmann et al., 2013). In contrast, limited road usage of some species, such as weasels, may cause their non-detection or low detection probability when surveying along roads (Ross et al., 2013; Chutipong et al., 2014); but their morphology and habits (low slung and fast moving) may also have hindered our ability to detect them via spotlight counts on vehicles going at a quite high speed. Sighting probabilities will also be affected by the degree of arboreality and the height at which a species usually forage, as the visibility of an individual foraging or resting in the crown of a palm tree is less than that on bare road. The strictly arboreal small-toothed palm civet may thereby be under-sampled compared to the common palm civet which was commonly observed on palm trees but also on the ground.

If the true composition of the small carnivore community is variable between plantations, it may also affect KAI_{SPL} and KAI_{FAE} of the whole small carnivore community and introduce bias in the comparison between plantations or regions at the community level. Difference in detection rates among species might represent a major source of bias, notably for spotlight counts. For faeces counts, different detection rate might also introduce a bias. Indeed, defecation rate is influenced notably by diet and by physiological variations among and between individuals (Andelt and Andelt, 1984). Plant consumption may for example induce the deposition of a higher number of faeces, as suggested by Cavallini (1994) for foxes. On another hand, a small carnivore community in which carnivorous species are relatively more abundant than frugivorous or omnivorous species may lead
to a higher KAI_{FAE} at the community level. Indeed, poorly digested items such as hair, teeth or bones are less vulnerable to rainfall flush or to consumption by coprophagous insects (compared for example to fruits or other soft organic matter); it may thus favor the persistence over time of faeces containing such macromains, thereby leading to a higher detection rate of faeces dropped by more strictly carnivorous species.

In terms of survey sites characteristics, plantation dirt roads used for faeces counts are quite similar across all four plantations (width and ground vegetation cover may vary according to road type, i.e. main road or collection road, but the proportion of each road type sampled is similar in each plantation). Therefore we may assume that the overall bias of faeces detection for a given community or species is about the same in each plantation, allowing comparisons among plantations. In contrast, for spotlight counts, we may assume different detection probability in Riau_2 compared to the other plantations. Indeed, as described in section II.1.2., although the oil palm habitat is quite similar in all four plantations, Riau_2 plantation design is characterized by a higher proportion of both winding roads and drainage ditches along roads. As we have experienced it, small carnivores may be detected far away along straight road thanks to their eye-shine; but in Riau_2 winding roads limit visibility far away along roads, and in addition drainage ditches bordering roads probably limit the use of roads as communication way for small carnivores. Thereby, detection probability of species preferentially using roads may be lower in Riau_2 compared to other plantations.

In addition to bias linked to sampling methods and to characteristics of features sampled (plantation roads and their borders), there may be question a bias linked to period of sampling (only carried out in dry season). Indeed, heterogeneous landscapes and practices provide opportunities for spatio-temporal variations in abundance and occupancy of carnivores in various habitats, notably linked to changes in habitat structure, resource availability, human activities such as hunting, and/or other biotic/abiotic factors such as competition with dominant predators (Burton et al., 2012; Lantschner et al., 2012; Kalle et al., 2014; Jennings and Veron, 2015). Within the oil palm habitat, as shown previously (see section II.1.2.), there is little variation in food resource, vegetation structure or human activity over the year or between years (except when replanting). Therefore we assume that the intrinsic attractiveness of the oil palm habitat does not vary much over time of between years. Nevertheless 1) variations in abundance in the oil palm habitat might occur due to temporal changes in the surroundings habitat, which we did not study, and 2) only part of the oil palm habitat was surveyed (roads and their border) therefore results are possibly biased if usage by small carnivores of these features is subject to temporal variation (Güthlin et al., 2012).

All these potential biases highlight the need to use multiple sampling techniques and methodology to detect the maximum number of species during surveys. In addition, faeces surveys should also include molecular analysis techniques in order to further increase the robustness of identification. Nevertheless, as argued below, we believe that our results provide a reasonable comparison of small carnivore abundance and diversity among plantations or regions within the study period.
• **Small carnivore abundance and species richness in Riau and Bangka plantations**

*Small carnivores are more abundant in Riau plantations than in Bangka plantations*

Even when considering suspected bias, our results confirm the prediction that small carnivores are more abundant in Riau plantations than in Bangka plantations.

Indeed, despite the more intensive sampling effort in Bangka, the mean kilometric abundance index (KAI) of wild small carnivores on the overall study period was about ten times greater in Riau than in Bangka as yielded by spotlight counts. The difference is less when considering the entire small carnivore community, because of the abundance of domestic/feral cats in Bangka, but it is still great (at least twice more in Riau than in Bangka). This trend is confirmed by faeces counts, which yield much higher mean KAI for the small carnivore community in Riau than in Bangka (more than ten times greater).

When focusing at the plantation level, index scales are quite similar in Bankga_1 and Bangka_2, whether for spotlight counts or faeces counts, thereby supporting a homogeneous “low abundance pattern” of wild small carnivores in Bangka. Scale of results were less homogeneous in Riau plantations: observations of faeces were slightly more in Riau_2 than in Riau_1, but on the contrary there was about two times fewer small carnivore sightings during spotlight counts in Riau_2 than in Riau_1. This contrast between the results from different methods in Riau plantations raises questions. The most likely explanation is that KAI\_SPL in Riau_2 is underestimated, because of lower detection probability of small carnivores, notably of leopard cats, during spotlight counts in Riau_2 compared to the others plantations, as explained above in the methodological bias section.

The leopard cat is a ground dwelling species which was seen most often walking on or crossing roads; the higher proportion of windings roads and drainage ditches along roads in Riau_2 compared to the other plantations would induce a lower detection rate of this species in Riau_2. Hence, in Riau_2, leopard cats may be in reality underestimated by spotlight survey method, and faeces counts would therefore be more representative of small carnivore abundance than spotlight counts. This hypothesis of lower detection rate in Riau_2 is consistent with the results of a camera trapping survey carried out on both Riau plantations from March 2012 to April 2013 (Jennings et al., 2015): leopard cats were captured in similar proportions in Riau_1 and Riau_2 (number of photographs per trap days: 8.9% and 7.8% respectively), which would let us believe that their true abundance is quite similar in both Riau plantations. The abundance index of the common palm civet was surprisingly much lower in Riau_2 (KAI\_SPL = 0.04) than in Riau_1 plantations (KAI\_SPL = 0.10). This might be partly due to a bias from a lower detection probability (see above), but it may also reflect a lower density of this species in Riau_2. Indeed, common palm civets are known to prefer tall trees with dense ferns for resting or foraging (Su and Sale, 2007; Nakashima et al., 2013; Rode-Margono et al., 2014). In Riau_2 plantation, suitable palm trees are less available because of younger trees (smaller trees) and peat areas (leaning trees); the oil palm habitat in Riau_2 would therefore be less attractive to common palm civet than other plantations.

Though species do not have an equal probability of being seen, thereby leading in underestimation of the abundance of some species, our overall results about species richness are consistent with those using other survey methods such as camera trapping, carried out in the same plantations in Riau (Jennings et al., 2015) or in other oil palm plantations (Scott and Gemita, 2004; Maddox et al.,
We can not reliably compare figures by species given that methods and environmental conditions might be different.
Abundance of these two species in oil palm plantations is most likely linked to a higher prey/food availability in such habitats, that is murids for leopard cats and oil palm fruits for common palm civets (Scott and Gemita, 2004; Rajaratnam et al., 2007; Nakashima et al., 2013). Presence of suitable rest sites (low-lying foliage if the understorey for leopard cats and high palm trees with dense foliage for common palm civets) probably also enhance the compatibility of the oil palm habitat for these species (Maddox et al., 2007; Nakashima et al., 2013). Food availability is indeed a key factor controlling carnivore occurrence probability and abundance (Burton et al., 2012), however, small carnivores may also benefit from loss of predators and competitors compared to less disturbed habitats (Watanabe, 2009; Mohamed et al., 2013; Bashir et al., 2014). Indeed, they have little chance to encounter large carnivores such as clouded leopard or sun bear in the oil palm habitat (though sun bear was detected by camera trapping in Riau_2). And, although the oil palm habitat may provide enough food resources to support other small carnivores, wild small carnivores, from which leopard cats and common palm civets may face serious competition, are rare in the oil palm habitat, as suggested by our results and by our literature review (see below).

In addition to the leopard cat and the common palm civet, two other species were observed occasionally in our study sites during spotlight surveys: the Malay civet, which was detected on both Bangka plantations and in Riau_1, and the small-toothed palm civet, which was sighted only in Bangka_1 and Riau_1. When detected, they were in low abundance: KAI-SPL of 0.003 for the Malay civet (same KAI-SPL on the three plantations) and of 0.004 or 0.012 for the small-toothed palm civet (for Riau_1 and Bangka_1 respectively). During camera trapping surveys in Riau plantations (Jennings et al., 2015), the only other wild small carnivore captured in addition to leopard cat and common palm civet was the Malay civet, and it was in low abundance comparatively to the two other species (1.6% of wild small carnivores photographs and occupancy of 0.111). The Malay civet mainly occurs in primary and secondary forest but it may be found in disturbed habitats or plantations (Giman et al., 2007; Meijaard and Sheil, 2008; Mathai et al., 2010; Jennings and Veron, 2011). Scott and Gemita (2004) reported, from their spotlight night survey in oil palm habitat compared to forest and scrub habitats, that all the three sightings of Malay civet were from in oil palm areas rather than either forest, scrub or an ecotone habitat. Occurrence of this species in oil palm plantations was also reported by other authors, generally in low abundance (Ross, 2009a; Jennings et al., 2010b; Wahyudi and Stuebing, 2013; Azhar et al., 2014a), and probably foraging for rodent prey, as they are one of the most carnivorous civet species.

To our knowledge, the present study reported the first record of small-toothed palm civet within oil palm habitat. According to Eaton et al. (2010), this species is widespread and often locally common in mainland Southeast Asia, Borneo and Sumatra. Nevertheless, it was never recorded by the increasing number of camera traps surveys carried out in oil palm plantations and records were rare even in other habitat types. However, it has been suggested that the paucity of records is due to the use of ground-level camera traps, which severely reduces detection of this strictly arboreal species, and that direct observations such as spotlights counts are more appropriate (Walston and Duckworth, 2003; Duckworth and Nettelbeck, 2007; Wilting et al., 2010; Willcox et al., 2012; Chutipong et al., 2014).

Though we did not detect them, other species are potentially present on our study sites as they are known to inhabit Sumatra and/or Bangka and they have already been recorded within oil palm habitat from our literature review (see Table 1 in section I.3.3). The fact that these species were not
encountered in our study sites may reflect the methods we used to detect them, as described above, but more probably their true rarity in oil palm habitat. Indeed, small carnivore species richness in oil palm habitat is generally reported as poor comparatively to that of forest habitats (Maddox et al., 2007; Wahyudi and Stuebing, 2013).

...and leopard cats and other wild felids are definitely absent from Bangka

According to diversity and evenness indices calculated from spotlight surveys, the community of small carnivores appears less diverse in Bangka plantations than in Riau plantations. The absence of wild felids in the oil palm landscape in Bangka was confirmed by spotlight counts and interviews among plantation workers and local hunters. This result is in accordance with our literature review and data mining from more or less recent wildlife inventory surveys carried out in Bangka island (see section I.3.3.): to our knowledge, no wild felids have ever been recorded from Bangka island. Therefore, the lack of records for felids in Bangka during our spotlight counts is surely not an issue of detectability due to sampling design or methods. The reason of their absence in Bangka is in question. Did they become extinct on this island? According to Watanabe (2009), although there are thousands of islands of various size in east Asia, wild cat populations are only present on 15 islands, and most cats species are only found on the largest islands. This may be explained by the fact that mammalian carnivores suffered higher extinction rates than other groups on post-Pleistocene islands (Heaney, 1984, 1986; Meijaard, 2003; Lomolino et al., 2010; Louys, 2014). The leopard cat is an exception as it occurs on several small islands such as Iriomote Island (298 km²) in Japan (Watanabe, 2009). Results obtained by the author suggested that island size is not a good predictor of the distribution of the leopard cat, but that the probability of existence of the leopard cat on an island increases with species richness of potential prey, or with decreasing species richness of potential competitors; moreover, the authors showed that the existence of viverrids negatively affected the existence of the leopard cat, while those of other carnivore families did not. Due to the relative richness of species from the Viverridae families in Bangka (5 species) compared to the other islands studied by the author (Watanabe, 2009), the leopard cat would have faced serious competition. Anthropogenic pressure leading to the loss of forested habitats (see Bangka landscape characterization in section II.1) might also have been a cause of extinction.

- **What could explain such a difference in wild small carnivore abundance in Bangka plantations compared to Riau plantations?**

Our results indicate that wild small carnivores were less abundant in Bangka than in Riau plantations, and that, their community appeared less diverse in Bangka than in Riau (in peculiar with no felids in Bangka). The absence of wild felids in Bangka is presumably linked to biogeographic issues, but what could explain the difference in estimated abundance for remaining species, i.e. civets, which have a mean kilometric abundance index (KAI) about three times lower in Bangka than in Riau? We discuss below the potential causes for this lower abundance of wild small carnivores in Bangka compared to Riau.

*Food resource?*
As previously mentioned, food resources are a key factor for controlling small carnivore abundance; nevertheless in our study sites we presume that food resource is not a good candidate to explain differences in small carnivore abundance between regions. Indeed, palm fruits are equally available for frugivorous species, and for carnivorous species, rat populations were estimated to be even higher in Bangka plantations than in Riau plantations. Moreover, the dominant rat species is of a bigger size in Bangka (R. tanezumi versus R. tiomanicus in Riau), but though it might be a problem for the barn owl (see section III.1.), it is presumably not a limiting factor for small carnivores. Indeed, Bonnaud (2011) reported that size of feral cat prey may reach more than 2 kg (lagomorphs constituting the largest prey). Moreover, R. tanezumi has been found to be an important prey for leopard cats in some areas (Fernandez and de Guia, 2011; Shehzad et al., 2012; Lorica and Heaney, 2013); and even Sundamys muelleri and Leopoldamys sabanus, which are large-size rats\(^3^8\), are consumed (Rajaratnam et al., 2007).

**Hunting?**

According to interviews and from our opportunistic observations during field surveys, hunting is much more common in Bangka plantations than in Riau plantations. When hunters were occasionally interviewed, they said they were hunting wild boars\(^3^9\), and less frequently civets. According to hunters, civet populations in Bangka were reduced due to previous heavy hunting pressure for exportation to China. Indeed, civets are hunted and traded for local and international consumption throughout Southeast Asia (Shepherd and Shepherd, 2010), and they are a preferred food in China where they are also used for skins or musk (Corlett, 2007). Common palm civet may also be killed as they are seen as a threat to orchard fruits and poultry, or captured for trade as pets (Shepherd, 2008; Nijman et al., 2014). The increasing demand for civet coffee production is an additional threat for this species (Shepherd, 2012; D’Cruze et al., 2014). Shepherd (2012) surveyed wildlife markets in Indonesia and reported the common palm civet to be the most numerous species observed. Malay civet is also hunted or killed as a pest (Jennings and Veron, 2009; Jennings et al., 2010b). Very little is known of the extent of the trade in civets in Indonesia, or the impact trade may have on wild populations (Shepherd, 2008); but high demand for these products very probably increase hunting pressure and may have led to the rapid population decline in Bangka, notably for the more common palm civet which is usually widely distributed in oil palm plantations.

**Landscape context?**

Small carnivore abundance and richness is known to be influenced by habitat configuration at the landscape level. Surveying mammals in oil palm landscapes, Azhar et al. (2014a) showed that overall mammal species richness, and carnivore abundance, increased significantly with the cumulative area of forest patches within 5 km of each site. Many other studies around the world have shown that a mosaic configuration, with forest or semi-natural habitats fragments retained, enhances biodiversity within plantations, and that species richness and abundance in agricultural areas increases with proximity to forested or semi-natural habitat (Duelli and Obrist, 2003; Ricketts, 2004; Cunningham et al., 2008; Gervais et al., 2012; Burel et al., 2013a; Lucey et al., 2014). As

\(^3^8\) Lekagul and McNeely (1988) reported an average weight of 397 g for S. muelleri and 343 g for L. sabanus, compared to about 100 g for R. tiomanicus and 150-230 g for R. tanezumi (Aplin, 2003).

\(^3^9\) The muslim majority avoids consuming wild boar for religious reasons, however, according to Luskins et al. (2014), there is a substantial local and export demand driven by Chinese and Christian Batak. In addition, wild boar hunting is encouraged by plantation managers (personal observations), as the animal damage crop.
described in section II.1., the Bangka plantation landscapes (within and around the plantations) is much more diverse than Riau plantations: many patches of semi natural (forest like) habitats are retained within Bangka plantations, and the forest or forest like habitats cover larger parts of the matrix within a 15 km buffer around Bangka plantations. In contrast, in Riau the landscape is relatively homogeneous, with a dominance of oil palm habitat. Landscape configuration within and around the plantations would thereby be more favorable to small carnivore richness and abundance in Bangka plantations than in Riau. This might explain why the Malay civet and small-toothed palm civet were more abundant on Bankga plantations than in Riau plantations, given that they have been found to be more dependent on forested habitats (Colon, 2002; Jennings et al., 2010b; Rustam et al., 2012). However, the contradictory lower abundance of common palm civet in Bangka is still in question. We assume that a higher hunting pressure on the common palm civet (compared to others species, and compared to Riau; see above), combined with no or few opportunities for recolonization given the island landscape configuration, could be a possible explanation. Indeed, Bangka is a small island with no extensive area of “intact” or natural forest remaining and potentially acting as “source” habitat (see section I.2.3 and II.1.1). Whereas in Riau, persistence of extensive forest landscape, though quite far away from our study sites, could potentially act as source habitat for range expansion of small carnivores.

**Competition with other carnivores?**

As reported by Linnell and Strand (2000), competitive interactions (whether interference or exploitative competition) among predators have very important implications on carnivore demography. Given its insularity, its small size and the poor area of high forest habitat remaining, there are undoubtedly no more large carnivores (carnivores of high trophic level and forest-dependant) on island such as Bangka (Heaney, 1984, 1986; Meijaard, 2003), that may represent serious competitors or predators for small carnivores. Feral dogs may be abundant within oil palm plantations, as shown by our results, and their presence very probably interfere with wild carnivores (Vanak and Gompper, 2009; Hughes and Macdonald, 2013). Azhar et al. (2013a) reported that feral dogs can kill wildlife, including civets, and contribute to biodiversity loss in oil palm plantations in Malaysia. Domestic/feral cats might also represent a threat to wild small carnivores, through direct competition and/or disease transmission (Nishimura et al., 1999; Izawa et al., 2009; Medina et al., 2014). Therefore, a greater abundance of dogs or domestic / feral cats in Bangka plantations compared to Riau could negatively influence the wild small carnivore abundance in Bangka to a greater extent than in Riau. However, this hypothesis was not supported by statistical analysis of our results, as we found no difference in dog or domestic/feral cat abundance between the different areas.

**Rodenticide use?**

Indirect intoxication by rodenticide may also cause mortality of non-targeted carnivorous species preying mainly on rodents (Fernández and Rossi, 1998; Shore et al., 1999; Shore et al., 2003; Berny, 2007; Sage et al., 2010). Jacquot et al. (2013) have established the negative impact of rodenticide on fox populations in France: fox KAI were significantly and negatively related to rodenticide use in previous years. We previously reported an intensive and continuous use of rodenticide in Bangka plantations, versus no use of rodenticide in Riau plantations for more than ten years. Use of rodenticide might cause mortality of leopard cats or carnivorous civets such as the
Malay civet in oil palm plantations, as reported by Duckett (2008). However, unless they eat the bait itself, rodenticide use would not be a plausible explanation for low abundance of the common palm civet, given the highly frugivorous diet of this species.

- **Relationship between small carnivores’ abundance and rodent damage**

Our results showed a negative correlation between estimated rodent damage and estimated small carnivore abundance: rodent damage decreased when the kilometric abundance index of the small carnivores or wild small carnivore community increased. The same trend appeared at species level for the leopard cat and the common palm civet, whereas we did not detect any correlation between rodent damage and the abundance for the domestic/feral cat. Comparing plantations from the same region showed similar patterns (if we exclude the outlier points for Riau_2 in 2010): lower values of estimated rodent damage were observed in plantations where small carnivores (or wild small carnivores) were estimated to be more abundant, that is Riau plantations, whereas small carnivores (or wild small carnivores) were estimated to be less abundant in plantations where estimated rodent damage values were higher, that is Bangka plantations.

The differences in terms of abundance and diversity of the small carnivore community between Bangka and Riau suggests a differential prey intake, which may have indirect consequences on rodent damage. According to our results, small carnivores were more abundant in Riau plantations than in Bangka plantations. Moreover, in Riau plantations, the community of small carnivores was dominated by Felidae, notably the leopard cat. Whereas in Bangka, the wild species were mainly composed of the common palm civet, and the absence of wild felids was confirmed; and even though the small carnivore community was dominated by domestic/feral cats, they were estimated to be less numerous than leopard cats in Riau. The cats are hypercanivores, requiring a higher proportion of protein in their diet than many other mammals (Sunquist and Sunquist, 2002; Sunquist and Sunquist, 2009) and they are highly specialized for killing live prey. During a typical night’s hunting, a cat, such as the wild black-footed cat in South Africa, can kill between 10-14 rodents or small birds (Sunquist and Sunquist (2009) refering to Sliwa’s results). The leopard cat is known to feed mainly on rodents from the muridae family (Rabinowitz, 1990; Tatara and Doi, 1994; Khan, 2004; Grassman et al., 2005; Austin et al., 2007a; Shehzad et al., 2012; Lee et al., 2014c); *Rattus* spp. are the most common prey in agricultural landscapes such as sugarcane fields (Fernandez and de Guia, 2011; Lorica and Heaney, 2013) or oil palm plantations (Rajaratnam et al., 2007). On the other hand, wild small carnivores recorded in Bangka are either highly frugivorous (as is the common palm civet (Joshi et al., 1995; Nakashima et al., 2013) and the small-toothed palm civet (Corlett, 2011)), or mainly omnivorous (like the Malay civet, even if the latter is heavily specialized on rodents (Jennings and Veron, 2009)). We therefore could expect a higher predation pressure on rats from the small carnivore community in Riau plantations compared to Bangka.
In brief:
According to our results, small carnivores were much more abundant in Riau plantations than in Bangka plantations: KAI from spotlight counts were on average two-times greater in Riau than on Bankga, and those from faeces counts ten times greater in Riau than in Bangka. In Riau plantations, leopard cats represented the most abundant sightings within the small carnivore community, followed by the common palm civet. Whereas in Bangka plantations, the leopard cat was absent, and the small carnivore community was dominated by domestic/feral cats, followed by Viveridae. From our results, the small carnivore community appeared less diverse in Bangka plantations than in Riau plantations. Absence of wild felids in Bangka was confirmed by interviewees and is in accordance with our literature review.
Compared to small carnivore species that are expected to be present on respective islands, small carnivore species richness in oil palm plantations was poor. This result may reflect limitation in our survey methods, but more probably true rarity of most species in oil palm habitats. However, from our literature review, leopard cats and common palm civets are generally reported as common and relatively abundant in oil palm plantations. Our estimations of abundance for those two species in Riau plantations are consistent with those of other small carnivore surveys in oil palm plantations. In contrast, our figures in Bangka plantations are comparatively much lower.
Potential factors which could explain a lower abundance of wild small carnivores in Bangka plantations (compared to Riau ones) include rodenticide use, a higher hunting pressure, a higher abundance of domestic/feral cats (competition and/or disease transmission), and the absence of extensive areas of natural forest on the island.
Our results suggested a negative correlation between rodent damage and small carnivore abundance at community level, as well as at species level for the leopard cat and the common palm civet. Moreover, a similar pattern emerged when comparing plantations from the same region: lower values of estimated rodent damage were observed in plantations where small carnivores were estimated to be more abundant, that is Riau plantations, whereas small carnivores were estimated to be less abundant in plantations where estimated rodents damage was higher, that is Bangka plantations. The lower abundance of small carnivores in Bangka plantations, compared to Riau ones, and the absence of leopard cat - a hypercarnivore feeding mainly on muridae- probably resulted in a reduced off-take of rats by the small carnivore community in Bangka compared to Riau, thereby potentially impacting rat population and consequently rodent damage.
Introduction

Our objective is to investigate differences in the relative importance of small mammals in the diet of the small carnivore community between Bangka and Riau plantations. We presume that the proportion of small mammals in the diet of the small carnivore community in Riau is greater than in Bangka.

Faeces analysis was used to assess potential differences in food habits of the small carnivore community. We assessed the overall relative importance of each food item in the diet of the small carnivore community for each plantation by calculating frequency of occurrence of this food item combined with its estimated relative dry volume in faeces. Our results were first compared to data from the literature. Then we discussed observed differences among regions and plantations, focusing on the importance of small mammals.

Material and methods

Faeces analyses are commonly conducted for carnivores in the context of diet surveys (Long et al., 2008). Traditional methods mostly rely upon the morphological identification of undigested remains in the faeces (Reynolds and Aebischer, 1991; Kauhala et al., 1998; Remonti et al., 2007). New methods are currently being developed to investigate predator diets from their faeces through molecular analysis. They may be rapid and accurate, such as those based on next-generation sequencing technology (Galan et al., 2012; Shehzad et al., 2012), but they need qualified expertise and specialized laboratories, careful preservation and special handling techniques (Panasci et al., 2011). Moreover, they are quite expensive, and, most of all, these technologies require reliable baseline reference for DNA barcoding of potential preys. Although a clearer picture of rodent taxonomy is emerging in Southeast Asia (Pagès et al., 2010), allowing these new methods to give promising results for rodent barcoding (Galan et al., 2010; Galan et al., 2012), knowledge is still lacking to discriminate and identify all prey species based on molecular identification (Chaval et al., 2010; Blasdell et al., 2015). Because of these financial and technical constraints linked to molecular analysis methods, and because of time constraints and other priorities set in the framework of this study, we used the less complex, though less accurate, method based on macroremains (undigested remains) analysis. This method enables us to assess the relative importance of small mammals in the diet of the small carnivore communities in Riau and Bangka plantations.

Field sampling and scat analysis

Small carnivore faeces collected were those counted for estimation of abundance, between 2010 and 2012. Sampling design, faeces identification methods, etc. have already described in the section III.2.1 “Faeces count”. All small carnivore faeces were collected, except very old and degraded ones (disintegrated and without the smooth outer coating). Faeces were collected in separate plastic bags\textsuperscript{40} and immediately frozen on return form the field for later treatment.

\textsuperscript{40} with a view of further DNA analysis for predator identification and/or in depth diet analysis, special care was taken while collecting faeces, in order to prevent contamination across faeces or from human DNA: we avoided contact with bare hands and used wooden sticks as collecting tools, renewing these for each faeces.
Only faeces combining the following criteria were kept for the diet analysis: 1) complete i.e. with no missing part (be it fresh or old), 2) surely or very probably being a faeces from a small carnivore (degree of certainty of 1 or 2 as depicted in section III.2.1). In addition, due to time constraints, only some years were included in the analysis, based on the sample size. Due to the small sample size on both Bangka plantations compared to Riau ones, keeping only one year may have biased the results when comparing both regions. Similarly there were few faeces in Riau_1 compared to Riau_2. Therefore, for Bangka, the faeces collected during three years were considered for the analysis, whether for Riau_1 only two years were retained and for Riau_2 only one year. Table 17 details the total number of faeces retained for the diet analysis.

<table>
<thead>
<tr>
<th>Year</th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Total Riau</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
<th>Total Bangka</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>11</td>
<td>13</td>
</tr>
<tr>
<td>2011</td>
<td>13</td>
<td>78</td>
<td>91</td>
<td>5</td>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td>2012</td>
<td>35</td>
<td>0</td>
<td>35</td>
<td>5</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>48</td>
<td>78</td>
<td>126</td>
<td>12</td>
<td>21</td>
<td>33</td>
</tr>
</tbody>
</table>

Faeces were extracted from the freezer, weighed, then immediately sub-sampled for later DNA analysis (out of the scope of this study). After decontamination in an autoclave for 20 mn at 120 °C, faeces were soaked in water for one night at room temperature to soften them. The macroscopic fractions (bones, hair, feathers, teeth, grass, fiber, etc.) were then gently disaggregated by washing the material under tap water through a 0.5 mm mesh sieve. All recovered macroremains were oven dried (temperature about 50 °C for 10 to 24 hours, depending on the type of macroremains and their volume) then kept in individual plastic bags for later identification.

Macroremains were visually identified, if necessary under a microscope (Nikon SMZ 745T). Plastics and such material were not considered as food items and were not taken into consideration for the analysis. Food items were separated into the following categories, based on the presence and/or characteristics of hair, bones, teeth, nails, feathers, scales, leaves, fruit seeds or nuts, and fiber: small mammals (all “mammals” were considered as “small mammals”, as we assume there was very little chance for small carnivores to prey on medium or large mammals), birds, reptiles, fish, amphibians, grass, plant material other than grass, eggs, and unidentified. Grass was separated from other plant material (such as fruits, seeds, etc.) as we assumed it was ingested not as part of the diet for food and energy purpose but either accidentally, or intentionally to aid hair elimination or to control parasitism (Chame, 2003; Krishnakumar and Balakrishnan, 2003; Lee et al., 2013); this habit is common for carnivores, notably for felids. Palm fruits were specifically identified (within plant material). Due to rarity of identifiable teeth and skull remains (as reported by Day (1966)), we could not make the distinction between rodent and non-rodent within small mammal prey remains (and furthermore between rat or non-rat), unlike we could do for barn owl pellets. Faeces may contain fur ingested during grooming. Hairs from grooming were differentiated from hairs from mammal prey, based on length and color, and were not taken into account.

For each faeces, we recorded the occurrence of each food category, and an estimate was made, by eye, of the relative volume of dry macroremains of each category in the given faeces. Results were expressed, for each food category, as:
- %FO: percent frequency of occurrence in faeces, i.e. number of faeces containing macroremains of the given food category x 100 / total number of examined faeces;
- %VOt: estimated percent dry volume in the overall diet, i.e. mean percent volume of the given food category as estimated in dry macroremains, considering the total number of examined faeces.
- %VOp: estimated percent dry volume when present, i.e. mean percent volume of the given food category as estimated in dry macroremains, considering only faeces containing that food category.

According to Zabala and Zuberogoitia (2003), the combination of the volumetric and frequency methods gives a general idea of the trophic habits of a species or a community (given that the volumetric results show the relative importance of the food category in the diet and the frequency one shows how often it is eaten), and is particularly adapted to comparisons between areas. The authors also reported that frequency of occurrence expressed as a percentage of the total number of faeces is more widely used in the western literature than frequency of occurrence expressed as a percentage of the total occurrence of all food items, and is of more biological significance. Plotting volumetric methods (percentage in all examined faeces and in faeces where remains were present) against %FO was inspired by Kruuk and Parish (1981). The %FO (x) of each main food item was plotted against its %VOp (y), (xxy)/100 equalling %VOt and all points with equal xxy being then connected by isopleths (Kruuk and Parish, 1981; Remonti et al., 2007).

**Statistical analysis**

We aimed at detecting differences in feeding behavior of the small carnivore community between Riau and Bangka, notably related to the overall importance of the small mammal category; results were also examined at plantation level to identify variation that might be obscured at the regional level. Given the importance of the food category “plant material (excluding grass)”, similar analysis as for small mammals items were also carried out for this food item. Generalized linear mixed-effects models (GLMM) of the binomial family were used to investigate variability in the probability of presence (presence/absence) of each food item in small carnivore faeces among regions, with plantations included as random effect (to account for pseudo-replications within plantations). Likelihood ratio tests were used to test for the effect of each variable (i.e. p-values were obtained by comparing, via anova, the model with the variable in question and the reduced model without the given variable). To test for differences of frequency of occurrence of a given food item among plantations, we used another series of generalized linear models of the binomial family, with no random effect and excluding the variable region. Analysis of variance was performed on those models; coefficients associated with these models selected enabled us to compare plantations two by two, whether or not they were from the same region. For %VOp and %VOt, we used the same approach, except that models were linear regressions. In all but one case (i.e. for %VOp as response variables for plant material food items), we failed to detect any effect of Year; consequently, in all these cases, the variable Year was dropped from the model.

Models assumptions about homoscedasticity and normality were checked by visual inspection of the plots of the residuals against the fitted value; normality was formally confirmed by One-sample Kolmogorov-Smirnov tests. When non homogeneity of variance was suspected for non-mixed effect models, permutation tests enabled us to confirm the effect of variables. As pointed out in section III.1.2. and II.3.2., $R^2$ definition and calculation for mixed-effect models is under debate (Xu, 2003; Edwards et al., 2008; Nakagawa and Schielzeth, 2013). To assess the overall goodness-of-fit of linear mixed-effects models, we used the $R^2$ of the correlation between the fitted and observed values, as suggested by Byrnes (2008). For generalized linear mixed-effects models, we calculated two pseudo $R^2$: marginal $R^2$, which describes the proportion of variance
explained by the fixed effect alone, and conditional $R^2$, which describes the proportion of variance explained by both the fixed and random effects (Nakagawa and Schielzeth, 2013). For non-mixed generalized linear models, we used McFadden approach, calculating pseudo-$R^2$ as $1$-residual deviance/null deviance (Faraway, 2006). For non-mixed linear models, we used the adjusted-$R^2$ as commonly reported. Adjusted $R^2$ and pseudo $R^2$ of models selected are given for information purposes only, in Appendix 6, as they cannot be interpreted independently or compared across datasets: they are valid and useful in evaluating multiple models predicting the same outcome on the same dataset, with $R^2$ of the same type (in this situation, the higher adjusted $R^2$ or pseudo $R^2$ indicates which model better predicts the outcome).

Analyses were performed using R version 3.3.0 (R Core Team, 2014). Either package lme4 version 1.1-7 or nlme version 3.1-117 were used for modelling. The package pgirmess version 1.5.9 was used for permutation test and One-sample Kolmogorov-Smirnov test. The package Ggplot2 version 1.0.0 was used for most graphics.

**Results**

Out of a total of 159 analyzed faeces (see Table 17), 311 food items were identified, of which 36.7% were small mammals items (37.7% in Riau and 32.2% in Bangka).

Percent frequency of occurrence (%FO) and percent volumes (%VOp and %VOt) of each food category in each plantation are reported in Figure 49 (see Appendix 6 for more details).

In one plot, Figure 49 makes it easy to compare the relative importance of each food item in the diet of the community on a given plantation, or to compare the importance of a given food item among plantations. For example, it indicates that the category “small mammals” has overall the same importance in the diet of the community in Riau_1 and Bangka_2 (in term of volume in the overall diet), as their points are located along the same %VOt isopleth (above 50%), however, in Riau_1, small mammals occurred more frequently in faeces than in Bangka_2 (cf. %FO in abscissa), but in lower volume in each faeces (cf %VOp in ordinate).
Figure 50: Diet composition of small carnivore community in Riau and Bangka oil palm plantations, based on prey remains identified from faeces. %VOp (estimated dry volume when present) versus their %FO (frequency of occurrence in faeces); isopleths connect points of equal estimated dry volume in the overall diet (%VOt). Number of faeces analyzed: Riau_1 = 48, Riau_2 = 78, Bangka_1 = 12, and Bangka_2 = 21.

Figure 49 (see Appendix 6 for more details) shows that, in both Riau plantations, small mammals rank first and dominated the other items in terms of frequency of occurrence (%FO) in faeces: mean of 74.6% at regional level, with 81.2% in Riau_1 and 70.5% in Riau_2 for small mammals, versus < 40 % for each other food items). And, when they occurred, their mean estimated volume was respectively 77.1% in Riau_1 and 73.6% in Riau_2 (mean at regional level: 75.1%). In Riau plantations, others items quite frequently found in faeces were, by order of decreasing importance, grass, insects and arachnids, and plant material (other than grass), with mean of %FO at regional level of 38.1%, 34.9% and 30.9% respectively. When taken, these items represented in terms of volume (mean at regional level): 20%, 45.9% and 54.6% respectively. Other identified food items were rarely taken (less than 6% for each, in each Riau plantation).

In Bangka, small mammals made up a large volume of the diet when taken (respectively 84.1% and 93.9% in Bangka_1 and Bangka_2), and in Bangka_2 these were taken the most frequently, with a percentage of 71.4%. However, in Bangka_1, frequency of occurrence for small mammals was only 41.7%, ranking second after plant food items (other than grass), which occurred in 66.7% of faeces, and represented 73.3% of the volume of faeces whenever present. Other identified food items were rarely taken in Bangka plantations, with a maximum FO of 14.6%, except for insects and arachnids food items which set apart with a FO of 42.2% at regional level.

Frequency of occurrence of small mammals in the diet of the small carnivore community in Bangka was of 60.6% compared to 74.6% in Riau, but we failed to detect statistical difference between both regions (p=0.124). We also failed to detect significant differences between regions for volumetric consumption of small mammals when considering all faeces (VOt, p= 0.92). When considering
only faeces in which small mammal food items were present, the volume represented by small mammals was significantly higher in Bangka (%VOp=91.4%) than in Riau (%VOp=75.1%) (p=0.028); though this result should be treated with caution because of lack of convergence of the model; moreover, when focusing at the plantation level, we failed to detected differences (p=0.117). In Bangka, seeds, fruits and leaves (“plant material excluding grass” food category) had an overall higher importance in the diet of the small carnivore community at the regional level: it was more frequently taken in Bangka than in Riau (FO of 51.1% in Bangka and 30.9% in Riau, p=0.035), although we failed to detect a difference at the plantation level (p=0.094). We also failed to detect a difference between regions in terms of volume in faeces (p=0.14 for VOt, p=0.06 for VOp but convergence issue). However, with analysis at the plantation level, the plant material (excluding grass) food category was found to be significantly higher in Bangka_1 (48.7%) compared to each of the other plantations (VOt ranging from 14.7% to 20.5%; p-value ranging from 0.002 to 0.0145); and we failed to detect differences of %VOt among Bangka_2, Riau_1 and Riau_2 (p>0.05).

The imprecision in the estimation for Bangka was large comparatively to Riau (notably in Bangka_1), due to small sample size in Bangka; this can be visualized from the wide and overlapping confidence intervals for the means as presented in Figure 50 for small mammals (see details in Appendix 6 for others food items).

![Figure 51](image_url): Frequency of occurrence (%FO) and volume (%VO) of small mammal food items in faeces of the small carnivore community in Riau and Bangka plantations, with lines representing 95% confidence intervals and dots representing means. Data include year 2011 for Riau_2 plantation, year 2011 and 2012 for Riau_1, and year 2010 to 2012 for both Bangka plantations. Results are expressed as percentage of the total number of faeces (for %FO and %VOt) or as percentage of the faeces whenever small mammal remains are present in the faeces (%VOp).
About model assumptions for mixed models:\footnote{For non-mixed effect models, models assumptions will not be discussed, given that permutation test was used to confirm effects of variables when assumptions were not upheld.}

- Models assumption about homogeneity of variance were not likely to be upheld in many cases, but given that the models were not used for predictions, this issue is not critical.
- In all but one situations (for the model with %VOp as a response variable with plant material food item), normality of the distribution of residuals was lacking. For small mammal food items and frequency of occurrence as a variable response, the null hypothesis was accepted, and the risk to accept H0 wrongly due to absence of normality is unlikely. The same is the case for %VOt as a response variable for plant material food items or small mammal food items. However, for plant material food items with frequency of occurrence as a variable response, as well as for small mammal food items with %VOp as a variable response, the null hypothesis was rejected, and it is not possible to say whether this is due to differences among regions or due to lack of normality of the residuals.

In conclusion, though we failed to detect differences of small mammal consumption among regions and plantations in most cases, diet patterns suggested that the diet of the small carnivore community in Bangka may be different than in Riau, at least for Bangka_1: vegetable food such as seeds, fruits and leaves were more important than in Riau plantations. However these results should be treated with caution, because of the imprecision of the estimations due to the very small sample size in Bangka (33 faeces analyzed in Bangka comparatively to 126 in Riau).

**Discussion**

- **About methodological biases**

Many authors have compared traditional scat analysis methods and investigated their limitations in assessing carnivore diets (Corbett, 1989; Reynolds and Aebischer, 1991; Carss and Parkinson, 1996; Ciucci et al., 1996; Zabala and Zuberogoitia, 2003; van Dijk et al., 2007; Crimmins et al., 2009; Klare et al., 2011).

The main bias associated with methods relying on macroremains analysis is related to differential digestibility, especially for the volumetric method, as some kind of food will be underestimated when taking into consideration only the macroscopic fraction (i.e. macroremains). For example, Reynolds and Aebischer (1991) showed that consumption of earthworms and birds by the foxes cannot be adequately assessed when ignoring the microscopic fraction. Moreover, hairs are usually better preserved in faeces than fruits, which are digested and may be washed out: only a smaller fraction of soft plant material, the fibers, are retrieved and count as “macroremains”, thereby frugivorous food part in the overall diet might be underestimated (Reynolds and Aebischer, 1991; Carss and Parkinson, 1996).

In addition, before faeces collection, corpophagous insects, which are quite active in the tropics, may preferentially consume some components, thereby excluding them from the analysis.

Our results might also be biased because of sampling methods. Indeed, faeces were collected along roads, therefore the proportion of different prey species found in the faeces are biased in favor of those small carnivores species, such as felids, that often travelled such routes and mark them with
faeces (Macdonald, 1980; Gordon and Stewart, 2007; Long et al., 2008); and felids are known to mainly feed on small mammals (Sunquist and Sunquist, 2009). Therefore, the proportion of mammals in the diet of the small carnivore community as assessed from our faeces analyse might be overestimated, in equal proportion to the proportion of felids within the community.

At species level, most of these biases would be offset in a comparative approach among regions and plantations, by the fact that these biases are likely to be the same across each plantation or region. However, at the community level, the amplitude of the bias would be linked to species composition of the community, which has been shown to be different e.g. between Riau and Bangka (see previous section).

Moreover, comparison between Bangka and Riau might also be biased by the low sample size in Bangka comparatively to Riau (only 33 faeces collected and analyzed in Bangka plantations, against 126 in Riau).

- **Comparison of overall results with literature**

Small carnivores exhibit a wide range of feeding habits from principally vertebrate and/or invertebrate feeders to predominantly frugivorous species, and most species may have a quite variable diet, depending on food resources available (Gilchrist et al., 2009; Jennings and Veron, 2009; Sunquist and Sunquist, 2009; Corlett, 2011).

Our results show the importance of small mammals in the diet of the small carnivore communities in our study sites: small mammals prey were often consumed (frequency of occurrence ranged from 41.7% to 81.2%), and when consumed they represent a large bulk of the diet (ranging from 73.6% to 93.9% of the dry volume of the faeces). Apart from small mammals, we reported the importance of plant material –excluding grass- (frequency of occurrence in faeces of 30.9% in Riau plantations and 51.1% in Bangka; estimated dry volume in overall diet of 16.9% in Riau and 28.4% in Bangka) as well as insects and arachnids (frequency of occurrence in faeces of 34.9% in Riau plantations and 42.4% in Bangka; estimated dry volume in overall diet of 15.7% in Riau and 4.6% in Bangka). Grass was also quite frequently taken, at least in Riau (38.1%). Birds, reptiles, amphibians, fish, molluscs and crustaceans were only occasionally or rarely taken.

The overall dominance of small mammals in the diet of the small carnivore community in our study sites is consistent with, on one hand, the abundant rodent food resources within the plantation as described in section II.2., and, on the other hand, spotlight counts (see section III.2.1) indicating the overall dominance of felids, i.e. hypercarnivores, within the small carnivore community: felids (leopard cats, domestic or feral cats, undetermined wild felids) represented between 66% and 82% of all small carnivores observed.

We found only few studies reporting the diet of a whole small carnivore community in the tropics (Rabinowitz and Walker, 1991; Ray, 1998), with most research being focussed on either one or few species (Joshi et al., 1995; Chuang and Lee, 1997; Colon, 1999; Angelici, 2000; Rajaratnam et al., 2007; Su and Sale, 2007; Silva-Pereira et al., 2011; Lee et al., 2014c), or including large carnivores (Ray and Sunquist, 2001; Mukherjee et al., 2004).

Ray (1998), collecting small carnivore faeces in an African rainforest, reported a frequency of occurrence of 49.3% for small mammals (mammals <1kg), but he mentioned that the small carnivore community was primarily composed of insectivorous species (frequency of occurrence of
arthropods was 78%). Other prey occurring were herpetofauna (18.4%), mammals >1kg (16.8%), fruit (11%), fish (3.9%) and birds (5%). The dominant role played by arthropods in the diets of tropical forest carnivores, due to this widely available and productive food source, was underlined by Ray and Sunquist (2001). In agricultural landscapes such as oil palm or sugar cane plantations, in Southeast Asia, small mammals -usually rodent pests- or fruits were reported as the most common food for carnivorous and frugivorous small carnivore species respectively (Scott and Gemita, 2004; Rajaratnam et al., 2007; Fernandez and de Guia, 2011; Loria and Heaney, 2013; Nakashima et al., 2013). For example, Rajaratnam et al. (2007) found that mammals and notably murids occurred in respectively 97.2% and 90.3% of leopard cat faeces in an oil palm landscape, with frequency of occurrence for herpetofauna, invertebrates, grass and birds being respectively 19.4%, 11.1%, 11.1% and 5.6%. For common palm civets in oil palm plantations, Nakashima et al. (2013) found that wild plant fruits and oil palm fruits occurred in 45.1% and 44 % of faeces respectively, compared to 16.5%, 13.1% and 2.1 % for millipedes, rodents and insects.

**About the place of small mammals in the diet of small carnivores in Riau compared to Bangka**

Statistical tests did not suggest any different frequency of occurrence (%FO) in faeces or volumetric consumption of small mammals by the small carnivore community in Bangka compared to Riau, except for volumetric consumption in faeces where small mammals food items were present (%VOp), but this last result should be treated with caution because the model lacked convergence. Statistical differences among plantations were not detected either, whatever the variable studied (%FO, %VOt, %VOp) though, at first sight, in Bangka_1, the estimated mean volume on overall faeces (%VOp) appeared lower than in the three other plantations, as did the frequency of occurrence. The fact that we could not detect differences between Riau and Bangka (and notably between Bangka_1 and others plantations) may be due to the lack of statistical power because of low sample size.

Analyzing results for other food items, our results suggest that the place of the “plant material excluding grass” food category in the diet of the small carnivore community was not the same in Riau plantations and in Bangka plantations. In Bangka, seeds, fruits and leaves had an overall higher importance in the diet of the small carnivore community than in Riau (32.7% vs 17.6%). This is mainly due to the different diet pattern in Bangka_1, where this vegetal category ranked first in terms of frequency of occurrence and volume whenever present, whereas for the other plantations it is the small mammal category which ranked first. Bangka_1 was the plantation which appeared different from the others when analyzing %VOt at plantation level: the volume in overall diet of the plant material (excluding grass) food item was significantly higher in Bangka_1 than in the other plantations.

Reduced food availability can cause a shift in the diet of generalist carnivores. Seasonal variation in predation on rodents by tropical small carnivores has been demonstrated in forest environments, likely linked to peaks in prey availability -the latest being governed by prey vulnerability to predation rather than by abundance- (Ray, 1998). However, studies conducted in oil palm (Rajaratnam et al., 2007) and sugarcane plantations (Loria and Heaney, 2013) reported no significant seasonal difference in prey composition for the leopard cat with respect to wet or dry season. In our study, sites were compared at the same season. Moreover, within the oil palm habitat, rodent damage data suggested an overall high and more or less constant rodent prey availability (see
section II.2). In addition, similar biophysical conditions and agricultural practices (see section II.1.2.), by providing similar habitat and microhabitat, would be likely to result in similar prey vulnerability to predation. Similarly, oil palm fruits are constantly available throughout the year in the studied oil palm plantations, and oil palm fruit is likely to be a major food for frugivorous species in oil palm plantations, as demonstrated for the common palm civet by Nakashima et al. (2013). Therefore, we assume that variation in small mammal consumption by the small carnivore community among Riau and Bangka plantations, relatively to fruit consumption, might not be explained by variation in food availability, but might rather reflect variation in species composition within the small carnivore community.

As shown previously (section III.2.1.) the small carnivore community (including domestic/feral species) in Riau is dominated by the leopard cat, which represented 57% of sighting in Riau_1 and 42% in Riau_2. Our results on small carnivore diet profile in Riau plantations is likely to reflect this dominance: small mammal prey dominates in terms of frequency of occurrence (81.2% in Riau_1 and 70.5% in Riau_2) and of dry volume in faeces when present (77.1% in Riau_1 and 73.6% in Riau_2), and grass was also frequently present (39.6% in Riau_1 and 37.2% in Riau_2). From our literature review, the leopard cat is an hypercarnivore, and feeds mainly on small mammals (Sunquist and Sunquist, 2009; Shehzad et al., 2012; Lee et al., 2013). Grass was also reported as frequently present in leopard cat faeces: e.g. Rabinowitz (1990) found grass in 48% of faeces. In a study conducted in an agricultural landscape composed of two oil palm plantations and an adjacent forest reserve on Borneo, Rajaratnam et al. (2007) found that small mammals occurred in 97.2% of leopard cat faeces, and grass in 11.1%, with frequency of occurrence for other items being below 20%. Scott and Gemita (2004) also reported that small mammals were the main prey of leopard cat in an oil palm plantation in Sumatra, both in terms of frequency of occurrence and proportion in faeces. Similarly, Lorica and Heaney (2013) studied the diet of the leopard cat in a sugarcane plantation on a Philippine island and found that mammals were present in 96% of scats and grass in 33%, reptiles in 20%, amphibians in 8% and insects in 4%.

In Bangka_1, the overall higher importance of plant material (excluding grass), would suggests that the proportion of more strictly carnivorous species in the small carnivore community is less than in Riau. At first sight, differences among regions is not consistent with previous results showing that in Riau plantations, felids i.e. hypercarnivores (leopard cats, domestic or feral cats, undetermined wild felids) represented 66% and 75% of the community in each plantation respectively, when in Bangka they represented 75% and 82% (see section III.2.1.). However, there are no wild felids in Bangka, and if we exclude domestic/feral cats, the common palm and the small toothed palm civets are the most abundant species within the wild small carnivore community in Bangka, whereas in Riau plantations these species rank second after the leopard cat. Moreover, the high consumption of plant material (excluding grass) in Bangka_1 compared to Bangka_2 may be explained by the fact that the civet group represented a larger proportion of the small carnivore community (including domestic/feral cats) in Bangka_1 comparatively to Bangka_2. Despite their taxonomic status within the Carnivora, the Paradoxurinae species feed extensively on fruit: common palm civet prefers fruits when available and small toothed palm civets are probably highly frugivorous (Jennings and Veron, 2009; Corlett, 2011; IUCN, 2014) (though, Lekagul and McNeely (1988), previously described this species as omnivorous, feeding mainly on live prey). In addition, domestic and feral cats probably depend more or less on human-derived food resources, and may therefore eat fewer small mammals than leopard cats. Watanabe et al. (2003) analyzed contents and distribution of feral cat faeces on Iriomote Island in Japan. Their results indicated a high dependency on garbage for food, though feral cats also preyed upon various animals ranging from mammals to insects (35%
insects, 26% birds, 9.7% rodent, 3.2% amphibians). In addition, Wood and Chung (2003) (citing Bunting (1939)) reported that attempts to introduce domestic/feral cats into oil palm plantations were successful only if extra food was provided for the cats.

To sum up, 1) the absence of leopard cat in Bangka plantations versus their abundance in Riau plantations, 2) the fact that civets -mainly common palm civets which are highly frugivorous- were the only species of wild small carnivores detected in Bangka plantations, and 3) the fact that the civet group represented a larger proportion of the small carnivore community (including domestic/feral cats) in Bangka_1 compared to Bangka_2 and Riau plantations, may explain that small mammals take more place in the diet of the small carnivore community in Riau, and that in Bangka_1, where seeds, fruits and leaves had an overall higher importance in the diet of the small carnivore community compared to other plantations.

To conclude, though small mammal consumption patterns were quite similar on both Riau plantations, the situation appeared more heterogeneous on Bankga plantations, notably with regard to vegetable food item, which formed a higher proportion of the diet in Bangka_1 compared to each of the other plantations, and ranked first before small mammal food items (in Bangka_1 only). Both results on volume and occurrence in Bangka are not very robust, given the imprecision of the estimation (due to the low sample size in Bangka comparatively to Riau), therefore it is hard to state clearly. However, our results broadly suggest that different diet patterns exist between Riau and Bangka, reflecting small carnivore community composition, and this result is consistent with our hypothesis that the small carnivore community in Riau may have a higher prey intake of small mammals than in Bangka.

Most small mammals taken are probably rodents: because they are dominant in our study sites (see section II.2) and because they are the preferred prey of most carnivorous species, notably those known to be present at these sites: the leopard cat, the domestic/feral cat and the Malay civet. In China, Bao et al. (2005) reported a frequency of occurrence of rodents of 82.4% for a small carnivore community composed of Canidae, Mustelidae and Felidae. The leopard cat was found to prefer rats and mice, as depicted in many studies (Rabinowitz, 1990; Tatara and Doi, 1994; Khan, 2004; Bao et al., 2005; Grassman et al., 2005; Austin et al., 2007a; Fernandez and de Guia, 2011; Lorica and Heaney, 2013; Bashir et al., 2014; Lee et al., 2014c). In oil palm plantations in Malaysia, Rajaratnam et al. (2007) reported that murids comprised 92.8% of the mammalian prey consumed by the leopard cat and occurred in 90.3% of faeces. According to Corlett (2011), rodents are the most consistent component in the diet of the three Asian Viverra species, including the Malay civet. Bonnaud et al. (2011) reported that rats or rabbits were the most important prey in the diet of feral cats on islands worldwide.

This study is a first step in diet analysis of the small carnivore community in oil palm plantations, and should be complemented by a more in-depth study using molecular biology techniques. Through DNA recovered from faeces, it should be possible 1) to assign each faeces to a small carnivore species, and 2) to identify food items with a higher taxonomic resolution, thereby assessing the part of each small carnivore species in rodent pest control.
In Brief:
Our analysis showed the importance of small mammals in the diet of the small carnivore communities in our study sites: small mammal prey were often consumed, and when consumed they represented a large bulk of the diet.
However, when comparing the respective place of both small mammals and plant material (excluding grass) food items in the diet, our results suggest that plant material (excluding grass) had an overall higher importance in the diet of the small carnivore community in Bangka compared to Riau, whereas in Riau small mammals were more important. Indeed, small mammals ranked first in both Riau plantations, whereas, in Bangka_1, this food item ranked second after plant material (excluding grass). Moreover, plant material (excluding grass) was more frequently encountered in faeces of the small carnivore community in Bangka compared to Riau, and, in Bangka_1, volumetric consumption of this food item (in all faeces) appeared significantly higher than in each of the other plantations.
Considering the food habits of small carnivores as detailed in the literature, this result is consistent with the composition of the small carnivores community in the four plantations as described in section III.2.1., and would suggest that small mammals, notably rodents, may be less important in the diet of small carnivores in Bangka compared to Riau.
III. 3. CONCLUSION

In this section, we have investigated and compared, among plantations and regions, the abundance and diversity of small carnivores, as well as diet of the barn owl population and the small carnivore community. Barn owl reproduction patterns were also compared, as it may suggest differential food intake. Main results are synthetized in Table 18.

Some main differences emerged from the comparison between Riau and Bangka systems:

- For the barn owl population:
  - There was only one breeding season in Bangka plantations compared to two in Riau. Given that reproduction and breeding increase food requirement, this would presumably lead to a lower prey intake for barn owls in Bangka plantations compared to Riau.
  - Prey taken as food by the barn owl was more diverse in Bangka plantations than in Riau, and the proportion of rats in the barn owl diet was slightly less in Bangka than in Riau. The difference in diet was not great, but this does not determine the extent of the impact on rat population dynamics.
  - Our results support the prediction that barn owl predation pressure on rats would be less in Bangka plantations than in Riau. However, the differential impact on rat population dynamics is still under question.

- For the small carnivore community:
  - According to abundance indices, small carnivores were much more abundant in Riau plantations than in Bangka. Moreover, the leopard cat was absent in Bangka plantations while being the dominant species in Riau plantations.
  - Small mammals are an important part of the diet of the small carnivore community in all plantations; however, our results suggest that the small carnivore community in Riau plantations may feed more on small mammals compared to the community in Bangka, where plant material took more importance in the diet. This result would reflect the variation in species composition of the small carnivore community between Riau and Bangka.
  - Our results suggest a negative correlation between rodent damage and small carnivore abundance, be it at community level or for the leopard cat alone.
  - Our results support the prediction that small carnivore predation pressure on rats would be less in Bangka plantations than in Riau, and therefore supports the broad hypothesis that small carnivores play a role in rodent control in oil palm plantations.

Table 18: Diet and/or abundance of two rat predators (barn owls and small carnivores): main differences between Riau and Bangka plantations.

<table>
<thead>
<tr>
<th></th>
<th>Barn owls</th>
<th>Small carnivores</th>
<th>KAI*</th>
<th>Small mammals in diet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Breeding season</td>
<td>Rodent in diet</td>
<td>Faeces</td>
<td>Spotlight</td>
</tr>
<tr>
<td>Riau</td>
<td>++</td>
<td>+++</td>
<td>1.12</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.78</td>
<td>0.16</td>
</tr>
<tr>
<td>Bangka</td>
<td>+</td>
<td>++(+)</td>
<td>0.07</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.20</td>
<td>0.12</td>
</tr>
</tbody>
</table>

*KAI: Kilometric Abundance Index
IV. SPATIAL DISTRIBUTION OF SMALL CARNIVORES WITHIN OIL PALM PLANTATIONS AND CORRELATION TO HABITAT

IV.1. INTRODUCTION

As highlighted in the general introduction, it is known that predator community composition and distribution is influenced by landscape configuration. Landscape configuration might therefore be critical for small carnivore persistence within oil palm plantations. However little is known about small carnivore habitat use in oil palm landscapes. Consequently, with a view to suggesting appropriate land-use management for small carnivore enhancement within oil palm plantations, there is a need to investigate spatial distribution of small carnivores in these areas.

Our objective is to investigate the heterogeneity of spatial observations of small carnivores within each oil palm plantation, and to investigate correlation to habitat, comparing spatial patterns among plantations. For this, we had two approaches. In the first, we looked for clustering in our observations, and broadly analyzed (visually) their distribution in the landscape. In the second, we tested if some focal habitats such as forest, the central area of oil palm plantation or human settlements had a positive (attractive) or negative (repulsive) effect on the distribution of small carnivores. Because habitat preference may be different among species (Burton et al., 2012), we analyzed the data not only at community level, but also at species level when possible. Our hypothesis is that there is a spatial heterogeneity in small carnivore observations within the oil palm habitat, and that this heterogeneity is linked to nearby habitats. We predict that there are more observations of wild small carnivores nearby forest habitat, and less in central parts of the oil palm habitat or nearby human settlements, except for domestic or feral cats which would rather be observed nearby human settlements.

IV.2. MATERIAL AND METHODS

**Small carnivore sampling**

We investigated small carnivore distribution within and on the boundary of oil palm habitat from field surveys previously carried out to assess their relative abundance among plantations (see III.2.1): presence records were compiled from: 1) direct sightings during night time spotlight counts from a vehicle along plantation dirt roads, and 2) faeces counts on fixed transects, walked along plantation dirt roads. More details about the methodology for spotlight and faeces counts can be found in section III.2.1. Pedestrian transects were walked only once a year; spotlight routes were surveyed three times each year, except in 2010 when we surveyed only once, and yearly observations were pooled. Given the potential for confusing faeces of sympatric small carnivore species (Ray and Sunquist, 2001; Davison et al., 2002; Chame, 2003; Long et al., 2008), we pooled all faeces collected within a “small carnivores” category and considered the community level, including faeces of domestic/feral cats. During spotlight counts, identification to species was almost always possible, therefore analyses were carried out at different taxonomic levels: for the small carnivore community, for the “wild small carnivore community” (excluding domestic/feral cats), and at species level (including domestic/feral cats).
Habitat mapping

A database of the global land cover map or forest cover map for insular South East Asia are available on the web (Miettinen et al., 2012; Hansen et al., 2013a), but they were criticized for their inaccuracies in distinguishing vegetation types at the local scale (Dong et al., 2014; Tropek et al., 2014). Therefore, we produced our own land cover maps for each oil palm plantation and its surroundings, based on visual interpretation of satellite images and ground truthed observations. Material and methods for mapping are detailed in section II.1.1.b.

The following main habitat types were considered: forest (or forest like habitat, such as complex rubber agroforestry systems called “jungle rubber”; hereafter, the term “forest habitat” will be use either for forest habitat or for forest like habitat), tree plantation, oil palm, mosaic_1, mosaic_2, shrub, savannah, mining, human settlement, human various. Main roads and watercourses were also represented. “Mosaic 1” and “mosaic 2” habitats are both patchworks of smallholder farms within a matrix of either shrubby savannah for “mosaic 1”, or forest (or forest like) habitat for “mosaic 2”; cultivated areas of “mosaic 2” are a mix of subsistence crop farms and palm or rubber smallholder plantations, whereas for “mosaic 1” young oil palm or rubber plantations dominate. “Human settlement” habitat groups areas with relatively high population density, such as villages or village areas, mills and dispensaries; “human various” habitat groups all other areas with human activities but with less human presence than “human settlement” (“human various” may thus include air strips, petroleum or gas exploitation areas, cemeteries, etc.). More details on all habitat type descriptions may be found in section II.1.1.b.

Clusters detection and distribution

We first identified potential clusters of observations of small carnivores, in each plantation, from spotlight and faeces counts respectively. Cluster detection was carried out only when there was more than one observation per plantation for the given category (community or species level).

In R software (R Core Team, 2014), each spotlight route was divided into successive 100 m segments, and each pedestrian transect was divided into successive 50 m segments (using thintrack function from pgirmess package, which was developed specifically for this purpose; Giraudoux (2014)). We used a 50 m interval for faeces because observations were more numerous and much closer together (often less than 100 m) than spotlight counts, thereby a smaller interval would provide more accurate results. Each observation was reported to the nearest interval, and the total number of observations for each interval was calculated (using knearneigh function from spdep package) and georeferenced to the centroid of the given interval.

We tested if observations were randomly distributed among intervals, following a Poisson distribution (H0), or if low (fewer observations than random) or high (more observations than random) clusters of observations occurred on some intervals (H1). The existence of these spatial clusters was investigated with Kulldorff method using SatScan version 9.1.1 (Kulldorff and Inc., 2011). The principle is to gradually scan a circle window across space (the windows being in turn centered on each interval centroid), and note the number of observed and expected observations inside the window at each location. The risk ratio RR is calculated as the risk estimated within the windows, divided by the risk estimated outside the windows, it is therefore a measure of the gap/difference between the real number of observations in each interval and the number of observations expected under the null hypothesis (if the risk was the same everywhere). RR is <1 for low rate cluster and >1 for high rate cluster. A p-value is assigned to each cluster according to Monte Carlo hypothesis testing (by comparing the rank of the maximum likelihood from the real
data set with the maximum likelihoods from the random data sets). Only clusters with a p-value <0.05 were retained as most likely clusters (i.e. cluster least likely to be due to chance). We verified the absence of spatial autocorrelation of observations (independence of sampling units / number of intervals) by modelling variograms, in R software. The variogram plots semivariance as a function of distance between observations. To verify whether an increase of semivariance with distance could possibly be attributed to chance, we computed variograms from the same data (with 99 permutations), after randomly re-assigning measurements to spatial locations. If the sample variogram (corresponding to our data set) falls within the range of the random variogram, complete spatial randomness may be a plausible hypothesis, and thereby the absence of spatial correlation is likely (Bivand et al., 2008). We may therefore conclude that results of our previous Kulldorff analysis are not biased by pseudo replicates due to non-independence of sampling units.

Once most likely clusters were identified, we broadly assess influence of habitat on their distribution by visual analysis of cluster location on habitat map, and we compared spatial patterns among plantations to search for similarities.

**Distance of observations to selected habitat**

We investigated if focal habitats such as forest (or forest like) habitat, oil palm edge and human settlement had a attractive or repulsive effect on the distribution of small carnivore observations. For this, we tested if Euclidian shortest distances (simple measure of nearest-neighbour-distance; Kindlmann and Burel, 2008) from observations and a given focal habitat were in average smaller or longer than those of randomly distributed observations, by developing our own one-tailed hypothesis test as described below. Analysis was carried out only when there was more than one observation per plantation for the given category (community or species level). Our null hypothesis $H_0$ is that observations are randomly distributed; the alternative hypothesis $H_1$ is our prediction. Hypothesis testing related to each focal habitat is detailed in Table 19.

<table>
<thead>
<tr>
<th>Question</th>
<th>Focal habitat</th>
<th>$H_0$</th>
<th>$H_1$ (prediction)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Did forest or forest like habitats have an attractive effect on small carnivores?</td>
<td>Forest or forest like habitat (include complex rubber agroforest)</td>
<td></td>
<td>Attractive effect on small carnivores: $D_{\text{obs}} \leq D_{\text{random}}$</td>
</tr>
<tr>
<td>Did oil palm edge have an attractive effect on small carnivores (i.e. repulsive effect of central area of oil palm plantation)?</td>
<td>Oil palm edge</td>
<td></td>
<td>Attractive effect on small carnivores: $D_{\text{obs}} \leq D_{\text{random}}$</td>
</tr>
</tbody>
</table>
| Did human settlements have a repulsive effect on wild small carnivores and attractive effect on domestic/feral cats? | Human settlement | | Repulsive effect on wild small carnivores: $D_{\text{obs}} \geq D_{\text{random}}$
Attractive effect on domestic/feral cats: $D_{\text{obs}} \leq D_{\text{random}}$ |
For the second hypothesis/question, our aim was to test if small carnivores were less encountered within the central area of the oil palm plantation, i.e. central area had a repulsive effect. We did this by asking: “did the edge of the oil palm habitat have an attractive effect on small carnivores”.

The following methodology has been repeated for each focal habitat in each plantation, for spotlight and faeces counts respectively.

The habitat map used was the vector layer produced as described previously in material and methods, from which we created a raster layer (with 30x30m pixels). Based on this raster habitat map, we first created a raster « distance to » layer for each focal habitat, such that each pixel was assigned a value for distance to the given focal habitat; to do so we used QGIS version 2.2.0 (R Core Team, 2014) with GRASS extensions.

Then we used R software (R Core Team, 2014) to analyse distances of observations to the given focal habitat. As for cluster detection, each spotlight route was divided into successive 100 m segments, and each pedestrian transect was divided into successive 50 m segments; then each observation was reported to the nearest interval, and the total number of observations for each interval was calculated and georeferenced to the centroid of the given interval. In a first step, we calculated the mean distance to the focal habitat of all observations, as followed: we first calculated the mean distance to the focal habitat corresponding to each interval i.e. to its centroid (using rwhatbufNum function of pgirmess package to extract pixels values of “distance to” raster for each points of an interval); then we calculated the mean of those distances, taking into consideration intervals with at least one observation. The second step was to calculate mean distance to the focal habitat for random observations. To this end we randomly selected, with replacement (as their might be more than one observation by interval), a number of intervals equivalent to the ones for which observations were really made. Then we calculated the mean distance of those random observations to the focal habitat as described previously. This was repeated one thousand times. In a last step, we looked how many times “by chance” we obtained a mean distance to the given focal habitat even lower -or greater, depending on H1- that the mean distance obtained from real observations. If the mean distance of random observations was lower (for H1: \(D_{\text{obs}} \leq D_{\text{random}}\) -or greater (for H1: \(D_{\text{obs}} \geq D_{\text{random}}\)- than the mean distance of real observations in less than 5% cases, then we rejected H0 with a risk \(\leq0.05\), and consequently H1 was likely.

In addition to mean distance, we also calculated, at species level, the observed maximum distance to forest habitat or oil palm edge, as well as the observed minimum distance to human settlements (from the “distance to” raster layer and R software).

IV.3. RESULTS

Numbers of observations at community level and species level are detailed in Table 20. Distribution analyses were based on much more observations in Riau than in Bangka (nearly ten times more).
Table 20: Number of observations of small carnivores in each plantation, from 2010 to 2012.

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Faeces counts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small carnivores</td>
<td>104</td>
<td>238</td>
<td>18</td>
<td>28</td>
</tr>
<tr>
<td>Spotlight counts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small carnivores (total)</td>
<td>155</td>
<td>102</td>
<td>56</td>
<td>66</td>
</tr>
<tr>
<td>Domestic/feral cat</td>
<td>13</td>
<td>30</td>
<td>43</td>
<td>53</td>
</tr>
<tr>
<td>Leopard cat</td>
<td>89</td>
<td>43</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Common palm civet</td>
<td>45</td>
<td>20</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Small-toothed palm civet</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Malay civet</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Undetermined wild cat</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Undetermined civet</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

IV.3.1. Clusters of observations

As detailed in Table 21, we detected high or low rate clusters (respectively higher or lower rate of observations than random) only in some cases. Sometimes, no clusters were detected, either because observations were evenly distributed or because of very few observations per plantation (e.g. only 2 observations for the Malay civet in Bangka_2).

Probable absence of spatial autocorrelation is supported by our results, for all observations (see variograms and detailed analysis in Appendix 8).

Table 21: Presence (P) or Absence (A) of clusters of small carnivore observations in each plantation. NA for not applicable, i.e. no or only one observation for this species.

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Faeces counts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small carnivores (including domestic/feral cat)</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
</tr>
<tr>
<td>Spotlight counts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild small carnivores</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Leopard cat</td>
<td>P</td>
<td>P</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Common palm civet</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Malay civet</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>A</td>
</tr>
<tr>
<td>Small-toothed palm civet</td>
<td>na</td>
<td>na</td>
<td>A</td>
<td>na</td>
</tr>
<tr>
<td>Domestic/feral cat</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
</tr>
</tbody>
</table>

Figure 51 shows spatial distribution of clusters for spotlight observations and faeces observations, with associated risk ratio (RR).

Figure 52 shows spatial distribution of individual observations.
Clusters of FAECES observations

(a) Small carnivore community (including domestic/feral cats)

**Figure 52:** Spatial distribution of clusters of small carnivore observations (faeces observations), in each Riau and Bangka plantation, with associated risk ratio. Routes surveyed are colored in white. Dots represented clusters with respectively higher (black filled with white border) or lower (white filled with black border) rates of observations. Black circles are surrounding clusters, to ease their identification. Associated risk ratio and p-value are annotated nearby circles surrounding clusters.
Clusters of SPOTLIGHT observations

(b) Small carnivore community (including domestic/feral cats)

**Figure 51:** Spatial distribution of clusters of small carnivore observations (spotlight observations), in each Riau and Bangka plantation, with associated risk ratio. Routes surveyed are colored in white. Dots represented clusters with respectively higher (black filled with white border) or lower (white filled with black border) rates of observations. Black circles are surrounding clusters, to ease their identification. Associated risk ratio and p-value are annotated nearby circles surrounding clusters.

No clusters were detected for Bangka_2. See Figure 52b for spatial distribution of observations.

Legend:
- primary road
- secondary road
- river
- forest or forest like
- tree plantation
- oil palm
- mosaic_2
- mosaic_1
- shrub
- savannah
- mining
- human settlement
- human various
- swamp

Small carnivore observation
- higher rates of observation (RR>1)
- lower rates of observation (RR<1)
Clusters of SPOTLIGHT observations

(c) Wild small carnivore community (excluding domestic/feral cats)

Legend (for habitat legend, see previous page):
- higher rate of observation (RR>1)
- lower rate of observation (RR<1)

No clusters were detected for Bangka
See Figure 52c for spatial distribution of observations

(d) Leopard cat

No clusters were detected for Bangka
See Figure 52e for spatial distribution of observations

Figure 51: cf title and notes previous page
Clusters of **SPOTLIGHT** observations

(e) Common palm civet

RIAU_1

RIAU_2

No clusters were detected for Bangka

See Figure 52g for spatial distribution of observations

Malay civet and Small toothed palm civet

No clusters were detected

See Figure 52h and 52f for spatial distribution of observations

Legend:

- primary road
- secondary road
- river
- forest or forest like
- tree plantation
- oil palm
- mosaic_2
- shrub
- savannah
- human settlement
- human various
- swamp

Small carnivore observation

- higher rates of observation (RR>1)
- lower rates of observation (RR<1)

**Figure 51:** cf title and notes previous pages.
Clusters of SPOTLIGHT observations

(f) Domestic/feral cats

Legend:
- Habitat type
  - forest or forest like
  - tree plantation
  - oil palm
  - mosaic_2
  - mosaic_1
  - shrub
  - savannah
  - mining
  - human settlement
  - human various
  - swamp

Small carnivore observation
- higher rates of observation (RR>1)
- lower rates of observation (RR<1)

Figure 51: cf title and notes previous pages.
If we first take interest in the distribution of clusters of faeces (Figure 51(a)) or spotlight counts (Figure 51(b)) from the small carnivore community, our results indicate:

- For Riau_1: higher rate clusters of faeces observations were detected around the conservation area (the big swamp forest area in Southeast of the plantation); high rates clusters were also detected in the central part of the oil palm habitat. Faeces clusters with lower rate of observations were detected in the central part of the oil palm habitat, and along the northern boundary, where a tarmac road with quite a lot of traffic lay few meters from the boundary. In comparison, high rate clusters yielded by spotlight counts (Figure 51(b)) were located near the conservation area only, and there were no low rate cluster.

- For Riau_2: high rate clusters of faeces observations were detected in the western part of the plantation, where the forest cover is the highest. Low rate clusters were detected in the eastern side of the eastern part of the plantation. Clusters yielded by spotlight counts (Figure 51(b)) showed similar patterns except that there was no low rate cluster.

- For Bangka_2: high rate clusters of faeces observations were detected in the south of the plantation, where the forest cover is highest. Low rate faeces clusters were detected in the northern area, where human presence and road traffic is higher due to concentration of human settlements (workers’ housing, office) and due to preferable access to mill and to the main road outside the plantation. Spotlights count observations yielded no clusters in Bangka_2.

- For Bangka_1: a high rate cluster of spotlight observations was detected in the south-west part of the plantation, whereas low rate clusters covered almost all the eastern part. No clusters were detected for faeces, and our results in Figure 52(a) did not reveal any specific pattern of spatial distribution of individual observations in relation to habitat or landscape.

If we now focus on the distribution of clusters from spotlight counts, considering only the wild small carnivores (Figure 51(c)):

- For Riau_1: two higher rate clusters were detected in the vicinity of the big swamp area in Southeast of the plantation (conservation area). Detected low rate clusters were concentrated around human settlements (mill, office, staff and workers’ housing), on the northern side of the main tarmac road crossing the estate (there is a lot of traffic along this road); some low rate clusters were also detected nearby swamp areas, along this road (south side).

- For Riau_2: a higher rate of observations was detected along the northern riparian forest corridor, in the western part of the plantation. Low rate clusters were found in the eastern part of the plantation, covering large areas (about half of routes). No clusters were detected in Bangka plantations. As shown in Figure 52(c), individual observations were widespread all over the plantations, without any obvious spatial pattern linked to habitat type or landscape.

Considering the leopard cat, as observed during spotlight counts (Figure 51(d)):

- For Riau_1: we did not detect any high rate clusters. We detected fewer observations than random (low rate clusters) on almost all routes in the central part and southern part of the

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42 See material and methods: a high rate cluster is a cluster with a risk ratio > 1 (more observations than random), a low rate cluster is a cluster with a risk ratio < 1 (fewer observations than random). Higher rate clusters are clusters with the highest risk ratio.
plantation, near or far from human settlements, and for some of them along or nearby the big swamp forest in the South.

- For Riau_2: high rate clusters were detected in the eastern part of the plantation, nearby the riparian forest corridor in the north. We did not detect any low rate clusters.

Leopard cats were absent from both Bangka plantations.

Considering the common palm civet, as observed during spotlight counts (Figure 51(e)):

- For Riau_1: two high rate clusters were detected at the same location as for wild small carnivores, i.e. in south-east of the plantation, in the vicinity of the conservation area (the big swampy forest area). We did not detect any low rate clusters.

- For Riau_2: a high rate cluster was detected in the western part of the plantation

Clusters detected in Riau plantations had a high risk ratio (respective RR of 85.2, 66.5 and 151.8) compared to those previously detected either for faeces or spotlight counts (RR ranging from 2.1 to 24.9). No clusters were detected in Bangka plantations. As indicated by Figure 52(g), individual observations were widespread all over the plantations, without any obvious spatial pattern linked to habitat type or landscape.

For the domestic/feral cat, clusters of spotlight counts observations were detected on the four plantations (Figure 51(f)):

- For Riau_1: high rate clusters were detected nearby human settlements (mill, office, staff and workers’ housing) along the main tarmac road crossing the plantation, which are in densely populated areas. We did not detect any low rate clusters.

- For Riau_2: high rate clusters were detected nearby human settlements, along the main tarmac road in between the two parts of the plantation. We did not detect any low rate cluster.

- For Bangka_1: high rate clusters were detected at two places on the boundary of the plantations; one place is an access gate/gateway to the plantation, whereas the other was located nearby a tiny forest patch and did not show any obvious characteristics linked to human settlements. A big area of low rate clusters was detected in the South-East of the plantation, in the vicinity of the big patch of degraded forest, which is also an area with quite a lot of traffic (access to the western part of the plantation).

- For Bangka_2: high rate clusters were detected around human settlements (workers and staff housing), but not only these. Low rate clusters were aggregated in the middle of the plantation.

Due to low sample size (2 to 4 observations per plantation), it was not possible to test for clustering for the Malay civet and the small-toothed palm civet. However, as shown on Figure 52(h), the four Malay civets observations were located along the boundary of the plantation only, nearby a forest patch and/or a shrubby swamp area. For the small-toothed palm civet, our results Figure 52(f) did not indicate any obvious pattern of spatial distribution which may be linked to landscape or habitat type.
(a) Small carnivore community (including domestic/feral cats)

Figure 53: Spatial distribution of small carnivore observations (faeces observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
(b) Small carnivore community (including domestic/feral cats)

**Legend:**
- river
- forest or forest like
- tree plantation
- oil palm
- mosaic_2
- mosaic_1
- shrub
- savannah
- mining
- human settlement
- human various
- swamp
- primary road
- secondary road
- small carnivore observation

**Figure 52:** Spatial distribution of small carnivore observations (spotlight observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
**Figure 52:** Spatial distribution of small carnivore observations (spotlight observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
Figure 52: Spatial distribution of small carnivore observations (spotlight observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
Figure 52: Spatial distribution of small carnivore observations (spotlight observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
Figure 52: Spatial distribution of small carnivore observations (spotlight observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
Figure 52: Spatial distribution of small carnivore observations (spotlight observations) in Riau and Bangka plantation; observations for which clusters were not detected. Routes surveyed are colored in white. Black filled circles represent observations, with diameter proportional to sample size.
IV.3.2. Euclidian distance to selected habitat

Detailed results of analysis for each focal habitat are presented next pages. Due to very low sample size (only 2 to 4 observations/plantation), results for the Malay civet and the small-toothed palm civet should be treated with much caution, and will therefore not be mentionned below.

- **Effect of forest habitat**

We predicted that forest habitat would have an attractive effect on the distribution of wild small carnivore observations within the oil palm habitat. At species level (observations yield by spotlight counts), our results supported this prediction only for the common palm civet in Riau_1. For other plantations and for the leopard cat, observations appeared to be distributed at random in relation to distance to forest habitat. For the domestic/feral cat, spotlight observations appeared to be distributed at random in relation to distance to forest habitat, as predicted. Regarding observations at community level for the whole small carnivore community (including domestic/feral cat), yielded by faeces counts, we detected an attractive effect of forest habitat on all plantations except Riau_2. Whereas with spotlight counts, we failed to detect any attractive effect of forest habitat on wild small carnivore community.

- **Effect of oil palm habitat**

We predicted that wild small carnivore observations would be less encountered within the center of the oil palm habitat, i.e that oil palm edge would have an attractive effect on the distribution of wild small carnivore observations within the oil palm habitat. At species level (observations yielded by spotlight counts), our results did not support this prediction, either for the leopard cat or for the common palm civet. Results at community level for wild small carnivores observed during spotlight survey did not support our prediction either. Regarding observations at the community level yielded by faeces counts (for the whole small carnivore community, including domestic/feral cat), we detected an attractive effect of oil palm edge only in Riau_1. For all other plantations, small carnivore observations were randomly distributed within the oil palm habitat. Concerning domestic/feral cats, we detected an attractive effect of oil palm edge habitat on the distribution of spotlight observations for Riau_2 and Bangka_1.

- **Effect of human settlements**

We predicted that human settlements would have a repulsive effect on the distribution of wild small carnivore observations within the oil palm habitat. This was supported by our results on spotlight counts, at community level only in Riau. At species level (spotlight counts), we detected a repulsive effect of human settlements for leopard cat on all plantations, and for the common palm civet only in Riau_2. Elsewhere, we could not reject the null hypothesis that observations were at random. As predicted, we detected an attractive effect of human settlements for domestic/feral cats spotlight observations.
Regarding observations at community level for the whole small carnivore community yielded by faeces counts, we could not reject the null hypothesis that observations were at random with regards to distance from human settlements.

The maximum distance from forest habitat at which an observation was made, considering the four plantations, was 6.6 km, 6.4 km, 3.8 km, 2.6 km, and 6.6 km for the leopard cat, the common palm civet, the small-toothed palm civet, the Malay civet and the domestic/feral cat respectively (spotlight observation). From the oil palm edge, it was 2.2 km, 2 km, 0.8 km, 0.3 km and 5.8 km for respective species. For minimum distance from any human settlement, results were 0.1 km, 0.1 km, 0.8 km, and 1.7 km, for the leopard cat, the common palm civet, the small-toothed palm civet, and the Malay civet respectively. Domestic/feral cats were also observed within human settlements.
Table 22: Results of analysis for distance to forest habitat of small carnivore observations. Analyses are based on Euclidian distances and investigated respectively mean distance (a)(b), and maximum distance to focal habitat (c). Results are presented (a) at the community level and (b) & (c) at the species level, including the domestic/feral cat. NA: Not applicable. In (a) & (b), cases for which H0 was rejected, i.e. for which H1 was likely, are in bold.

<table>
<thead>
<tr>
<th>(a)</th>
<th>Mean distance to forest habitat</th>
<th>P-value</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Faeces counts</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small carnivore community</td>
<td><strong>Riau_1</strong></td>
<td>&lt;1E-04</td>
<td>We detected an attractive effect of forest like habitat on small carnivores’ faeces distribution for Riau_1, Bangka_1 et Bangka_2 plantations, but not for Riau_2</td>
</tr>
<tr>
<td></td>
<td><strong>Riau_1</strong></td>
<td>0.054</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_1</strong></td>
<td>0.026</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_2</strong></td>
<td>0.041</td>
<td></td>
</tr>
<tr>
<td>Wild small carnivore community</td>
<td><strong>Riau_1</strong></td>
<td>0.164</td>
<td>We did not detect any attractive effect of forest like habitat on the distribution of wild small carnivore spotlight observations</td>
</tr>
<tr>
<td></td>
<td><strong>Riau_1</strong></td>
<td>0.164</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_1</strong></td>
<td>0.432</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_2</strong></td>
<td>0.190</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b)</th>
<th>Mean distance to forest habitat (spotlight counts)</th>
<th>P-value</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leopard cat</td>
<td><strong>Riau_1</strong></td>
<td>0.883</td>
<td>We did not detect any attractive effect of forest like habitat on the distribution of the leopard cat spotlight observations</td>
</tr>
<tr>
<td></td>
<td><strong>Riau_2</strong></td>
<td>0.414</td>
<td></td>
</tr>
<tr>
<td>Common palm civet</td>
<td><strong>Riau_1</strong></td>
<td>0.003</td>
<td>We detected an attractive effect of forest like habitat on the distribution of the common palm civet spotlight observations, only for Riau_1</td>
</tr>
<tr>
<td></td>
<td><strong>Riau_2</strong></td>
<td>0.294</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_1</strong></td>
<td>0.699</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_2</strong></td>
<td>0.082</td>
<td></td>
</tr>
<tr>
<td>Malay civet</td>
<td><strong>Bangka_2</strong></td>
<td>0.917</td>
<td>We did not detect any attractive effect of forest like habitat on the distribution of the Malay civet spotlight observations</td>
</tr>
<tr>
<td>Small-toothed palm civet</td>
<td><strong>Bangka_1</strong></td>
<td>0.94</td>
<td>We did not detect any attractive effect of forest like habitat on the distribution of the small-toothed palm civet spotlight observations</td>
</tr>
<tr>
<td>Domestic or feral cat</td>
<td><strong>Riau_1</strong></td>
<td>0.231</td>
<td>We did not detect any attractive effect of forest like habitat on the distribution of domestic or feral cat spotlight observations</td>
</tr>
<tr>
<td></td>
<td><strong>Riau_2</strong></td>
<td>0.279</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_1</strong></td>
<td>0.49</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Bangka_2</strong></td>
<td>0.532</td>
<td></td>
</tr>
</tbody>
</table>

| (c) | Maximum distance to forest habitat (spotlight counts) | | | |
|-----|-------------------------------------------------|--------|------|------|------|
| Leopard cat | Common palm civet | Malay civet | Small-toothed palm civet | Domestic or feral cat |
| Riau_1 | 6.6 km | 6.4 km | NA | 3.8 km | 6.6 km |
| Riau_2 | 3.7 km | 4.0 km | 0.3 km | NA | 3.3 km |
| Bangka_1 | NA | 2.5 km | 0.2 km | 1.8 km | 1.9 km |
| Bangka_2 | NA | 1.6 km | 2.6 km | NA | 3.9 km |
Table 23: Results of analysis for distance to oil palm edge of small carnivore observations. Analyses are based on Euclidian distances and investigated respectively mean distance (a)(b), and maximum distance to focal habitat (c). Results are presented (a) at the community level and (b) & (c) at the species level, including the domestic/feral cat. NA: Not applicable. In (a) & (b), cases for which H0 was rejected, i.e. for which H1 was likely, are in bold.

<table>
<thead>
<tr>
<th></th>
<th>Mean distance to oil palm edge</th>
<th>P-value</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Faeces counts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>Riau_1</td>
<td>0.045</td>
<td>We detected an attractive effect of oil palm edge habitat on small carnivores’ faeces distribution only for Riau_1, and not for Bangka_1, Bangka_2 nor Riau_2</td>
</tr>
<tr>
<td>carnivore</td>
<td>Riau_2</td>
<td>0.201</td>
<td></td>
</tr>
<tr>
<td>community</td>
<td>Bangka_1</td>
<td>0.344</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>0.062</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spotlight counts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild small</td>
<td>Riau_1</td>
<td>0.808</td>
<td>We did not detect any attractive effect of oil palm edge habitat on the distribution of wild small carnivore spotlight observations</td>
</tr>
<tr>
<td>carnivore</td>
<td>Riau_2</td>
<td>0.537</td>
<td></td>
</tr>
<tr>
<td>community</td>
<td>Bangka_1</td>
<td>0.069</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>0.317</td>
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<table>
<thead>
<tr>
<th>(b)</th>
<th>Mean distance to oil palm edge (spotlight counts)</th>
<th>P-value</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leopard cat</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Riau_1</td>
<td>0.973</td>
<td>We did not detect any attractive effect of oil palm edge habitat on the distribution of the leopard cat spotlight observations</td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.651</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Common palm civet</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Riau_1</td>
<td>0.175</td>
<td>We did not detect any attractive effect of oil palm edge habitat on the distribution of the common palm civet spotlight observations</td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.373</td>
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<tr>
<td></td>
<td>Bangka_1</td>
<td>0.207</td>
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<tr>
<td></td>
<td>Bangka_2</td>
<td>0.304</td>
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<tr>
<td></td>
<td>Malay civet</td>
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<td></td>
<td>Bangka_2</td>
<td>0.288</td>
<td>We did not detect any attractive effect of oil palm edge habitat on the distribution of the Malay civet spotlight observations</td>
</tr>
<tr>
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</tr>
<tr>
<td></td>
<td>Small-toothed palm civet</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_1</td>
<td>0.723</td>
<td>We did not detect any attractive effect of oil palm edge habitat on the distribution of the small-toothed palm civet spotlight observations</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td>Domestic or feral cat</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Riau_1</td>
<td>0.291</td>
<td>We detected an attractive effect of oil palm edge habitat on the distribution of domestic/feral cat spotlight observations only for Riau_2 and Bangka_1</td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.016</td>
<td></td>
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<tr>
<td></td>
<td>Bangka_1</td>
<td>0.008</td>
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<tr>
<td></td>
<td>Bangka_2</td>
<td>0.434</td>
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<table>
<thead>
<tr>
<th>(c)</th>
<th>Maximum distance to oil palm edge (spotlight counts)</th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Leopard cat</td>
<td></td>
<td>Common palm civet</td>
<td>Malay civet</td>
<td>Small-toothed palm civet</td>
</tr>
<tr>
<td></td>
<td>Riau_1</td>
<td>2.2 km</td>
<td>2 km</td>
<td>NA</td>
<td>0.8 km</td>
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<tr>
<td></td>
<td>Riau_2</td>
<td>2.1 km</td>
<td>1.7 km</td>
<td>0.3 km</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Bangka_1</td>
<td>NA</td>
<td>0.8 km</td>
<td>0.05 km</td>
<td>0.8 km</td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>NA</td>
<td>0.4 km</td>
<td>0.07 km</td>
<td>NA</td>
</tr>
</tbody>
</table>
Table 24: Results of analysis for distance to human settlements of small carnivore observations. Analyses are based on Euclidian distances and investigated respectively mean distance (a)(b), and maximum distance to focal habitat (c). Results are presented (a) at the community level and (b) & (c) at the species level, including the domestic/feral cat. NA: Not applicable. In (a) & (b), cases for which H0 was rejected, i.e. for which H1 was likely, are in bold.

(a) & (b) Mean distance to human settlements

<table>
<thead>
<tr>
<th>Faeces counts</th>
<th>Mean distance to human settlements</th>
<th>P-value</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small carnivore community</td>
<td>Riau_1</td>
<td>0.883</td>
<td>We did not detect any repulsive effect of human settlements on the distribution of wild small carnivore spotlight observations</td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.723</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_1</td>
<td>0.209</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>0.279</td>
<td></td>
</tr>
<tr>
<td>Wild small carnivore community</td>
<td>Riau_1</td>
<td>0.006</td>
<td>We detected a repulsive effect of human settlements on small carnivores’ faeces distribution</td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_1</td>
<td>0.959</td>
<td>in Riau plantations, but not in Bangka ones.</td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>0.178</td>
<td></td>
</tr>
</tbody>
</table>

(b) Mean distance to human settlements (spotlight counts)

<table>
<thead>
<tr>
<th>Leopard cat</th>
<th>Riau_1</th>
<th>0.001</th>
<th>We detected a repulsive effect of human settlements on the distribution of the leopard cat spotlight observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common palm civet</td>
<td>Riau_1</td>
<td>0.259</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.011</td>
<td>We detected a repulsive effect of human settlements on the distribution of common palm civet spotlight observations only for Riau_2</td>
</tr>
<tr>
<td></td>
<td>Bangka_1</td>
<td>0.361</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>0.725</td>
<td></td>
</tr>
<tr>
<td>Malay civet</td>
<td>Bangka_2</td>
<td>0.417</td>
<td>We detected a repulsive effect of human settlements on the distribution of the Malay civet spotlight observations only in Bangka_1</td>
</tr>
<tr>
<td>Small-toothed palm civet</td>
<td>Bangka_1</td>
<td>0.674</td>
<td>We did not detect any repulsive effect of human settlements on the distribution of the small-toothed palm civet spotlight observations</td>
</tr>
<tr>
<td>Domestic or feral cat</td>
<td>Riau_1</td>
<td>0.019</td>
<td>We detected an attractive effect of human settlements on the distribution of domestic/feral cat spotlight observations</td>
</tr>
<tr>
<td></td>
<td>Riau_2</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_1</td>
<td>0.018</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bangka_2</td>
<td>0.007</td>
<td></td>
</tr>
</tbody>
</table>

(c) Minimum distance to human settlements (spotlight counts)

<table>
<thead>
<tr>
<th>Minimum distance to human settlements (spotlight counts)</th>
<th>Leopard cat</th>
<th>Common palm civet</th>
<th>Malay civet</th>
<th>Small-toothed palm civet</th>
<th>Domestic or feral cat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riau_1</td>
<td>0.1 km</td>
<td>0.1 km</td>
<td>NA</td>
<td>0.8 km</td>
<td>0.03 km</td>
</tr>
<tr>
<td>Riau_2</td>
<td>0.1 km</td>
<td>0.6 km</td>
<td>1.7 km</td>
<td>NA</td>
<td>0.03 km</td>
</tr>
<tr>
<td>Bangka_1</td>
<td>NA</td>
<td>0.4 km</td>
<td>1.8 km</td>
<td>0.8 km</td>
<td>0.2 km</td>
</tr>
<tr>
<td>Bangka_2</td>
<td>NA</td>
<td>1 km</td>
<td>1.7 km</td>
<td>NA</td>
<td>≈ 0 km</td>
</tr>
</tbody>
</table>
IV.4. DISCUSSION

- **About methodological biases**

Both faeces counts and spotlight counts are prone to various sources of bias, notably in relation to various detection probabilities, as detailed in section III.2.1. For example, a lower detection probability might occur in areas with winding roads, compared to straight roads on which small carnivores may be detected from far away.

In addition, variations due to the season and year of sampling might occur, due to heterogeneous landscapes and practices that may provide opportunities for spatio-temporal variations in abundance and occupancy of carnivores in the various habitats, as mentioned in section III.2.1.

Our results should be interpreted with caution also and above all because of bias linked to methods of analysis.

Indeed, by using the Euclidian shortest distance we did not take into account the permeability of the various habitats and landscape features that facilitates or impedes to various degrees the movements of small carnivores among source patches (Taylor *et al.*, 1993; Tischendorf and Fahrig, 2000; Kindlmann and Burel, 2008). For example, the large river such as the one in Riau_2 which, in some places, separates the oil palm plantation from the connected forest patch, does represent an impassable barrier for some species; and crossing the very busy tarmac road in the middle of Riau_2 represents a “cost”. We therefore suggest, for future investigation, the use of other more complex methods taking into account landscape connectivity and effective distance, such as the those based on circuit theory or least cost path distance (Urban and Keitt, 2001; Adriaensen *et al.*, 2003; McRae *et al.*, 2008; Rayfield *et al.*, 2010).

In addition, for cluster detection, the spatial scanning window used with Satscan was a circle, which does not correspond to any structural or functional landscape unit (linked for example to topography, ecological corridor or other landscape features). Ellipse may also be used with Satscan, but more complex forms could not. In the future, when ecologically based hypotheses of space-used by small carnivores will be clearer, it might be interesting to work on space partitioning with ecological realities taken into account.

We may also question the statistical power of tests used and representativeness of results, notably for very small sample size such as for the Malay civet or the small-toothed palm civet (1 to 4 observations per plantation, see Table 20).

- **Trends in spatial distribution at species level, from spotlight observations**

**Leopard cat**

For the leopard cat, no homogeneous spatial pattern may be derived from our visual analysis of the distribution of clusters from spotlight observations: In Riau_2, more observations than random (high rate clusters) were detected nearby forest areas, but in Riau_1 fewer observations than random (low rate clusters) were observed nearby the big swamp forest area, as well as in the central part of the estate and/or nearby some human settlements. From statistical analysis based on Euclidian distance, we did not detect any attractive effect of forest habitat or oil palm edge habitat on the distribution of leopard cat observations during spotlight counts; and the leopard cat may be found as far as 6.6 km from the nearest forest patch. The non-attractive effect of oil palm edge or forest
habitat was confirmed by results of camera trapping carried out in both Riau plantations (Jennings et al., 2015): leopard cats were recorded deep within the plantation -up to 3.6 km from the edge-, and neither covariates represented by the distance to the nearest edge of an extensive area of lowland forest, and the distance to the nearest edge of the oil palm habitat, affected occupancy of the species within the oil palm habitat. Radio tracking of leopard cats in oil palm landscapes in Sabah Malaysia revealed that they significantly preferred the oil palm habitat over logged and secondary forest (Rajaratnam et al., 2007). In other research carried out in Sabah, two radio-collared leopard cat captured and released in dense secondary forest travelled over 25 km to a completely new home range mainly consisting of an oil palm plantation; they were then frequently recorded in this plantation by camera trapping (Ross, 2009b). The fact that the oil palm habitat may be more attractive than forested habitat, at least at night, is hardly surprising. Prey availability is known as a key factor controlling carnivore occurrence probability, density and distribution (Carbone and Gittleman, 2002; Burton et al., 2012). This was confirmed for the leopard cat: predictive modelling in Eastern Himalaya indicated that high rodent abundance, as well as tree cover, were the best predictors for the occupancy of the leopard cat (Bashir et al., 2014), and, in Thailand, Chutipong et al. (2013) reported that the leopard cat occurrence and abundance was correlated with abundance of murid rodents. Therefore, as suggested by Scott and Gemita (2004), the preference of the leopard cats for oil palm is probably due to the higher abundance of their primary preys, which are murid rodents and notably rats, in this habitat. Rajaratnam et al. (2007) suggest that preference of leopard cat for oil palm habitat is related to prey ‘catchability’, rather than high prey density alone: visibility and ease of movement in this habitat (sparse understorey, vast roads network) increasing the leopard cat hunting success. Moreover, the leopard cat is small enough to shelter in the low-lying foliage of the understorey for resting or hiding (Maddox et al., 2007), thereby enhancing the desirability of the oil palm habitat for this species. In addition, the nocturnal peak of activity for leopard cats has been shown to coincide with the activity pattern of their main prey, thereby maximizing encounter rates when the prey is active (Zieliński, 1988; Lynam et al., 2013; Bashir et al., 2014). During our spotlight counts, several individuals were observed with a small rodent, presumably a rat, in their mouth. To conclude, our results from spotlight counts, and knowledge about leopard cat feeding habits from our literature review, support the idea that leopard cats can actively hunt in oil palm plantations at night, and that this species may be found deep in the oil palm habitat.

Some low rate clusters were located nearby to human settlements, and we detected a repulsive effect of human settlements on leopard cat; however leopard cats may be observed close to human settlements (minimum distance to human settlements was about 100 meters). From literature review, leopard cats seems quite tolerant to human presence: they were found to come to the perimeter of villages (Rode-Margono et al., 2014), and occupancy modelling by camera trapping showed that the detection probability of the leopard cat was not influenced by human presence at the camera site (Bashir et al., 2014).

**Common palm civet**

In Riau_1 plantation, we detected two high rate clusters of observations located nearby the conservation area; however, no clusters of observations were detected in Bangka plantations, and in Riau_2 the only cluster, a high rate one, was not located close to a forest patch. From our analysis, the common palm civet may be found 6.4 km away from the nearest forest patch: and we did not detect any attractive effect of forest habitat or oil palm edge habitat on the distribution of common palm civet observations during spotlight counts, except in Riau_1. These results were confirmed by
camera trapping carried out in both Riau plantations (Jennings et al., 2015): neither distance to the nearest edge of an extensive area of lowland forest, nor distance to the nearest edge of the oil palm habitat affected the occupancy of the common palm civet within the oil palm habitat; and the species was recorded deep within the plantation (3.6 km from the edge). This is not surprising as the common palm civet is adapted to a wide range of habitats, including cultivated areas (Holden, 2006; Francis, 2008; Jennings and Veron, 2009; Chutipong et al., 2013), and even shows preference toward non-forest habitats (Stuebing and Gasis, 1989; Kalle et al., 2013; Rode-Margono et al., 2014). Its diet is mainly frugivorous and density and distribution of fruiting trees highly influences its spacing behavior (Joshi et al., 1995; Chutipong et al., 2013). In oil palm plantations, oil palm fruits constitute abundant food resources for the common palm civet. Nakashima et al. (2013) showed that, in an oil palm landscape, use of space by common palm civets is mainly determined by fruit availability and their home range include oil palm plantations where they forage at night. Our results, combined with knowledge on the diet of the species, support the fact that common palm civets actively use oil palm habitats for foraging at night, and that this species may be found deep in the oil palm habitat.

Our analysis showed a repulsive effect of human settlements on the distribution of the common palm civet for only one of the plantation out of the four. This is not surprising as common palm civets are highly tolerant to human activities and are often seen in and around human settlements (Francis, 2008; Jennings and Veron, 2009; Chua et al., 2012; Kalle et al., 2013; Rode-Margono et al., 2014; Spaan et al., 2014), presumably attracted by fruiting trees.

**Small-toothed palm civet**

For the small-toothed palm civet, our analysis did not reveal any specific pattern of spatial distribution, however, our results should be considered with caution due to the very low sample size. Though the small-toothed palm civet is widespread and often locally common in mainland Southeast Asia, Borneo and Sumatra (Corbet and Hill, 1992; Duckworth et al., 2008b; Eaton et al., 2010), very little is known on its ecology. Primary semi-evergreen forest, regenerated forest or unlogged forests have been reported as their preferred habitats (Syakirah et al., 2000; Jennings and Veron, 2009), however, the effect of logging on this species remains unclear (Meijaard and Sheil, 2008), as in Borneo sighting frequency was higher in logged forest than in primary forest (Heeydon and Bullow, 1996). Moreover, this species was already recorded in plantations in Indonesia and Malaysia: in rubber *Hevea brasiliensis* and in cocoa *Theobroma cacao* plantations (Harrison (1968); cited by Eaton et al. (2010)), as well as in coconut *Cocos nucifera* plantations (Miller (1901); cited by Willcox et al. (2012)). More recently, Eaton et al. (2010) reported the species to be present in highly modified habitats. To our knowledge, the present study is the first record of small-toothed palm civet being found within oil palm habitat. This might be at least partly due to the fact that most previous surveys in oil palm habitats used ground-level camera traps rather than spotlight counts, the latest method being more appropriate for arboreal species such as the small-toothed palm civet (Jennings and Veron, 2009).

**Malay civet**

For the Malay civet, the four observations made were all located at the boundary of the oil palm plantation, at the edge of the oil palm habitat (for two of them) and/or (for all of them) nearby a forest patch or a shrubby non-planted area. In addition to our survey observations, we made an incidental sighting of Malay civet, also along the oil palm habitat edge (in Bangka_2). The locations of our observations, at the interface of oil palm and non-oil palm habitat, are consistent with the
results of Jennings et al. (2015) who found that occupancy of the Malay civets camera-trapped in Riau_2 was influenced by distance from the edge of the oil palm habitat. Many other authors have reported the occurrence of the Malay civet in agricultural lands or plantations (Giman et al., 2007; Francis, 2008; Eng, 2011). Results of Eng (2011) indicated that this species uses the interface between Acacia plantations and forest remnants frequently. Studying the habitat use of the Malay civet in an oil palm landscape in Malaysia and comparing it with other studies, Jennings et al. (2010, 2011) reported that this species was sometimes found in plantations during the night to forage for food, but did not venture far from forested habitat, where they find more appropriate rest sites. From our results, the Malay civet was found only in the three plantations where the surrounding landscape is quite heterogeneous (Riau_2 and both Bangka plantations) and includes more forest or forest like areas. The species was not recorded in Riau_1 where the landscape is more homogenous and highly dominated by oil palm. Jennings et al. (2015) also reported that the Malay civet was camera-trapped in Riau_2 but not in Riau_1. Our results broadly support our hypothesis that forest habitat or oil palm edge may be attractive to the Malay civet, and that the ability of this species to survive in disturbed habitats might be influenced by the proximity of undisturbed habitats, as suggested by Colon (2002).

Domestic/feral cat

From statistical analysis based on Euclidean distance of observations, we detected an attractive effect of human settlements on the distribution of domestic/feral cats during spotlight counts, as predicted. Domestic cats are closely related to humans, and feral cats probably also forage in garbage (Watanabe et al., 2003). Our analysis of spotlight counts in Riau plantations also showed that more domestic/feral cats were observed (high rate clusters) near human settlements. However, in Bangka plantations, spatial distribution of clusters did not reveal such an obvious pattern (high rate clusters were not only detected near to human settlements), perhaps because in Bangka plantations feral cats were introduced within the oil palm habitat by plantation management, and thereby feral cats in Bangka might be less dependent on human settlements than domestic cats in Riau. Another hypothesis would be that, in Riau, domestic/feral cats are more restricted to human settlements surroundings, where competition with the leopard cat is less (as shown previously, leopard cats are globally less encountered nearby human settlements than in other parts of the oil palm habitat), whereas in Bangka plantations, because leopard cats are absent, domestic/feral cats may forage all throughout the oil palm habitat.

This issue of competition between species was raised previously on our discussion about the relative abundance of small carnivores species across plantations (III.2.1.). Coexistence of sympatric species is mediated by resource partitioning (Schoener, 1974), and competitive interactions among species have very important implications on carnivore abundance and distribution (Linnell and Strand, 2000). Competition for space and food resource is linked to carnivore morphology and body mass, feeding habits and foraging strategies, habitat preference, and/or difference in activity patterns (Rosenzweig, 1966; Palomares et al., 1996; Durant, 1998; de Almeida Jácomo et al., 2004; Romero-Muñoz et al., 2010). Partitioning and sharing of resources may explain patterns of spatial distribution observed within the oil palm habitat, such as for the domestic cat and the leopard cat, which are phylogenetically similar and may therefore face serious competition with each other. Spatial overlap among leopard cat and others wild cats species was studied in Sumatra (Pusparini et al., 2014; Sunarto et al., 2015), but we found no literature investigating space partitioning between our species of interest.
• **Analysis at community level versus species level, and differences between results from spotlight and faeces counts**

Highlighting the frequently complex relationships between landscape heterogeneity and carnivore ecology, Burton et al. (2012) reported that heterogeneity in species’ responses to landscape features is to be expected, thereby leading to some inconsistency in aggregate response interpreted at the community level.

We found that results from faeces counts at community level for all small carnivores, including domestic/feral cats, were not always representative of the aggregate response from species level, considering community composition as described in section III.2.1.\(^4^3\). For example, at community level, we detected an attractive effect of forest habitat for three plantations (all except Riau_2), whereas this attraction effect was not detected at species level for any of the five species (leopard cat, common palm civet, Malay civet, small-toothed palm civet, domestic/feral cat) whatever the plantation, except for the common palm civet in Riau_1.

On the contrary, our results from spotlight observations for the wild small carnivore community are globally consistent with the results at species level as detailed previously: we did not detect any attractive effect of forest habitat, or oil palm edge on observation distributions, and we detected a repulsive effect of human settlement only in Riau plantations.

Inconsistency from distance to focal habitat analysis results as yielded by faeces for the small carnivore community (forest attraction in all cases except one) *versus* those yielded by night spot counts at species level (globally no forest attraction either for wild small carnivores or for domestic/feral cats) may also be explained by the sampling method and the species activity. Indeed, spotlight counts take into account only individuals ranging within the oil palm habitat during the night, whereas faeces include day and night ranging (faeces might also be emitted by individuals ranging in the oil palm habitat during the day). During daytime, wild small carnivores would preferably range nearby forest habitat or at the oil palm edge, as shown by Jennings et al. (2015) in Riau plantations for the leopard cat (87% of the daytime detections recorded ≤0.2 km from the edge of the oil palm). Others authors have shown or suggested that, even for species commonly found in oil palm plantations such as the common palm civet and the leopard cat, though the oil palm habitat may be more attractive for foraging at night, those species preferably retreated to adjacent forest habitat during the day, where they may find more appropriate rest or breeding sites (Rajaratnam *et al.*, 2007; Mohamed *et al.*, 2013; Nakashima *et al.*, 2013).

Therefore, our contrasting results from night spot counts and faeces counts support the hypothesis that, though the oil palm habitat may be compatible for some wild small carnivores, those species may still need forest habitats for their survival in oil palm landscapes.

• **Differences among plantations: could “attractiveness” of forest fragments be link to their rarity or distribution in the landscape?**

From our results, it seems that there would be a kind of gradation in the attractiveness of forested habitat for wild small carnivores, from more attractive in Riau_1; less attractive in Riau_2 and not attractive in Bangka. Indeed, in Bangka plantations, we did not detect any clusters for common

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\(^4^3\) For the wild small carnivores: leopard cat and common palm civet are dominant in Riau plantations; common palm civet is dominant in Bangka plantations. For all small carnivores: leopard cat and common palm civet are dominant in Riau plantations, domestic cat is dominant in Bangka plantations.
palm civet (which is the most common wild small carnivore observed) nor did we for wild small carnivores at the community level; and individual observations for those two categories were widespread all over the plantations, without any obvious spatial pattern linked to habitat type or landscape. On the contrary, in Riau plantations, high rate clusters were detected for the wild small carnivore community and were located nearby the biggest forest habitats in the landscape (either the conservation area for Riau_1 or the riparian corridor for Riau_2). For the common palm civet, clusters detected in Riau_1 were located nearby the conservation area, whereas in Riau_2 the only high rate cluster detected was not located nearby a forest area.

We raise the hypothesis that the “attractiveness” of forest fragments would be proportional to their rarity and distribution in the landscape; in other worlds, more the forest habitat is clustered, more wild small carnivores are themselves clustered around these habitats. The opportunities for dispersion of wild small carnivores within and around the estate would be higher in Bangka than in Riau plantations, thanks to a mosaic landscape in Bangka including more forest habitats, and notably scattered fragments of forest like habitat (“enclaves” of jungle rubber agroforests) within the oil palm plantation (as described in section II.1. on landscape configuration), which may act as refuges or step zones. In Bangka_1 and Bangka_2 plantations, the total forest habitat within a 15km around the plantation represented 12 and 15% respectively, whereas it represented only 2 % in Riau_1 and 3.2 % in Riau_2 (Table 3 section II.1.1); and the mean distance of each point of the plantation to forest habitat was of 1574 m, 1490 m, 405 m and 546 m for Riau_1, Riau_2, Bangka_1 and Bangka_2 plantations respectively. In Riau_2, there is no forest fragment retained within the plantation, but two forest fragments of more than 200 ha are lying on its border. In Riau_1, oil palm habitat is highly dominant in the landscape and the only forest fragment in the vicinity is the conservation area (about 112 ha). Thereby, in Riau_1, the attraction of the only forest fragment on wild small carnivores would be high, with small carnivores ranging not far from this habitat. In contrast, wild small carnivores would be widespread within the plantations in Bangka as they may use the many forest fragments within or surrounding the plantation and range from one to the other.
In Brief:
From our spotlight counts, the common palm civet and the leopard cat may be found deep in
the oil palm habitat and we did not detect an attractive effect of forest habitat or oil palm
edge. Our results combined with knowledge about their diet from our literature review,
support the fact that the leopard cat and the common palm civet would preferably forage in
oil palm plantations at night. For the Malay civet, our results broadly support the hypothesis
that, though this species may use the oil palm habitat, it did not venture far from forest
habitat or oil palm edge. For the small-toothed palm civet, our analysis did not reveal any
specific pattern of spatial distribution within the oil palm habitat. However, our results for
those two last species should be considered with caution, due to the very low sample size. For
the domestic/feral cats, our results support the prediction that human settlements have an
attractive effect on this species, except in Bangka plantations where spatial distribution of
clusters did not reveal such an obvious pattern.
Our analysis on distance to focal habitat for faeces counts, at community level (entire small
carnivore community, including small domestic/feral cats) showed an attractive effect of
forest habitat, which is not the case for almost all spotlight counts observations. These
contrasting results from spotlight and faeces counts support the hypothesis that, though the
oil palm habitat may be habitable for some wild small carnivores, where they supposedly
forage at night, these species may still need forest habitats for their survival in oil palm
landscape.
Overall, our results confirm and strengthen those of others ecological studies on small
carnivore habitat preferences, and, to our knowledge, our study reported the first record of
the small-toothed palm civet within an oil palm habitat.
Our analysis also revealed differences among Riau and Bangka plantations: it seems that
there would be a kind of gradation in the attractiveness of forest habitat for wild small
carnivores, from more attractive in Riau_1; less attractive in Riau_2 and not attractive in
Bangka. We hypothesize that it may be linked to landscape configuration, and notably to the
relative abundance of forest fragments within and in the surroundings of each plantation:
wild small carnivores were more widespread within the plantation in Bangka as they may use
the numerous forest fragments within and surrounding the plantation as step zones, whereas,
in Riau plantations, forest habitat was more scare and clustered, notably in Riau_1 (only one
big forest fragment), and thereby small carnivores would not range very far from it.
V. GENERAL DISCUSSION AND CONCLUSION

In this last section, we will first recap the questions raised in the introduction and point out the original findings in this study. Then we will synthesize our main findings with existing studies and point out any limitations. Finally, we will discuss management implications of this work and identify research needs.

V.1. QUESTIONS RAISED AND ANSWERS TENTATIVELY GIVEN: DISCUSSION ON STUDY INPUTS AND LIMITS

V.1.1. Questions raised and originality of the present study

In this study, we took interest in two contrasted systems, Riau and Bangka, where rodent damage levels, and thus presumably rat population levels, were different: in Riau plantations rodent damage was maintained at an acceptable level, whereas in Bangka plantations a higher level of rodent damage persisted.

Rodent population dynamics may be influenced by many factors, including extrinsic ones such as food supply, predation and landscape (Krebs, 2013). Consequently, the first part of the study had its origin in the general question: what factors could contribute to explaining rat population limitation in Riau plantations compared to Bangka? More precisely, which assumption(s) could be made to explain such differences in rat abundance in both situations, with respect to small mammal community, agricultural practices, landscape characteristics, and the predator community?

As suggested our results in the first part of this study, small carnivores potentially contribute to rodent control through predation. However, most species populations are severely impacted by deforestation and habitat fragmentation (Prugh et al., 2008; Crooks et al., 2011); moreover, their ecology and notably their habitat use remains poorly understood (Holden, 2006; Duckworth et al., 2014). Thus, both from a conservation and a production point of view, it is necessary to assess which landscape configuration may enhance small carnivore persistence within oil palm plantations.

With this in mind, the second part of the study investigated the spatial distribution of small carnivores within the oil palm habitat, for a better understanding of small carnivore habitat use in oil palm landscapes.

The main questions raised in both parts of the study, and their links, are synthetized in Figure 14 in the general introduction.

First part of the study: what may contribute to explain rat population limitation in Riau plantations compared to Bangka?

We first needed to confirm that rat populations were different among our two systems, i.e. Riau versus Bangka. the question raised (section II) was the following: What are the differences in rat population levels and trends between oil palm plantations? As we did not have time to monitor rat populations, we used an indirect method, using existing data on rodent damage (routinely collected by PTSmart plantation staff) as a broad indicator of the relative size of the rat population.
We also characterized the small mammal community within the plantations. Questions raised were: what is/are the dominant small mammal species within the oil palm habitat, and what are the main characteristics of those species that may affect population density or an estimation of population density? In addition, because it may influence the spatial distribution of small carnivores, an issue analyzed in the second part of the study, we also raised the following question: does small mammal diversity exhibit a cline from the interior of the oil palm plantation to the fringes of the neighboring habitats?

Many factors potentially affect rodent population dynamics, including landscape configuration, habitat features and agricultural practices (Delattre et al., 1992; Lidicker, 2000; Morilhat et al., 2007; Delattre and Giraudoux, 2009; Krebs, 2013; Berthier et al., 2014). Therefore, we first compared our study sites in regards to their landscape and agro-environmental characteristics (section II). Questions raised were:

- What are the main differences in landscape configurations between Riau and Bangka (large landscape context: provincial and regional) and between plantations (within and surroundings of each plantation)?
- What are the main characteristics of the oil palm habitat in our study sites, and is this habitat different or homogeneous within and among the plantations?
- What are the differences in rodent pest management practices between the two systems? In particular, we aimed at investigating whether barn owl population level was similar in Riau and Bangka, and to characterize rodenticide use in the two systems.

Predation has often been reported as a fundamental cause of regulation, in association with food resources (Krebs, 2013). Food resource is seemingly not a limiting factor for rat growth in oil palm plantations, as reported in the literature (Lenton, 1984; Wood and Liau, 1984b), and as assumed for our study sites (see section II.1.2.). Here predation has been hypothesized as a major factor in determining the small mammal population, which we needed to investigate. We knew that barn owls were present in the two systems, but nothing was known about the small carnivore community. Consequently, questions raised were linked to the hypothesis inspired from Krebs (2013), i.e. the predation-as-limitation hypothesis, stating that a particular suit of predators, here small carnivores and barn owls, limits rat population density –here R. tiomanicus or R.tanezumi- so that their density averaged over a few years will be lower if predators are present/abundant -here in Riau plantations comparatively to Bangka. To explore the potential differential importance of predation among sites, we investigated the diet (and/or food intake and/or selective predation), as well as the abundance (and/or diversity) of barn owls and the small carnivore community (section III).

Questions raised for the barn owl population were:

- Are barn owls less abundant in Bangka plantations comparatively to Riau?
- Does rodent prey contribute a different proportion of the diet for barn owls in Bangka plantations compared to Riau?
- Are there and, if yes, what are the differences in barn owl breeding season(s) in Bangka compared to Riau, which, for a given barn owl population density, may explain a lower food intake in Bangka?
- How could we assess selective predation by the barn owl in relation to rat size or age?

Questions raised for the small carnivore community were:
Is the small carnivore community more abundant and more diverse in Riau plantations compared to Bangka?

Does rodent prey contribute a different proportion of the diet for the small carnivore community in Bangka plantations compared to Riau?

Second part of the study: what about spatial distribution of small carnivores within the oil palm habitat?

It is acknowledged that spatial heterogeneity affects ecological systems (Wiens, 1999), and that heterogeneity and connectivity are key concepts for biodiversity conservation and management in agricultural landscapes (Benton et al., 2003; Fahrig et al., 2011; Burel et al., 2013b), notably in relation to pest control (Tscharntke et al., 2005; Bianchi et al., 2006). Moreover, many studies investigated factors influencing the occurrence probability, density and/or distribution of small carnivores in East Asia or in the tropics, as reported in Table 22.

Table 25: Studies investigating factors influencing the occurrence probability, density and/or distribution of small carnivores in East Asia and in the tropics.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Taxa studied</th>
<th>Landscape type</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yasuda and Tsuyuki (2012)</td>
<td>mammalian communities</td>
<td>East Kalimantan</td>
<td></td>
</tr>
<tr>
<td>Mudappa et al. (2007)</td>
<td>small carnivores</td>
<td>fragmented forest landscape</td>
<td>India</td>
</tr>
<tr>
<td>Chutipong et al. (2013)</td>
<td>small carnivores</td>
<td>mosaic forest types</td>
<td>Thailand</td>
</tr>
<tr>
<td>Kalle et al. (2013)</td>
<td>small carnivores</td>
<td>forest reserve</td>
<td>India</td>
</tr>
<tr>
<td>Rode-Margono et al. (2014)</td>
<td>small carnivores</td>
<td>throughout Java</td>
<td></td>
</tr>
<tr>
<td>Sunarto et al. (2015)</td>
<td>cats</td>
<td>Central Sumatra</td>
<td></td>
</tr>
<tr>
<td>Watanabe (2009)</td>
<td>leopard cat</td>
<td>East Asian islands</td>
<td></td>
</tr>
<tr>
<td>Oh et al. (2010)</td>
<td>leopard cat</td>
<td>suburban environment</td>
<td>Japan</td>
</tr>
<tr>
<td>Mohamed et al. (2013)</td>
<td>leopard cat</td>
<td>commercial forest reserves</td>
<td>Borneo</td>
</tr>
<tr>
<td>Bashir et al. (2014)</td>
<td>leopard cat</td>
<td>biosphere reserve</td>
<td>India</td>
</tr>
<tr>
<td>Lee et al. (2015)</td>
<td>leopard cat</td>
<td></td>
<td>South Korea</td>
</tr>
<tr>
<td>Nakashima et al. (2013)</td>
<td>common palm civet</td>
<td>oil palm landscape</td>
<td>Borneo</td>
</tr>
<tr>
<td>Wilting et al. (2010)</td>
<td>flat-head cat</td>
<td>heterogeneous landscape</td>
<td>South-East Asia</td>
</tr>
<tr>
<td>Ramesh and Downs (2014)</td>
<td>genet &amp; mongoose</td>
<td>urban environment</td>
<td>South Africa</td>
</tr>
<tr>
<td>Widdows et al. (2015)</td>
<td>genet</td>
<td></td>
<td>South Africa</td>
</tr>
</tbody>
</table>

However, very limited studies took interest specifically in the distribution of small carnivores within oil palm plantations, with a view of providing management recommendations in order to enhance small carnivore persistence within oil palm plantations. Thus, in the second part of the study (section IV), we provided some insights into the spatial distribution of the small carnivore community within the oil palm habitat. Questions raised were:

- Is spatial distribution of observations homogenous or heterogeneous (existence of clusters of observations) within the oil palm habitat?
- Is spatial distribution of observations correlated to focal habitat such as forest, oil palm edge and human settlements?
- Are spatial patterns similar among plantations?

Originality of the study

This study is an original attempt to link barn owl population and the small carnivore community abundance and diet to rodent damage, within oil palm plantations, in various landscape contexts
(from a highly oil palm-dominated to a more diverse landscape) and management practices (heavy rodenticide use to no rodenticide). Although it is obviously not sufficient for understanding the role of both kinds of predators in the agroecosystems, it aims to improve our knowledge on the topic. It is also one of the first detailed studies taking interest in the distribution of small carnivores within the oil palm habitat (associated with a camera trap survey; see Jennings et al., 2015). Previous studies mainly focused on the occurrence of small carnivores within oil palm habitat in comparison to their occurrence in other habitats, but, to our knowledge, none have specifically investigated the distribution of small carnivores within the oil palm habitat, with the exception of Bateman et al. (2015) who examined variations in mammal numbers across a plantation in central Sumatra. Another originality is that our study sites were not adjacent or nearby extensive areas of continuous forest, on the contrary to almost all previous studies (e.g. studies in Borneo or in Jambi). Our results, at least in Riau, thereby give information about the persistence of small carnivores in such oil palm-dominated landscapes. These oil-palm dominated landscapes are becoming more and more common, and are likely to increase further (see section I.1.1.a), therefore our study have implications for future understanding of such agroecosystems.

In addition, most recent wildlife studies in oil palm landscapes use camera traps (see Table 1 in section I.3.3.). In the present study, we complemented an on-going camera trap survey in which we were associated (not in the scope of the present study; preliminary results are presented in Jennings et al., 2015) with two others methods: spotlight counts and faeces counts. To our knowledge, only one previous survey has combined these two methods to study small carnivore community occurrence and/or distribution in oil palm plantations (Scott and Gemita, 2004) and three have used either one or the other of the methods (Maddox et al., 2007: sign surveys; Gumal et al., 2014: walked spotlight transects; Bateman et al., 2015: walked day and night transects). Moreover, our results are based on a longer survey period and a greater survey effort than previous studies. We conducted surveys over three years, and, in total, we covered 3,003 km for spotlight counts and 478.44 km were walked for faeces collection. While, for example, Scott and Gemita (2004) conducted field surveys for only one year, covering 410 km and 11.5 km respectively for spotlight surveys and faeces collection; Bateman et al. (2015) covered about 670 km of pedestrian transects but it was not restricted only within the oil palm habitat. In addition, in the framework of our study, about 3,200 barn owl pellets, representative of diverse agroecological conditions found within the four studied oil palm plantations, were collected and dissected. To our knowledge, such an extensive survey on rat predators has never been carried out within oil palm plantations before.

V. 1.2. Synthesized results and discussion

After a brief point about the spatial scale issue, we will synthesize and discuss our results according to “packages” as defined in the questions-raised section.

Figure 53 to 57 are stemmed from Figure 14 in the general introduction and will progressively show the main results obtained.
A brief note about the spatial scale issue

Ecological processes (e.g. dispersal, predation, foraging) patterns and properties are scale dependent: they occurred at different spatial scales, and their effects and relative importance may change with the grain and extent of the landscape data considered (Turner et al., 1989; Bissonette, 1997; Schröder and Reuter, 2007; Fahrig et al., 2011; Smith et al., 2011). The fact that both local scale and landscape scale factors matter reinforces the need for a multi-scale approach to understanding the relationship between a species and its environment (Murray et al., 2008). In addition, given that most ecological processes and interactions related to mammals depend on scales much larger than a single habitat (as it is the case for predation), it is important to link spatial patterns and ecological processes at a landscape scale (Steffan-Dewenter et al., 2002). Consequently, in the present study, we broadly characterized the habitats and their configuration at a landscape scale, but we also focussed in on a finer description of the oil palm habitat. Moreover, assessment of abundance and diversity as well as spatial distribution was carried out at the stand scale (the oil palm habitat); and spatial distribution was not related to within habitat characteristics (e.g. to ground vegetation cover or height) but rather to the surrounding habitats (the extent of landscape data considered). However, though we took interest in the surrounding habitat in our analysis, we only assessed species abundance and distribution within the oil palm habitat; consequently this did not enable us to truly assess habitat preference and habitat use compared to other habitats, such as forest.
In addition to observation scales and scales of ecological phenomena, scales used in spatial statistical analysis should also be considered. Indeed, according to Dungan et al. (2002), “when scales of observation or analysis change, that is, when the unit size, shape, spacing or extent are altered, statistical results are expected to change.” For example, when identifying clusters of observations within the oil palm habitat, the shape of the spatial scanning windows used for statistical analysis was limited to a circle, which does not correspond to any structural or functional unit. A different window configuration, corresponding to a space partitioning better adapted to ecological realities, may have changed the results. However this could not be achieved with the software used, and we could not investigated for a more appropriate configuration due to time constraints.

V.1.2.a. Is rat damage and are rat populations different between plantations?

From our results (section II.2.2.), rodent damage within each region showed similar temporal patterns, and rodent damage levels in both Bangka plantations were globally higher than in Riau plantations.

Results of section II.2. confirmed that species richness of non-volant small mammals within the oil palm habitat was very low compared to surrounding habitats: it was basically restricted to Rattus spp., even in the fringes of the oil palm plantation (abrupt cline at the ecotone of the oil palm habitat). In each region, one species was over-dominant: R. tiomanicus in Riau plantations, and R. tanezumi in Bangka plantations, and most probably caused a very large part, if not all, of the rodent damage observed.

According to our literature review, the relation between rat abundance and crop damage can be complex, and rat damage is sometimes poorly correlated with rat populations (Liau, 1990; Sumantri and Wood, 2013). However, as we didn’t have sufficient time to monitor rat populations, we used existing data on rodent damage (routinely collected by PTSmart plantation staff) as a broad indicator of rat population relative size. Considering the probable bias due to the assessment method (notably linked to 1- the height of the palm trees in relation to the climbing ability of each Rattus species and/or the visual acuity of the observer, and 2- the proportion of loose fruits consumed compared to consumption of fruit bunches still on the tree) , we may infer that:

1) from damage indices, Rattus populations in oil palm habitats was relatively high (compared to neighboring habitats) and fluctuated slowly (except the very unusual outbreak in Riau_2 early 2010), with no obvious seasonal cycle. These trends confirmed results from existing studies in our literature review (Wood, 1984; Wood and Chung, 2003).

2) from damage indices, Rattus were more abundant in Bangka than in Riau, and rat population level was quite similar within each region.

Our assumptions about rat population dynamics and size in our study sites should be confirmed by appropriate trapping, as accurate knowledge on the prey resource is a fundamental prerequisite to better understanding prey-predator relationships (see research needs).
V.1.2.b. What contributes to explaining rat population limitation in Riau plantations compared to Bangka?

Table 23 synthesize main characteristics of Riau and Bangka agroecosystems.

**Table 26: Comparison of study sites: main characteristics of Bangka and Riau agroecosystems**

<table>
<thead>
<tr>
<th></th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plantation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biogeography</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sumatra Island</td>
<td>473 607 km²</td>
<td>Bangka Island</td>
<td>11 910 km²</td>
</tr>
<tr>
<td><strong>Landscape</strong></td>
<td>Mosaic diversity</td>
<td></td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td></td>
<td>Forest or forest like habitat</td>
<td>+/-</td>
<td>+</td>
<td>+++</td>
</tr>
<tr>
<td><strong>Rodent dominant species</strong></td>
<td><em>Rattus tiomanicus</em></td>
<td><em>Rattus tanezumi</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Rodent damage</strong></td>
<td></td>
<td></td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td><strong>Rodenticide use</strong></td>
<td>0</td>
<td></td>
<td>++</td>
<td></td>
</tr>
<tr>
<td><strong>Barn owl</strong></td>
<td>Average nest boxes density</td>
<td>+</td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean nest box occupancy rate</td>
<td>+</td>
<td>+/-</td>
<td>&lt;?→+++</td>
</tr>
<tr>
<td></td>
<td>Breeding season</td>
<td>++</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rodent in diet</td>
<td>+++</td>
<td>++(+)</td>
<td></td>
</tr>
<tr>
<td><strong>Small carnivores</strong></td>
<td><em>KAI</em>FAE</td>
<td>+++</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td></td>
<td><em>KAI</em>SPL</td>
<td>+++</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td></td>
<td>Diversity</td>
<td>Dominance leopard cat</td>
<td>No wild felids</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small mammals in diet</td>
<td>+++</td>
<td>++(+)</td>
<td></td>
</tr>
</tbody>
</table>

*KAI: Kilometric Abundance Index
Accumulation of "+" indicates an increase in intensity

Descriptive and comparatives approaches, such as the one in this study, are a preliminary and necessary step to improve our understanding of the underlying factors controlling rodent populations in oil palm plantations.

Below is an hypothetical table of general factors that could explain change in rat population abundance in our study sites (inspired from Krebs, 2013).
Table 27: Hypothetical table of general factors that could explain changes in rat population abundance in our study sites (inspired from Krebs, 2013)

<table>
<thead>
<tr>
<th></th>
<th>Rodenticide use</th>
<th>Poor weather</th>
<th>Food shortage</th>
<th>Parasite &amp; disease</th>
<th>Self regulation</th>
<th>Heavy predation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Reduced breeding</td>
<td>Social mortality</td>
</tr>
<tr>
<td>Riau</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0/(-)</td>
<td>0/(+)</td>
<td>0/(+)</td>
</tr>
<tr>
<td>Bangka</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>0/(-)</td>
<td>0/(+)</td>
<td>0/(+)</td>
</tr>
</tbody>
</table>

+ present
- absent
0 unknown or not studied

Some factors, such as parasites and diseases or self-regulation were not studied.

- Parasites and diseases: according to PTSmart research institute, there was no explicit sign of such mortality causes in any of our study sites (except the experimental one linked to biological control using Sarcocystis singaporensis). However, we cannot produce any data to confirm this statement.

- Self-regulation, e.g. reduced breeding and social mortality: according to Wood and Liau (1984b), in uncontrolled oil palm plantations (no rodenticide treatment and no barn owl introduction), the mechanisms limiting R. tiomanicus numbers (the dominant rat species in Riau plantations) appears to include intraspecific pressures on behavior, causing maternal inefficiency and/or outward dispersal of juveniles (usually unsuccessful). Nevertheless, it seems unlikely that self-regulation would explain on its own such differences in rat population abundance between Riau and Bangka, given notably that intraspecific pressure would be higher in Bangka than in Riau (higher rat population in Bangka: higher intraspecific pressure, inducing more self-regulation and not less self-regulation). Other intrinsic factors such as emigration would also not be a good candidate, given that the oil palm habitat is more favorable to rat proliferation than surrounding habitat types (greater food supply, less competition).

In the section below, we will focus on other factors.

- Could the agro-environmental conditions of our study sites be responsible?

We reported differences in oil palm habitat and landscape configuration. However, we argued previously that they may not explain the differences of rodent levels between Bangka and Riau plantations. On the contrary, management practices such as rodenticide use may affect rat population dynamics.

About food supply and weather

We previsously postulate that, in the conditions of our study sites, food availability is not a limiting factor in rat population growth and cannot explain the difference in abundance between Bangka and Riau plantations, given that oil palm fruits are abundant throughout the year in oil palm plantations. If there was a difference in food supply, it would have come from supplementary animal food (insects, snails, etc.) which would be limited in Riau comparatively to Bangka.

Though we have not specifically studied it, poor weather is also unlikely to be a good candidate in our area, although exceptionally heavy and prolonged rainfall could cause an occasional and local ‘extra’ mortality (Wood and Liau, 1984b).
About rodenticide use

In theory (PTSmart agricultural practices recommendation), the critical level of 5% of fresh damage observed on ripe fruit bunches is used as a threshold for treatment with coumatetralyl (rodenticide). However, in practice, plantation managers in Riau and Bangka react differently to rodent damage. In Bangka plantations, recommendation is implemented: rodenticide is systematically applied as soon as the threshold of 5% is reached. Whereas in both Riau plantations, rodenticide is never applied even though the 5% threshold is reached, which was not uncommon, notably in Riau_2 (e.g., in Riau_2, the proportion of blocks with rodent damage > 5% were of 5.7%, 1.8%, 0.5% and 0.3% in 2008, 2009, 2011 and 2012 respectively; and even in the outstanding peak of 2010, when more than 30% of blocks overtook the 5% threshold, the area was not treated with rodenticide, according to plantation managers).

It is still unknown to what extent rodenticide treatment affects rat population dynamics in Bangka, may it be on a short or a long-term basis. But apparently, it seems that rodenticide use may in the end have an opposite effect to the one anticipated: it would not greatly affect R. tanezumi in Bangka plantations, given the proven high degree of tolerance of this species to strong coumatetralyl exposure, as demonstrated by Andru et al. (2013). However, on the other hand, it could negatively affect predator populations through indirect intoxication, as demonstrated with other anticoagulants, e.g. bromadiolone for fox populations in the Doubs department in France by Jacquot et al. (2013), and warfarin or brodifacoum for barn owl population in oil palm plantations by Naim et al. (2011), and it would thus in turn limit their regulation on rat prey in Bangka plantations compared to Riau plantations.

![Two contrasting systems: RIAU “low” rodent damage versus BANGKA “high” rodent damage](image)

**What could explain the relative success in rodent pest control**

*Do small carnivores play a role?*

**Oil palm plantation agroecosystem**

<table>
<thead>
<tr>
<th></th>
<th>RIAU</th>
<th>BANGKA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landscape</td>
<td>Homogeneous: oil palm</td>
<td>Mosaic with forest like habitats</td>
</tr>
<tr>
<td>Oil palm habitat</td>
<td>Similar</td>
<td></td>
</tr>
<tr>
<td>Rodenticide</td>
<td>No</td>
<td>Heavy use</td>
</tr>
<tr>
<td>Rodent community</td>
<td>Rattus tiomanicus</td>
<td>Rattus tanezumi</td>
</tr>
<tr>
<td></td>
<td>Abrupt cline at oil palm edge</td>
<td></td>
</tr>
</tbody>
</table>

*Figure 55: From questions raised to main results: about the oil palm agroecosystem*
May it come from a differential predation pressure?

As pointed out in the general introduction, small mammal populations were shown to be affected by predators in many cases (Pearson, 1971; Erlinge et al., 1983; Korpimaki and Krebs, 1996; Hanski et al., 2001), but to what extent remains poorly understood.

About vulnerability to predation

From our observations and literature review, vegetation cover, hence supposedly refuge opportunities for Rattus populations, are roughly similar in the four plantations and are not a priori candidates for explaining a difference in rat population levels between Bangka and Riau (as caused by a difference in vulnerability to predation).

About barn owl abundance and food intake

Results of section II showed that barn owls were well established in both Riau and Bangka plantations, and we have no reason to suppose that barn owl populations in Bangka are significantly lower than in Riau.

However, results from section III suggested that, although rats represent a large part of the diet in all plantations, yearly, rat prey intake from the barn owl would be less in Bangka than in Riau plantations.

A standing hypothesis is that barn owl food requirements could be less in Bangka, given that there is only one main breeding season in Bangka comparatively to two in Riau, and that, according to Small (1990) and Lenton (1980), breeding considerably increases owl food requirements. The reasons for the difference in number and duration of breeding seasons between Riau and Bangka are under question and should also be investigated. We hypothesize that rodenticide might be a limiting factor for the barn owl reproduction rate (section III.1.2.): in Bangka, as a result of indirect intoxication, the barn owl may be too weak for two breeding seasons a year.

A second hypothesis is related to differential diet composition, which could also contribute to a reduced rat prey intake in Bangka. Indeed, our results suggest differences between Riau and Bangka in term of food resources used by the barn owl community: though rats still represented a very high, and the major part, of the diet in both cases (over 90 % frequency of occurrence in pellets), their importance in diet was less in Bangka than in Riau, and alternate prey contributed to a greater proportion of the diet in Bangka plantations compared to Riau. Reasons and consequences for differences in barn owl diet between the two agroecosystems are yet to be investigated. It may reflect either barn owl preference or prey availability (abundance and vulnerability) or both. For example, is it linked to rat prey size as hypothesized in section III.1.1. Indeed, R. tanezumi has a larger size than R. tiomanicus; which may induce differences in the functional responses of the predator community (rat intake). Selective predation related to age or sex of rats could affect rat population structure (Dickman et al., 1991; Kittlein, 1997), and in turn lead to a differential impact on rat population dynamics between Riau and Bangka; it is thus an important issue to investigate. As a first step to further test the hypothesis of barn owl preferential predation on younger rat individuals in Bangka compared to Riau, we provided in section III.1.3. a tool to assess the age structure of R. tiomanicus prey items from macroremains found in barn owl pellets in Riau plantations.
To conclude: barn owls predation is not a good candidate on its own to explain differences in rat population levels between Riau and Bangka, as it is presumably quite heavy in both areas. However, our results on reproduction and diet showed that something different is happening in Bangka compared to Riau, and that barn owl predation on rats might be slightly greater in Riau; the question remains whether it is sufficiently great as to contribute, with others factors, to a lower rat population in Riau. More precisely, the new question raised is: does the lower rat intake (or a potential selective predation related to age or sex) in Bangka plantations contribute to the greater rat population level compared to Riau? Another issue to be investigated (see research need) is linked to the impact of rodenticide use on barn owls, as it seems fundamental in order to advise plantation managers on their cultural practices: does coumatetralyl rodenticide use affect barn owl breeding seasons and reproduction rate in Bangka, and to what extent?

**About small carnivores abundance, diversity and diet**

According to our results (section III.2.1.), small carnivores were much more abundant in Riau plantations than in Bangka plantations: KAI (Kilometric Abundance Index) yielded from spotlight counts were on average two-times higher in Riau than in Bankga, and KAI yielded from faeces counts ten times greater in Riau than in Bangka. Four species of wild small carnivores were sighted: the leopard cat, the common palm civet, the small-toothed palm civet, and the Malay civet. To our knowledge, the present study represents the first record of small-toothed palm civet within oil palm habitat. On both Riau plantations, leopard cat represented the most abundant sightings within the small carnivore community, followed by the common palm civet (the small-toothed palm civet and the Malay civet were not or rarely seen). In Bangka plantations, the leopard cat was absent, and the small carnivore community was largely dominated by domestic/feral cats, followed by Viveridae (mainly common palm civet, then small-toothed palm civet, and the Malay civet). From our results, the small carnivore community appeared less diverse in Bangka plantation than in Riau plantations. Absence of wild felids in Bangka was confirmed by interviews and is in accordance with literature review.

Compared to small carnivore species that are expected to be present on each island, small carnivore species richness in oil palm plantations was poor. This result may reflect limitation of our survey methods or statistical analysis\(^4\), but is more likely to reflect true rarity of most species in oil palm habitats.

From our literature review, leopard cats and common palm civets are generally reported as common and relatively abundant in oil palm plantations, attracted by an abundant food resource, i.e. respectively rats and oil palm fruits (Rajaratnam et al., 2007; Nakashima et al., 2013). Our estimations of abundance for these two species in Riau plantations are consistent with those of other small carnivore surveys in oil palm plantations. In contrast, our figures in Bangka plantations are comparatively much lower. For wild felids, the situation is specific and their absence in Bangka is very probably linked to biogeographical issues (see section III.2.1.). We may question what could explain a lower abundance of wild small carnivores in Bangka plantations, compared to Riau ones. Though rat population level is lower in Riau, rats are still very abundant, and given that rat population may only decrease temporarily (just after treatment) and

\(^4\) Rather than using linear mixed-effect with KAI (Kilometric Abundance Index: number of observations/kilometer) in response variable to test for difference between small carnivore abundance among plantations or regions, we could have modelize a count (number of observations) as a function of the logarithm (ln) of the number of km (in offset variable) using a poisson regression.
locally (block scale), the amount of food for predators is likely to be enough throughout the year and at the plantation level to sustain predators populations. Food shortage is thus presumably not an issue. However, *R. tanezumi*, the dominant rodent prey in Bangka, has a great tolerance to rodenticide (Andru *et al.*, 2013), and, because they are repeatedly feeding on resistant live rats which have accumulated rodenticide residues in their tissues, predators may suffer from indirect intoxication (Newton *et al.*, 1999; Naim *et al.*, 2011). Within the oil palm habitat, there are no major differences in habitat features that may more or less favor the abundance of small carnivores among plantations; although, it is plausible that the lower palm tree height (in Riau_2) would be less favorable to more or less arboreal small carnivores species, such as the common palm civet, which have shown preference for the tallest trees for resting (Joshi *et al.*, 1995). A greater human disturbance and a higher hunting pressure in Bangka plantations also probably affects small carnivore populations. Landscape heterogeneity in and around Bangka plantations would, a priori, favor a more abundant and diverse small carnivore community. However, as discussed previously (section III.2.1.), the absence of extensive areas of natural forest in Bangka island, in association with a high hunting pressure, may have contributed to extinction or abundance reduction of some small carnivores.

Our results (section III.2.2.) showed the importance of small mammals in the diet of the small carnivore communities in our study sites: small mammals were often consumed, and when consumed they represent an overwhelming bulk of the diet. The overall dominance of small mammals in the diet of the small carnivore community in our study sites is consistent with, on one hand, the abundant rodent food resources within the plantation, and, on the other hand, spotlight counts (see III.2.1) indicating the overall dominance of wild or domestic felids, i.e. of hypercarnivores, within the small carnivore community.

Besides this, our analysis also suggests that small mammals may have more importance in the diet of the small carnivore community in Riau compared to Bangka: this food item ranks first in both Riau plantations; whereas in Bangka_1, plant material (excluding grass) had an overall higher importance in the diet of the small carnivore community, both in terms of frequency of occurrence and volume in total faeces. We assume that variation in small mammal consumption by the small carnivore community among Riau and Bangka plantations, relatively to fruit consumption, may not be predominately explained by variation in food availability, but rather by variation in species composition within the small carnivore community. Indeed, considering food habits of small carnivores as detailed in the literature -notably: the leopard cat mainly preying on rats and mice when available (Rajaratnam *et al.*, 2007; Lorica and Heaney, 2013), the common palm civet is highly frugivorous (Jothish, 2011; Nakashima *et al.*, 2013), and the domestic/feral cat relying more on human-derived food (Watanabe *et al.*, 2003),- our results on diet at the community level is consistent with the composition of the small carnivore community in the four plantations as described previously, and would suggest a higher prey intake of small mammals, notably rodents, in Riau compared to Bangka.

To our knowledge, this study is the first one taking an interest in the diet of the small carnivore community within oil palm plantations. Though, our results were limited by the methods used and notably by our inability to validate our field-based identification as “small carnivore” (given that visual assignment based on faeces size and morphology might be problematic; see section III.2.1.). To address this issue of species identification, rapid and simple “host-faecal-test” using real-time PCR could be developed (Dinkel *et al.*, 2011). As a result, our results should be treated with
caution, given the small sample size in Bangka and the unbalanced design (more faeces collected in Riau). Statistical analyses were also limited by our inability to explore more complex models or approaches.45

Lastly, our analysis suggested a negative correlation between rat damage and small carnivore abundance at community level, as well as at species level for the leopard cat and the common palm civet: lower values of rodent damage were observed in plantations where small carnivores were more abundant, that is Riau plantations, whereas rodents damage were higher in plantations where small carnivores were less abundant, that is Bangka plantations. However, correlation doesn’t mean causality, and lower rat damage might only be concomitant with an incidental greater abundance of small carnivores. And even if not only contingent, it doesn’t tell us whether the greater abundance of small carnivore is a necessary condition (must be present in every low rat population level) whether this is and/or a sufficient cause (can cause by itself a low rat population level), as defined by Krebs (2013).

However, although this study does not reveal the mechanisms behind the observed relationship, these results support our hypothesis of a lower predation pressure from small carnivores as one possible explanation for greater rodent damage in Bangka.

To conclude, the lower abundance of small carnivores in Bangka plantations, compared to Riau, and the absence of leopard cats -a hypercarnivore feeding mainly on muridae- in Bangka probably induce a lower off-take of rats by the small carnivore community in Bangka compared to Riau, thereby potentially impacting rat populations and consequently rodent damage. Our results suggest that one mechanism controlling rat populations in Riau plantations could be small carnivore predation; however, this factor is probably not sufficient and it may only contribute to regulating rat populations, in association with others factors, such as predation by other predators (e.g. barn owls, reptiles, etc.), or factors mentioned above. The extent to which small carnivores contribute to rodent control thus remains under question.

45 for example using predicted means, i.e. LSmeans, of VO and FO per plantation and compare them with Tuckey’s test may have better taken into account the unbalanced design.
Figure 56: From questions raised to main results: about barn owls and small carnivores

About others predators

Other rat predators, such as snakes (notably pythons and cobras) or monitor lizards (Varanus spp.), were not studied. The rate of rat predation by monitor lizards is presumably low, as indicated by results of Uchida (1966) who investigated the potential of Varanus indicus as a rat-control agent on a Western Caroline Islands. Similarly, because they are ectotherms and have subsequently low prey intake, snakes would probably have a very limited impact on rat population, and, according to Wodzicki (1973), who examined the relationship of five predators with their rodent prey, domestic/feral cats would do better that monitor lizards. However, a potential difference in reptile abundance between Bangka and Riau plantations, which could be assessed by further research, may result in a different impact on rat populations in both areas (directly or indirectly, see predators interaction below), thereby contributing more or less in rodent control.

About predator interactions

Predator interactions should also be taken into consideration when discussing the effect of predator(s) on prey populations. On our study site, we should question potential interference, either competition or facilitation, among species of the small carnivore community, but also between small carnivores and barn owls, or others rat predators like snakes, which may be more or less abundant among plantations.

46 Species of pythons that may be found in Riau and Bangka are the reticulated python (Python reticulatus) and the short-tailed python (P. brongersmai) (Kasterine, 2012).
For example, small carnivore predation may be complementary to barn owl predation, because of resource partitioning: small carnivores may prey on large-sized rats (Rajaratnam et al., 2007, found that Leopoldamys sabanus\textsuperscript{47} occurred in 12.5\% of leopard cat scats), thereby complementing barn owl predation which focuses on low or medium-sized rats. Moreover, they both have different foraging areas: barn owls hunt in open areas, while small carnivores may preferentially hunt in shrub areas, because of greater ambushing opportunities. In contrast, coexistence of sympatric species such as the domestic and wild cats might induce more competitive interactions (see section V.1.2.3.).

In addition, multiple predators have effects that cannot be predicted as simply the sum of their single effects, as one species of predator may either facilitate or hinder the success of another (Sih et al., 1998; Embar et al., 2014). About small carnivores and barn owls for example; as demonstrated for vipers and barn owls (Embar et al., 2014), we may hypothesise that small carnivores, ambushing in shrubs, could indirectly facilitate barn owl hunting by causing rats to bias their microhabitat use more towards open areas, and thus provide barn owls with better hunting opportunities. Therefore, we assume that a higher abundance of small carnivores may facilitate barn owl hunting success, which would favor predation on rats in Riau plantations compared to Bangka where small carnivores are relatively less abundant. Among the small carnivore community, taking the example of feral cats and leopard cats in oil palm plantations in Indonesia, Silmi et al. (2013a) suggested that the presence of both species did not affect negatively the other cat species, since leopard cats are strictly nocturnal and feral cats exhibit crepuscular and diurnal activity. However we did not find any other results supporting this hypothesis.

➢ To conclude

According to Popper (2005), a theory in the empirical sciences can never be proven or logically verified, but it can be falsified. The findings of the present study did not falsify the hypothesis that greater small carnivore predation pressure on rats contributes to a lower rat population level in Riau plantations compared to Bangka plantations. More specifically:

1) our results complement previous evidence that leopard cat (and common palm civet) populations may persist in oil palm plantations, seemingly benefiting from an abundant food resource, i.e rats for the leopard cat and oil palm fruits for the common palm civet;
2) our results suggest that predation pressure on rats was greater in Riau than in Bangka; and we believe that this is largely due to a differential predation from the small carnivore community (notably the leopard cat) rather than from the barn owl population. We also believe that rat regulation is more a predator community process than a single predator effect.
3) and, finally, our results broadly support the hypothesis that small carnivores play a role in rat control, notably the leopard cat given its diet mainly based on murids and the fact that this species represents the most abundant sighting within the small carnivore community in Riau plantations (about half the total sightings).

Therefore, small carnivore predation would be a promising candidate for a necessary condition, although inferences about the effect of this predator category on rat population regulation is still limited by substantial uncertainty. It may be necessary, but is it sufficient? As reported by Krebs (2013), the hypothesis that predation is necessary and sufficient to produce prey population

\textsuperscript{47} See previously: Lekagul and McNeely (1988) reported an average weight of 397 g for S. muelleri and 343 g for L. sabanus, compared to about 100 g for R. tiomanicus and 150-230 g for R. tanezumi (Aplin et al., 2003).
fluctuations is generally strongly rejected, but another hypothesis might be valuable for our systems and is yet to be confirmed: predation is necessary but not sufficient to regulate prey populations, i.e. predation mortality is only a single factor in a multifactor explanation with multilevel processes (Sinclair, 2003; Krebs, 2013), as exposed in Table 24. Therefore, the possible role of other factors such as disease or rodenticide should be investigated as well.

Within this multilevel process, landscape may also affect spatial distribution of both small mammals and small carnivores, and thus their presence/abundance within a specific habitat (Delattre et al., 1992; Lidicker, 2000), here the oil palm habitat. The issue of small mammal species richness and distribution within the oil palm habitat has been raised previously (very low species richness compared to surrounding habitats; abrupt cline at the ecotone of the oil palm habitat). In the next section, we will investigate spatial distribution of small carnivores within the oil palm habitat. Indeed, the presence or even abundance of a species within an habitat does not imply its long-term survival in this habitat. The next question to address is the extent to which small carnivores rely on forest fragments or other habitats for survival within oil palm plantations.

V.1.2.c. What about spatial distribution of small carnivores within the oil palm habitat?

In section II.1.1., our analysis of land use at the regional/provincial level was based on literature reviews and existing maps. However, we produced our own map and landscape metrics to describe and analyze the landscape at a finer scale, i.e. within and around each plantation. This map was used to investigate whether spatial distribution of small carnivores within the oil palm habitat was linked to surrounding habitat distribution.

We reported from our spotlight counts that the common palm civet and the leopard cat may be found deep in the oil palm habitat, and we did not detect attractive effect of either forest habitat or oil palm edge on either species (be it from visual analysis of clusters distributions, or from statistical analysis of distance of observations to focal habitat). These results, combined with knowledge about these species’ diet from our literature review, support the fact that the leopard cat and the common palm civet would forage in oil palm plantations at night, seemingly attracted by an abundant food resource (Scott and Gemita, 2004; Rajaratnam et al., 2007; Nakashima et al., 2013). We detected a repulsive effect of human settlements on leopard cats in all plantations, and for the common palm civet in only one plantation out of the four; moreover both species have been observed very close to human settlements (as close as to 100 m). These results strengthen the results of previous studies, which suggest that the leopard cat and the common palm civet were quite tolerant and highly tolerant to human presence, respectively, and can do well in agricultural areas (Duckworth et al., 2008c; Sanderson et al., 2008).

For the Malay civet, our results broadly support the hypothesis that, though this species may use the oil palm habitat, it did not venture far from the forest habitat or oil palm edge; this has also been reported in other studies (Jennings et al., 2010b; Jennings and Veron, 2011) and in other landscapes (Eng, 2011). As suggested by Colon (2002), the ability of this species to survive in disturbed habitats might thus be influenced by the proximity of undisturbed forest habitats. For the small-toothed palm civet, our analysis did not reveal any specific pattern of spatial distribution within the
oil palm habitat. However, our results for these two last species should be considered with caution due to a very low sample size.

For the domestic/feral cats, our results support the prediction that human settlements have an attractive effect on this species, except in Bangka plantations where spatial distribution of clusters did not reveal such an obvious pattern. The fact that, in Riau plantations, domestic/feral cats are more restricted to human settlement surroundings might be partly explained by resource partitioning and competitive interactions with the leopard cat, which preferentially forage far from human settlements, whereas domestic/feral cats are closely related to humans and may forage on garbage (Watanabe et al., 2003). In Bangka, there is not such a coexistence/competition issue, given that the leopard cat is absent, thus domestic/feral cats may forage all around the oil palm habitat, and not preferentially on garbage near human habitation.

Our analysis on distance to focal habitat for faeces counts at community level showed (in all plantations except one) an attractive effect of forest habitat, which is not the case for almost all spotlight counts observations, be it at community or species level. These contrasting results from spotlight and faeces counts support the hypothesis that, though the oil palm habitat may be suitable for some wild small carnivores, where they supposedly forage at night, those species -or at least most species-, may still need forest habitats for their survival in oil palm landscapes.

Our results also suggest that the spatial configuration of forest fragments, and notably their degree of isolation, might be of importance to enhance the dispersion of small carnivores within the oil palm habitat (see section IV.4.). Indeed, in the homogenous oil palm landscape of Riau plantations, spotlights observations of the wild small carnivore community were aggregated nearby the biggest forest area in the landscape (and the only for Riau_1), whereas in Bangka we did not detect any cluster of observations. The fact that wild small carnivore observations were widespread within the plantation in Bangka might reflect a greater opportunity of dispersion, thanks to a mosaic landscape including more forest habitats, and notably scattered fragments of forest or forest like habitat (enclaves of complex rubber agroforests) within the oil palm plantation, which may act as refuges or stepping stones. As reported by Fischer et al. (2006), increasing the permeability of the agricultural matrix facilitates species movement and bolsters species persistence in the landscape. Therefore, minimizing the distance between forest (or forest like habitat) and oil palm habitat would increase the ability of species to use the plantation.

Interpretation of our results is limited by the bias linked notably to the method of analysis used, e.g. the euclidian distance, which did not take into account the permeability of the various habitats and landscape features that may facilitate or impede movement of small carnivores. For example, the more dense drainage network in Riau_2, the presence of a busy tarmac road crossing Riau_1, and the large river bordering Riau_2 to the West, might influence small carnivore movements within the given plantation. Thus, methods based on least cost path distance (Adriaensen et al., 2003) or circuit theory (McRae et al., 2008), for example, should be investigated when further exploring our data set.
Globally, our findings confirm and strengthen those of other ecological studies on small carnivore habitat preferences, highlighting the importance of creating suitable rest sites within oil palm habitat and retaining forest habitat for the long-term persistence of small carnivores within oil palm landscapes (Mudappa et al., 2007; Jennings et al., 2010b; Nakashima et al., 2013; Jennings et al., 2015). However, for the leopard cat, which is obviously the main rat predator within the small carnivore community from our study sites, and which was found to be abundant in a highly homogenous oil palm landscape (Riau_1), it is still under question to what extent this species relies on forest fragments for persistence within oil palm plantations.

V.1.2.d. From questions raised to main answers

Figure 57 is an overview of Figures 54 to 56 and sums up our main results, as stemmed from questions raised in the general introduction.
Two contrasting systems:
RIAU “low” rodent damage versus BANGKA “high” rodent damage

Two different prey-predator systems

What could explain the relative success in rodent pest control

Small carnivores may play a role

Landscape has an influence
Spatial distribution of small carnivores within the plantations is linked to habitat

Oil palm plantation agroecosystem

Barn owls
Predator Community

Small carnivores

Proportion of rodent in diet: RIAU > BANGKA
Reproduction (food requirement): RIAU > BANGKA
Abundance: RIAU > BANGKA

Importance of small mammals in diet: RIAU ≠ BANGKA
Abundance: RIAU >> BANGKA
Diversity: RIAU (+ leopard cat) > BANGKA (no leopard cat)

Rat prey intake greater in Riau than in Bangka?

Small carnivore spatial distribution within plantations and correlation to habitat

> Importance of forest habitat/ non-oil palm habitat different according to species
Leopard cat, common palm civet: no attractiveness of oil palm edge or forest habitat
Malay civet: probable attractiveness of oil palm edge

> Oil palm habitat → foraging area at night?

Figure 58: From questions raised to main results: an overview
V.2. PERSPECTIVES AND RESEARCH NEEDS

This exploratory work is a baseline providing insights into potential directions for further research, and there are still a lot of questions to address, notably the following: to what extent does leopard cat predation contribute to the regulation of rat population level? Is leopard cat predation on rats complementary to barn owl predation (rat size, foraging areas, etc.)? What is the real impact of rodenticide treatment on *R. tanezumi* populations in Bangka? What is the impact of rodenticide use (indirect intoxication) on predators (barn owls and small carnivores) in Bangka? Does the leopard cat rely on forest fragments for resting and breeding, or may it persist in oil palm plantations, taking advantage of oil palm microhabitat features?

- **Additional research actions to strengthen or complete our results**

  **Barn owl selective predation related to rat age**

To investigate if the dietary response of barn owls is either linked to prey availability or to barn owl preference, barn owl diet and behavior could be monitored in the same time and location as prey communities in the field. As previously mentioned, barn owl pellets could be analyzed in order to investigate barn owl selective predation related to rat age. In this study, we provided a tool to assess the age structure of *R. tiomanicus* prey items from macroremains found in barn owl pellets in Riau plantations. The model could be extended to *R. tanezumi* in Bangka plantations. Then age structure of the prey population in the field could be compared to that found in pellets, in order to further explore predation patterns and therefore better predict the potential demographic impact of barn owl predation on rat prey.

  **Barn owl abundance**

In addition, data could be acquired to better assess barn owl abundance, notably in Bangka, in order to confirm our hypothesis of similar abundance levels in Riau and Bangka. For this, ongoing permanent data collection carried out by plantation staff should be closely monitored and cross checked to ensure reliability.

  **Predator faeces identification**

Emerging analytical techniques such as molecular biology on faeces DNA may further increase the robustness of faeces identification as “small carnivores”. Species-level assignment (Farrell *et al.*, 2000; Mukherjee *et al.*, 2010; Michalski *et al.*, 2011; Roques *et al.*, 2011) would also enable us to detail faeces abundance according to species, and perhaps to detect elusive or rare species that have not been not encountered during spotlight counts (Davison *et al.*, 2002; Mukherjee *et al.*, 2010). Moreover, thanks to the development of techniques that enable individual identification (microsatellites nuclear markers), we could count leopard cat individuals and estimate population size (Waits and Paetkau, 2005; Goossens and Salgado-Lynn, 2013).

  **Small carnivore and barn owl diet**

Predator diet may also be investigated more accurately thanks to molecular approaches (Galan *et al.*, 2010; Galan *et al.*, 2012; Shehzad *et al.*, 2012), in order to better assess which rodent species are consumed and what is the relative importance of *R. tiomanicus* in Riau and *R. tanezumi* in Bangka.
in the diet of predators, both at population (barn owls)/community (small carnivores) and at species level (small carnivores). This analysis could also be useful to confirm if *R. tiomanicus* and *R. tanezumi* are almost the only rodent prey consumed by the barn owls in Riau and Bangka respectively. It is indeed a prerequisite to the applicability of the tool we have developed to investigate barn owl selective predation on *R. tiomanicus* in Riau (and similarly for the tool to be developed for *R. tanezumi* in Bangka).

**Spatial distribution of small carnivores**

To strengthen and/or complete our analysis, methods taking into account the complexity of the landscape structure should be investigated. For example, methods relying on effective distance and not euclidian distance, such as those based on least cost path distance or circuit theory, could be used.

**Small mammal community composition**

Small mammal community composition within the plantations could be better assessed, by upscaling rodent trapping and using various types of trap and various trap locations (arboreal traps, etc.). According to our results and to our literature review, there is an undoubted overdominance of *R. tiomanicus* in Riau. But, in Bangka, though *R. tanezumi* appears to be dominant according to literature review, results suggested that its dominance would be less than *R. tiomanicus* in Riau; moreover the assessment was based on only one type of bait and trap48. A better assessment of prey availability might inform results of the predator diet survey.

**Spatial analysis of rat damage**

Spatial analysis of rat damage could be carried out, and correlation to environmental conditions (neighboring habitats, etc.), management practices, small carnivore abundance and barn owl nest boxes occupancy could be explored. Spatial pattern of barn owl diet could also be investigated, given that block scale data are available: barn owl pellets were collected in every block, only part of them (representative of the various landscape situations of the plantation) have been dissected and analyzed, but the others are available for further dissection. If differential patterns emerged, the link with local agroecological conditions could be explored as suggested above.

- **Long-term research perspectives to be addressed**

**Rat population dynamics**

Most of all, it is necessary to better characterize rat population demography and population dynamics (*R. tiomanicus* in Riau and *R. tanezumi* in Bangka), as it remains a “black box” although it is fundamental to better understanding at prey-predator relationships. We based our analysis on available data, i.e. rat damage, which may be only poorly correlated with rat population size, as pointed out in section II.2.2. Local investigations are strongly needed 1) to determine rat population sizes, and long term dynamics in our study sites, and 2) more specifically to monitor short-term changes in rat population demography in Bangka plantations as a consequence of rodenticide

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48 See section II.2.1.: exploratory trapping carried out in Riau plantations with various types of baits and traps (see Box 3.; results not mentioned in this study) suggested that the bait and trap used for our further intensive trapping (cage trap bait with oil palm fruit) were adapted/successful for non-volant small mammals found in the oil palm habitat, however, this issue should be confirmed by a better framed and longer experiment.
treatment, and investigate demographic processes involved in rat population recovery after treatment.

**Rodenticide effectiveness and negative impact**

What are the real benefits of rodenticide treatment compared to its adverse effects, particularly the potential indirect intoxication of rat predators? Does the use of rodenticide worsen the rat problem by disturbing the natural balance and increasing rat resistance? Olea *et al.* (2009) pointed out the lack of scientific evidence on side-effects on wildlife in decision making for chemical rodent control practices, and argued for the implementation of environmentally sustainable management, based on the precautionary principle. Moreover, a long-term collaborative research program undertaken in France to monitor grassland vole population has shown that a toolbox of mitigation measures, including modification of agricultural practices and habitat manipulation, has successfully led to the control of the vole *Arvicola terrestris* Linnaeus density, with a lesser impact on wildlife through a constant decrease in treatment intensity (Delattre and Giraudoux, 2009; Jacquot *et al*., 2013; Coeurdassier *et al*., 2014). In South-East Asia, ecologically-based rodent management has also been successfully implemented in rice cropping systems (Singleton *et al*., 2004).

To address this issue related to rodenticide in Bangka plantations, the first step would be to assess the real impact of rodenticide treatment on *R. tanezumi* populations, as emphasized above: to what extent does rodenticide treatment directly affect the rat population? Treatment may be inadequate because *R. tanezumi* showed a high tolerance to rodenticide and/or because of treatment modalities (date, frequency, spatial extent, etc.). Keeping in mind that, to be efficient, control measures should be implemented before the outbreak, otherwise the pest population will be so high that it can hardly be reduced.

As a supplement, the negative impact of rodenticide on barn owl reproduction and chicks survival in Bangka plantations should be investigated. Previous studies have showed that barn owls would be relatively tolerant to coumatetralyl compared to the second generation rodenticide (Duckett, 1984; Fisher *et al*., 2003a; Naim *et al*., 2011). However, we previously suggested that the lower reproductive frequency in Bangka compared to Riau might be caused by rodenticide. Indirect intoxication of small carnivores should also be assessed: non-invasive techniques such as analysis of rodenticide residues in faeces might be used (Sage *et al*., 2010; Jacquot, 2013).

**Leopard cat ecology**

The leopard cat, because of its rat-based diet and tolerance to human modified habitat, has a great potential for rat control in oil palm plantations. The ways to enhance their persistence in oil palm plantations should therefore be investigated, for example by studying its spatio-temporal behavior and microhabitat use. Lorica and Heaney (2013) reported that sugarcane fields in the Philippines support populations of leopard cats throughout the year, and that reproduction occurs within these populations, even though the sugarcane plantation is a highly disturbed habitat (harvest cycle induced regular destruction of vegetation cover), with only very small and scattered patches of non-agricultural vegetation. This result gives hope for the persistence of the leopard cats in oil palm plantations. A previous study showed that, within an agricultural landscape in Borneo, leopard cats prefer oil palm habitat to secondary forests fragments for foraging at night, but suggested that those fragments may be crucial for the survival of the leopard cat in oil palm landscapes, thanks to their dense ground cover appropriate for resting and breeding (Rajaratnam *et al*., 2007). However, as
highlighted by Mohamed et al. (2013), it is unclear whether the leopard cat is resident or in transit in the oil palm habitat, traveling from neighboring forests into plantation to forage, and it is still unknown which degree of alterations the leopard cat tolerates. In other words, it is still under question whether the leopard cat can be sustained within oil palm habitat, or only persists in this habitat because of the presence of secondary forest fragments within the plantation matrix or at a wider landscape scale, where the animal may return for resting or breeding. To address this question, leopard cats could be fitted with radio-collars and tracked. New GPS equipment and techniques now enable the monitoring of animal movements in real time. Investigating time spent in the oil palm habitat and at what period of the day/night, coupled with microhabitat characterization, may enable us to find out if leopard cats do use specific microhabitat features within the oil palm habitat (such as oil palm fronds piles, old log cavities, etc.) for resting/refuge during the day. This experiment could be carried out in Riau_1, which is the most homogeneous oil palm landscape of our four study sites.

What about an exclusion experiment?
To test the necessary role of small carnivores in controlling rat population level, one way is to extirpate them or reduce their abundance (Korpimaki and Krebs, 1996), however such experimental removal are very difficult to implement because of the large geographical scale range of most predators, and because of ethical (risk of harming wildlife) and managerial constraints (Sih et al., 1985; Krebs, 2013). Consequently, such exclusion experiments involving mammals are rare. One example is the research carried out in Kenya to test the effect of mammalian herbivores declines on plant communities (Young et al., 1997; Young et al., 2013). To test the effect of leopard cat and others ground dwelling small carnivores on rat population and rat damage, one could think of an exclosure experiment with areas from which these predators species are excluded, using fences, and compare such manipulations to control sites at which they are still abundant.

V.3. MANAGEMENT IMPLICATIONS

Our results support the hypothesis that, in an assemblage of predators, barn owls and leopard cats would be the best candidates for biological control of rats (given their diet and their abundance in oil palm plantations). In addition, our results showed that the distribution of wild small carnivores within the oil palm habitat was positively correlated to neighboring forested habitat and oil palm edge, and negatively correlated to human settlements, but to a lesser degree for the leopard cat and the common palm civet, which appeared to be widespread in the oil palm habitat. Our results also suggest that the abundance and degree of isolation of forest fragments might be of importance to enhance the dispersion of small carnivores within the oil palm habitat. Thus, although more research still needs to be done before appropriate and accurate advice can be given, some leads may be suggested, based on our results and on previous research. Because there is a need for a system and multi-level approach to enhancing biodiversity and supporting sustainable pest management (Fitzherbert et al., 2008; Koh and Sodhi, 2010; Yaap et al., 2010), multiple and complementary recommendations should be considered.
V.3.1. Enhancement of rat predators within oil palm plantations: benefits and limits

- **Which specie(s) to promote?**

Promoting a variety of natural predators, including small carnivores, is a way to increase the effectiveness of ecologically based rodent management (but see below about competitive interactions). Importance of species for rat control depends of course on their diet and hunting success, but also on their ability to adapt to the oil palm habitat.

In addition to barn owls which are already “adopted” by plantation managers, enhancement of highly carnivorous species such as wild cats should be encouraged, given their preference and ability to prey on rats. For example, Mukherjee *et al.* (2004) showed that one jungle cat eat three to five rodents per day in a dry forest of western India. In South Africa, Olbricht and Sliwa (1997) reported that during a typical night’s hunting, the black-footed cat usually killed between 10 to 14 rodents and small birds per night, one male being observed catching 12 rodents in three to five hours. To our knowledge, no study has yet assessed the mean daily number of rats consumed by the leopard cat in an oil palm plantation. However, the leopard cat is known to feed mainly on rats when available (see literature review of Shezard *et al.*, 2012). Thus this species should particularly be taken into consideration for pest control, given its additional ability to adapt to human-modified habitats, and therefore its potential for survival in oil palm landscapes, as confirmed by our results. Other wild cat species, such as the marbled cat or the flat-headed cat are highly dependent on primary forest or other specialized forest habitats (Sunquist and Sunquist, 2009), so their conservation in oil palm landscapes is more challenging. The benefit of other more common small carnivores, such as the Malay civet, or other vertebrate predators known to feed on rats, such as the monitor lizard or snakes, should also be considered. Monitor lizards, cobras and pythons are found to be abundant in oil palm plantations in Southeast Asia, attracted by rodent proliferation (Shine *et al.*, 1999a; Fitzherbert *et al.*, 2008; Koh and Gan, 2008; Koh and Sodhi, 2010; Yaap *et al.*, 2010). Protecting and enhancing small carnivores are of particular interest in areas where barn owl introduction has failed, such as in Borneo. Similarly, in newly planted or young oil palm plantations, attempts to introduce barn owls are limited by environmental conditions: 1) barn owls apparently suffer from hotter conditions in nest boxes because of lack of shade due to low tree height (Small, 1990; Charter *et al.*, 2010), and 2) cover-crops provide ample shelter for rats, thereby hindering barn owl hunting success (Noor Hisham and Cik Mohd Rizuan, 2013).

- **Bearing in mind possible effects of intraguild interactions and competition**

Enhancing a wide variety of predators is generally assumed as more “efficient” for pest control than focusing only on one or two predators; however, one should bear in mind that interactions between predators are not always, or not only, in favor of pest regulation (Tylianakis and Romo, 2010). Indeed, predator competition or interference may hinder the success of one of the predators or result in a shift in its diet resource, thereby resulting in a lesser effect (or at least a more complex effect) on prey demography than the predicted sum of individual effects of each predator (see section 1.2.2

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49 In Kalimantan (Indonesian part of Borneo), attempts to introduce barn owls have failed: barn owls are raised then introduced in nest boxes, but nest boxes are soon found to be empty (barn owls are disappearing: they may desert nest boxes for unknown reasons) (Mohd Naim and Sudartha Ps, com.pers.).
Almost nothing is known about rat predator interactions in oil palm landscapes, so speculations on this issue should be taken with caution. Interactions between domestic/feral cats and leopard cats are a good example of the question raised.

Domestic cats also feed on rodents so they may represent an additional predation pressure on rats, thereby contributing to the control of this pest. However, they may face competitive interactions between each other, one species precipitating a shift in the habitat use of the other species. From our results on spatial distribution, domestic / feral cats may be complementary to wild small carnivores due to space partitioning: the first being attracted by nearby human habitation, while small carnivores are found further away. Moreover, when comparing abundance of both species from plantation to plantation, we found that domestic cats were the less abundant in Riau_1, where leopard cats were the most abundant. In Bangka, where leopard cats are absent, the domestic cat has apparently occupied the vacant niche and is widespread all over the plantations. Silmi et al. (2013a) carried out camera trapping in an oil palm plantation in Aceh. They found population levels of these two small carnivores, i.e leopard cats and feral cats were quite similar, and they suggested that the presence of both species did not negatively affect the other cat species, since leopard cats are strictly nocturnal and feral cats exhibit crepuscular and diurnal activity. Moreover, the authors reported that “the presence of feral cats did not seem to affect the distribution of leopard cats in the plantation landscape, as both species were generally recorded from the same areas”. However, the scale of their experiment was quite limited in time (1 month) and space (20 camera traps deployed in a 1600mx2000m grid), moreover the authors did not bring up detailed results to support this assumption; and we did not find any other study investigating one or the other assumptions about space partitioning or overlapping between leopard cat and feral cat.

Risk of species introduction

The issue of intraguild interactions brings us to the danger of species introduction. The temptation could be great to introduce domestic cats into oil palm plantations or leopard cats to Bangka island. An early approach to manipulate domestic cats took place in the forties, with an attempt to establish cat farms in oil palm plantations (Bunting, 1939). Wood and Chung (2003), reporting this attempt, indicated that the cats survived if extra food was provided, and that the cat populations themselves were disrupted by predators, thus the method was not developed further. Research on rat control by domestic cat introductions was also carried out by Sime Darby in Malaysia (Shanmugam S., pers.com.).

Be it effective or not for rat control, unexpected consequences of species introductions may alter ecological processes and greatly affect both man and nature (Lodge, 1993; Elton, 2000), especially on small islands. The domestic/feral cat is often reported as one of the worst invasive mammalian predators, being a primary extinction driver for at least 33 insular endemic vertebrates (Nogales et al., 2013). The impacts of competition are notably stronger between closely related species (Diamond and Case, 1986), through hybridization, disease transmission and behavioral changes, as well as competition and direct predation impacts (Hervias et al., 2014; Medina et al., 2014). So any introduction attempts, specifically for cat species, should be considered with great caution.

To conclude, as highlighted by Linnell and Strand (2000): “manipulating carnivore numbers (reintroduction or control) [is] hard to predict. Changes in number of one carnivore species can lead

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30 Unfortunately we couldn’t find published or unpublished results on this experiment, thus we cannot give their conclusions.
to direct increases or decreases in the number of other carnivores, with resulting complex changes in prey populations”.

V.3.2. How to enhance rat predators within oil palm plantations?

Enhancing or protecting natural predators such as barn owls and small carnivores, notably leopard cats, probably contributes in rat control, as suggested by previous studies for barn owls (see the review paper from Wood and Chung, 2003) and by our results for small carnivores. However, it is a real challenge to enhance most small carnivores, given their population decrease consequently notably to habitat destruction and fragmentation, combined with hunting. Bangka forests and agroforests are undergoing more and more land clearing for oil palm cultivation and tin mining (see section I and II.1.). The heavy hunting pressure and absence of extensive intact forest landscape in Bangka, in conjunction to this habitat modification at island level, have very probably lead to the decrease of small carnivores in Bangka Island, and thereby on our study sites also, and this phenomenon is assumed to be exacerbated in the future. Similarly, in Sumatra, and over the whole of Indonesia, predictions indicate accelerating deforestation and continuous biodiversity loss (Koh and Ghazoul, 2010; Carlson et al., 2012; Harris et al., 2013; Lee et al., 2014b). So, in general, small carnivore population decrease is alarming, at least for the less human tolerant species. Even for leopard cat and common palm civet, which are widespread species categorized as “Least concerned” (IUCN, 2014), we don’t really know their degree of dependence on forest habitat. Other rat predator taxa such as reptiles are also heavily harvested (mainly for commercial trade) and the long-term sustainability of the high off-take of these species has been questioned, although monitor lizards (Varanus spp.), cobras and pythons can be abundant in human modified habitats and notably in oil plantations (see section V.3.1.) (Shine et al., 1999b; Shine et al., 1999a; Azhar et al., 2013a). Consequently, enhancing and protecting rat predators is a challenge, even for the barn owl in some areas (see section V.3.1.).

Though protected areas are a crucial tool for the conservation of biodiversity, their unprotected surroundings may be an important part in many species ranges, and thus variations in habitat quality outside a protected area may greatly affect the population dynamics (Baeza and Estades, 2010). Moreover, it is recognized that effective strategies for the conservation of biodiversity must take multiple spatial scales into consideration (Meentemeyer and Box, 1987; Fischer et al., 2004; Franklin and Lindenmayer, 2009). In planted forest or agricultural areas, management decisions at both the stand and landscape scales should be related to each other, and both will influence habitat quality for wildlife in the region (Lantschner et al., 2012). Therefore, to enhance persistence of small carnivores or other rat predators in oil palm landscapes, appropriate land use planning at macro and micro level, in hand with wildlife-friendly farming practices and controlled hunting/harvesting, should be considered. Our results have shown that attractiveness of oil palm habitat and spatial distribution of small carnivores in the oil palm plantation may vary according to species, therefore, land-use and practices should be adapted to the species targeted. Below, we suggested some management practices that may benefit small carnivores, or other rat predators.
Manage habitat at different scales: stand and landscape

Oil palm plantation landscaping: retain natural forest patches within the plantation

Our results on both abundance and spatial distribution of small carnivores strongly support previous evidence that leopard cat and common palm civet populations can persist in oil palm plantations, but they also highlights the importance of retaining forest habitat in the landscape, which might be crucial for some species such as the Malay civet. The fact that other species were poorly or not detected in the oil palm habitat during our survey is probably due to their preference or dependence for/on forest habitat rather than to methodological biases (see section III.2.1.). Even for the widespread leopard cat, as pointed out previously (see section V.2), we still don’t clearly know what are the effects of habitat loss and fragmentation (Zanin et al., 2015) and to what extent retaining forest fragments in oil palm landscapes would be crucial for the persistence of the species in those landscapes. However, it should also be noted that for the leopard cat, Bernard et al. (2014) reported a higher photographic rate (camera traps) in all forest patches within an oil palm plantation than in continuous forest. This result may confirm that, for this species, an oil palm landscape retaining forest fragments is a profitable habitat.

Therefore, we recommend preserving or reestablishing forested areas embedded within the oil palm plantation/concession[^1]. Several authors, based on their results, have advocated the retention of natural forest patches for biodiversity enhancement, be it specifically within oil palm plantations (Maddock et al., 2007; Rajaratnam et al., 2007; Gervais et al., 2012; Azhar et al., 2013b; Bernard et al., 2014; Lucey et al., 2014; Bateman et al., 2015), or more generally in agricultural landscapes (Fischer et al., 2006; Cunningham et al., 2008; Burel et al., 2013a) or tree plantations (Lindenmayer et al., 1999; Lindenmayer and Hobbs, 2004; McShea et al., 2009; Lantschner et al., 2012).

Studying mammal richness in forest remnants within an oil palm plantation, Bernard et al. (2014) showed the central role of habitat quality, patch size, and degree of isolation from continuous forest habitat.

An abundant literature reported that, to enhance the conservation value of forest remnants, their degree of isolation is of importance: connectivity should thus be maximized via strips/corridors or stepping stones (Taylor et al., 1993; Laurance and Gascon, 1997; Taylor et al., 2006; Lees and Peres, 2008; Prugh et al., 2008; Gilbert-Norton et al., 2010; Brodie et al., 2015). As suggested by our results minimizing the distance between forest (or forest like habitat) and oil palm habitat would increase the ability of species to use the plantation. Indeed, at the community level, small carnivores encountered within the oil palm habitat were mostly found near forest edge (attractiveness of forest habitat). Moreover, as pointed out previously (V.1.2.c.), the fact that small carnivore observations were widespread within the oil palm habitat in Bangka plantations (and not aggregated nearby big forest fragments like in Riau plantations) suggested that the numerous forest-like enclaves may favor small carnivore dispersion opportunities within the plantation.

We have assessed the influence of surrounding habitat types on the distribution of small carnivores, but we have not investigated the influence of surroundings habitat quality or patch size. Although

[^1]: It should be noted that if forest fragments cover large areas, the company should work effectively with the government to convince them that conservation areas are part of their business model for sustainable development, and provide them with evidence of active management on the ground. Indeed, in Indonesia, when land has been allocated to a company (e.g. oil palm company) for agriculture purpose, if significant areas are not converted to oil palm and set aside for protection by the company, they are considered as “unproductive” and can therefore be taken back by government and reallocated to another company. (Paoli and Schweithelm, 2014).
some species are heavily dependent on non-disturbed forests, for many other species, forested fragments are important even if degraded; and within small carnivorous mammal species, habitat generalists and/or more frugivorous species such as mongooses and civets, are less affected by logging or moderate habitat disturbance, which may even have a positive effect (Meijaard et al., 2005; Mudappa et al., 2007). Results of Azhar et al. (2014a) showed that size of patches of remnant rainforest were important factors influencing the richness of mammal species in oil palm landscapes, all species being more likely to be recorded in plantations supporting large areas of native forest. The issue of size is still under debate: some arguing that small fragments can be valuable (Turner and T. Corlett, 1996), others that maintaining small forest fragments are useless for effective conservation strategy and that investment in such practices should be better directed toward the protection of contiguous forest (Edwards et al., 2010; Edwards et al., 2012). Definitely, the smaller the fragments are, the greater they are exposed to edge effects and to hunters/poachers (Canale et al., 2012). Obviously, there is no fixed and global “best size” of forest remnants to be recommended to plantation managers: it is species specific (requirements are highly variable across different taxa, depending on their relative sensitivity to edge and area effects), and context specific (habitat quality including the surrounding environment, etc.) (Laurance and Laurance, 1999; Lees and Peres, 2008; Pardini et al., 2010). Our results suggested that some small carnivore species might take advantage of even small and degraded habitats to survive within oil palm landscapes: some civets still persisted in Bangka plantations, a landscape with 1) few small enclaves of disturbed forest-like habitat (rubber agroforests) within the plantation and 2) no extensive and/or well preserved forest in the surrounding areas (nor on the island). To conclude, a) not only the proportion of habitats, but also quality and their design, is of importance when identifying the maintenance of forest fragments for shaping oil palm landscapes; b) few general rules may be brought out, but identifying the more profitable characteristics of the landscape mosaic is mainly taxa dependent, not to say species dependent, and is yet to be investigated for many taxa (Debinski and Holt, 2000).

Forest fragments within the plantation are prone to disturbance activities from local communities or plantation workers (easy access, sometimes conflicting land use status, etc.), and notably to heavy hunting/harvesting pressure as emphasis in section III.2.1. and as reported by Azhar et al. (2013a). This may represent a major threat for rat predators, notably small carnivores. Therefore, there is a need to control hunting/harvesting/logging practices (see Appendix 9), and to closely monitor predator populations.

It must be noted that the impact of retaining forest fragments in/around the plantation may also have negative impacts on production/yield, for example by enhancing the abundance of some pests. In their literature review on the impact of landscape composition on biological control effectiveness, Bianchi et al. (2006) and Veres et al. (2013) reported that landscapes with higher proportions of semi-natural areas exhibited higher natural enemy populations and lower pest abundance respectively, i.e higher pest control in fields. However, that it is not the case everywhere: for example, in oil palm plantations in South America, attacks of oil palm trees by the root minor Sagalassa valida Walker are particularly developed along forest boundaries or riparian areas, and seem to be linked to the presence of a spiny palm tree of the Bractis genus which is the main host plants of this pest (Genty et al., 1978; Mariau, 2001). Martin et al. (2013) results show that, by altering natural enemy interactions, landscape complexity can provide ecosystem services as well as disservices constraining pest control. Edwards et al. (2014), argue that there is no evidence to
support arguments that forest should be retained within or adjacent to oil palm monocultures for the provision of ecosystem services that benefit yield. Definitely, it is highly context dependent.

**Large scale landscaping (regional level or upper)**

Most species, notably mammalian carnivores, are particularly vulnerable to fragmentation and connectivity-loss of habitat, and though some may persist in fragmented landscapes with altered community structure, most require large areas for their long term-survival (Mudappa et al., 2007; Crooks et al., 2011; Pe’er et al., 2014). Moreover, beyond the maintenance of large contiguous forest blocks, landscape scale mosaic and connectivity might be crucial for maintaining a metapopulation structure in fragmented landscapes, as shown for the tiger potentially using mosaics of plantations as additional roaming or foraging zones, riparian forests as corridors and smaller forest patches as stepping stones (Sunarto et al., 2012). As suggested previously (section III.2.1.), the depauperate small carnivore community in Bangka might be partly explained (in conjunction with a high hunting pressure and biogeographic issues) by the absence of large contiguous areas of undisturbed or poorly disturbed forest potentially acting as source habitat for further range expansion, compared to Riau province landscape which retains some extended areas of well-preserved forests, even if they are relatively far from the studied plantations (about 30 km). Consequently, plantations have to address large landscape-level considerations, e.g. landscape-level impacts within the landscape beyond their boundaries, to plan the development within their boundaries. That is to say that plantation management should consider the broader landscape when identifying HCV (High Conservation Value) areas or species and designing land-use at a plantation scale, with a view of ensuring spatial coherence. However, although areas set aside for conservation at the plantation scale may have the potential to make a substantial contribution to the viability of a species population, they are often of quite reduced area and they will surely not ensure the viability of the given species on their own. Therefore, as pointed out notably by Bateman et al. (2015), conservation efforts coordinated across multiple sites would enhance the likelihood of the persistence of sustainable populations; moreover, favoring the establishment of contiguous conservation areas that span concessions may reduce costs and provide win-win outcomes for both conservation and landowners. But such a collaborative landscape approach is really challenging, and would need not only coordination between oil palm companies, but also involvement of governments, NGOs, financial institutions and other stakeholders, and should include legal requirements and incentives (Koh and Sodhi, 2010; Paoli et al., 2010; Yaap et al., 2010; Bateman et al., 2015).

*Maintain microhabitat as a refuge for small carnivores within the oil palm habitat*

Cultural practices among plantations may vary, thereby impacting vegetation cover for example, and in turn providing habitat of variable quality for small carnivores. We have described the oil palm habitat of our study sites in section II.1.2. We reported that the oil palm habitat did not vary much among our studied plantations, therefore it was not considered as a potential factor to explain the difference in small carnivore abundance among these plantations. We did not consider microhabitat either when analyzing spatial distribution of small carnivores within the oil palm habitat; however we recommended further investigation of this issue for the leopard cat, with more adapted methods (see research need). Indeed, according to our literature review, the characteristics of the microhabitat may play a crucial role in the abundance and distribution of small carnivores within the oil palm habitat; and the ability for small carnivore populations to persist in agricultural
landscapes may depend greatly on their ability to use the cultivated area, which is species specific. Enhancing the structural complexity of commercial plantations, notably through the maintenance of understorey vegetation, could enrich the presence of mammals within them (Hartley, 2002; Ramirez and Simonetti, 2011). According to Lindenmayer and Hobbs (2004), reviewing fauna conservation in Australian plantation forests, at stand level, structural complexity is of importance for fauna, with many species responding positively to the presence of native understorey plants, the presence of windrowed logs, and logging slash\(^{52}\) on the forest floor. In oil palm plantations, Mohamed et al. (2013) and Rajaratnam et al. (2007) results suggested that dense vegetation and rotting logs in interrows may provide adequate rest sites for the leopard cat. Similarly, dense ground cover also appeared to be an important habitat component for providing day beds for the Malay civet (Colon, 2002; Jennings et al., 2006; Eng, 2011). In contrast, the common palm civet was shown to preferentially use the dense canopy of the tallest trees, be it in forest or in oil palm plantation, for resting (Joshi et al., 1995; Su and Sale, 2007; Nakashima et al., 2013). In oil palm plantations this species notably selected oil palm trees with dense mats of ferns and larger numbers of leaves as preferable rest sites (Nakashima et al., 2013).

Therefore, by adapting agricultural practices (pruning, slashing, etc.), the presence of features such as dense vegetation, dead logs (providing caves and tree hollows), epiphytes along oil palm trunks (providing dense vegetation mat), etc. should be increased in oil palm blocks, thereby providing more suitable rest or den-sites for small carnivores within the oil palm habitat, as suggested by Jennings et al. (2015). Although it will probably not be practical to adopt some practices over the entire plantation (for example stop pruning will make it more difficult to harvest the oil palm bunch), some parts of blocks could be managed specifically for favoring small carnivores (with also a control/restricted access, as to avoid as much as possible disturbance by human presence). In addition to such practices, plantation management could favor replanting practices such as differed failing with underplanting\(^{53}\), instead of clear cutting of senescent plantations, in order to minimize disturbance associated with this practice. Moreover, as suggested by Luskin and Potts (2011), the oil palm matrix quality could also be improved by manipulating the temporal scale associated with the oil palm lifecycle, e.g. by creating a patchwork of different aged stands, thereby enhancing a greater diversity of microclimate and vegetation structure, and minimizing spatial scale of disturbance when replanting. As highlighted by the authors, these methods should be adapted to realistic conditions, given their induced management constraints and yield effects for the producers.

➢ Take a fresh look at rodenticide usage

Our results suggested that rodenticide treatment in Bangka plantations does not have the expected effects (rat population not regulated on a long term) and we hypothesized that it may negatively affect barn owl breeding. Thus, there is obviously an issue to address with rodenticide use: what are the real benefits of rodenticide treatment regarding rat resistance and costs, notably the one linked to indirect intoxication of rat predators? Do rodenticide treatments worsen the rat problem by disturbing the natural balance? Moreover, control measures that are implemented after the critical

\(^{52}\) Logging slash is coarse and fine woody debris generated during logging operations or through wind, snow or other natural forest disturbances (Source: Wikipedia).

\(^{53}\) In order to minimize the yield gap and spread the economic loss caused by clear cutting of large areas of senescent plantations, some managers favor under-planting methods, whereby young palms are planted under old palms, which are gradually poisoned. However, poisoned palms left to decompose result in infestation of *Oryctes sp. a rhinoceros* beetle, which is a serious pests in immature and young palms.
level of the pest is reached are likely too late, as the pest population is already so high that control efforts will hardly reduce it.

It appears that plantation management perception of rodent damage threshold may be crucial. We have previously reported the different perceptions between Riau and Bangka (see section II.3.1.). Bangka management applying rodenticides as soon as the damage threshold is reached, while Riau management tolerates damage above the threshold, dealing with the risk in a long term approach. Maybe Bangka plantation managers should consider such an approach, stop using rodenticide and tolerating higher levels of damage to test what happens? This “experiment” could be carried out on one Bangka plantation, while the other would continue current practices, meanwhile long term research on rat population dynamics and predators (small carnivores and barn owls) abundance would be carried out on both plantations. The problem being that those plantations are connected to/bordered by other oil palm plantations: it would be preferable to study isolated plantations to avoid rats immigration from surroundings plantations, or others interferences. Moreover, most positive consequences of a stop in using rodenticide (linked for example to indirect intoxication of predators) might only be visible in the long-term; and, obviously, plantations managers might be reluctant to stop using rodenticide given the (perceived) immediate risk of allowing rat populations to grow. Thus, it might be more “acceptable” to first monitor the short-term effect of rodenticide on rat population, and then, if results are in favor of minor effects, to put in place such a comparative experiment (with and without rodenticide use respectively on the two Bangka plantations).

Plantation managers should bear in mind that pesticides other than rodenticides may also cause indirect intoxication of rat predators. For example, barns owls were reported to be “apathetic”, with even some cases of population decrease, after spraying of an insecticide (Marshal®) to get rid of Oryctes spp. (a Scarabaeidae larvae mining gallery into oil palm stem or fronds): it thus seems plausible that barn owls would have been intoxicated after ingestion of Oryctes spp., or ingestion of rats preying on Oryctes spp. (Jacquemard J.C., com.pers.). Indeed, the active ingredient of Marshal® product, Carbosulfan, was shown to have a detrimental effect on the development of avian embryos (Taparia et al., 2014).

To conclude, adapting practices and land-use to enhance biodiversity, notably small carnivores, within oil palm plantations, could really be a win-win strategy for both conservation and production.
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### Appendix 1: Carnivore species in Sumatra and Bangka islands

**Table 1**: Small, medium and large sized carnivores species potentially present in Sumatra and/or Bangka island (Source: cf next page)

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common name</th>
<th>IUCN Red List Status</th>
<th>Population Trends (IUCN)</th>
<th>SUMATRA</th>
<th>BANGKA</th>
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<tbody>
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<td>Felidae</td>
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<td>Sunda Clouded leopard</td>
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<td>Paradoxurus hermaphroditus</td>
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<td>Viverra tangalunga</td>
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<td>LC</td>
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<td>Viverricula indica</td>
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<td>Dhole</td>
<td>EN</td>
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<td>Domestic dog</td>
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<td>Ursidae</td>
<td>Helarctos malayanus</td>
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<td>VU</td>
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DD: Data Deficient; LC: Least Concern; NT: Near threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; SU: Sumatra; BA: Bangka

Present | Absent | Status uncertain
References


Appendix 2: Deforestation around Riau_1 plantation

Figure 1: Deforestation between 2000 and 2011 in West/Northwest of Riau_1. Big red crosses indicate location of forest fragments totally cleared. (Source: Satellite images Landsat 2000 and Spot 2010-2011)
### Table 1: Area per planting year (in % of total oil palm habitat)

<table>
<thead>
<tr>
<th>Year</th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
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<tbody>
<tr>
<td>1986</td>
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<td>-</td>
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<td>1987</td>
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<td>4.6</td>
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<td>2002</td>
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<td>1.8</td>
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Appendix 4: Detailed results for analysis of barn owl nest box occupancy rate and of eggs in nest boxes

Table 1: Linear models used to test for the statistical differences among regions and plantations of 1) pellets occurrence within barn owl nest boxes, and 2) number of eggs within barn owl nest boxes: results of analysis of variance and goodness of fit test. The symbol * indicates the significance level associated to the p-value: * for P ≤ 0.05, ** for P ≤ 0.01 and *** for P ≤ 0.001. See material and methods section for Pseudo R² calculation.

<table>
<thead>
<tr>
<th>Model retained Variable</th>
<th>Covariates</th>
<th>Random effect</th>
<th>Pseudo R²</th>
<th>Analysis of variance Difference tested</th>
<th>p-value</th>
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<td>Region</td>
<td>Plantation</td>
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<td>Marginal R²</td>
<td>0.111</td>
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<td></td>
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<td>Conditional R²</td>
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<td></td>
<td></td>
<td></td>
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<td>Riau versus Bangka</td>
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<td>Pellet occurrence</td>
<td>Plantation</td>
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<td>0.073</td>
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<td>Number of eggs</td>
<td>Region</td>
<td>Plantation</td>
<td>0.869</td>
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</tr>
<tr>
<td>Number of eggs</td>
<td>Plantation</td>
<td>NA</td>
<td>0.059</td>
<td></td>
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</tr>
</tbody>
</table>

For the analysis of variance:
- Riau versus Bangka: 0.064
- All plantations: <0.00001***
- Riau_1 versus Riau_2: <0.00001***
- Bangka_1 versus Bangka_2: <0.00001***
- Riau_2 versus Bangka_1: <0.00001***
- Riau_2 versus Bangka_2: <0.00001***
- Riau_1 versus Bangka_1: 0.250
- Riau_1 versus Bangka_2: <0.00001***

For the analysis of variance:
- Riau versus Bangka: 0.014*
- All plantations: 0.096
### Table 1: Linear models used to test for statistical significance of differences in small carnivores KAI (kilometric abundance index) among regions and plantations: results of analysis of variance and goodness of fit test. Small carnivore category included domestic/feral cats, whereas wild small carnivore category excluded domestic/feral cats. The symbol * indicates the significance level associated to the p-value: * for \( P \leq 0.05 \), ** for \( P \leq 0.01 \) and *** for \( P \leq 0.001 \). See material and methods for \( R^2 \) calculation.

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<th>Covariates</th>
<th>Random effect</th>
<th>( R^2 ) or pseudo ( R^2 )</th>
<th>Analysis of variance Differences tested</th>
<th>p-value</th>
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<td><strong>Small carnivores</strong></td>
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<tr>
<td>KAI_{spl}</td>
<td>Region</td>
<td>Plantation</td>
<td>0.585</td>
<td>Riau versus Bangka</td>
<td>0.036*</td>
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<td>Region</td>
<td>Plantation</td>
<td>0.539</td>
<td>Riau versus Bangka</td>
<td>0.006**</td>
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<td>KAI_{apl}</td>
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<td>Riau_1 versus Riau_2</td>
<td>0.081</td>
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<td>Bangka_1 versus Bangka_2</td>
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<td>Riau_1 versus Bangka_1</td>
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<td>Riau_1 versus Bangka_2</td>
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<td>Riau_1 versus Bangka_2</td>
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<td>Riau_1 versus Bangka_1</td>
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<td>Riau_1 versus Bangka_2</td>
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<td>Bangka_1 versus Bangka_2</td>
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</tr>
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<td>Riau_1 versus Bangka_1</td>
<td>0.0007***</td>
</tr>
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<td></td>
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<td></td>
<td>Riau_1 versus Bangka_2</td>
<td>0.0007***</td>
</tr>
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<td>Riau versus Bangka</td>
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<td>Plantation</td>
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<td>NA</td>
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Appendix 6: Detailed results for diet analysis of the small carnivore community (frequency of occurrence and estimated dry volume)

Figure 1: Dispersion of measurements for frequency of occurrence (%FO) and dry volume (%VO) of small mammal food items in faeces of the small carnivore community in Riau and Bangka plantations. See material and methods section III.2.2. for data and results description. Data include year 2011 for Riau_2 plantation, year 2011 and 2012 for Riau_1, and year 2010 to 2012 for both Bangka plantations. FO single measurement is representative of all faeces, whether VO single measurement is representative of one faeces. Results are expressed, for volume, in percent of the total volume of the faeces but considering only faeces containing that food category (%VOp) and, for frequency of occurrence, in percent of the total number of faeces (%FO). For boxplots: boxes contain the middle 50% of the data; horizontal solid lines in boxes represent the median value, and the white diamond the mean, end of vertical lines represent the minimum and maximum value, and small circles are outliers. Total number of faeces analyzed was 48 in Riau_1, 78 in Riau_2, 12 in Bankga_1 and 21 in Bangka_2.
Table 1: Frequency of occurrence (FO) and volume (VO) of food items found in faeces of the small carnivore community, with their confidence intervals (CI). Volumes are calculated either in overall diet, i.e. among all faeces (VOt), or only in faeces where the food item is present (VOp).

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<th>Riau_1</th>
<th>Riau_2</th>
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<td></td>
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</tr>
<tr>
<td>Grass</td>
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<td></td>
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<td></td>
<td></td>
</tr>
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<td>Molluscs &amp; Crustaceans</td>
<td>3.2</td>
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<td>8.4</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
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<td>Eggs</td>
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<td>2.1</td>
<td>0.1</td>
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</tr>
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<th>Food Item</th>
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<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
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</thead>
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<td>43.4</td>
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<td>2.0</td>
<td>26.5</td>
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<tr>
<th>Food Item</th>
<th>Riau</th>
<th>Riau_1</th>
<th>Riau_2</th>
<th>Bangka</th>
<th>Bangka_1</th>
<th>Bangka_2</th>
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<tr>
<td>Only one value of VOp</td>
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<td>Grass</td>
<td>7.9</td>
<td>4.8</td>
<td>11.6</td>
<td>6.8</td>
<td>2.7</td>
<td>12.3</td>
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<tr>
<td>Birds</td>
<td>1.2</td>
<td>0.1</td>
<td>2.9</td>
<td>0.9</td>
<td>0</td>
<td>2.7</td>
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<tr>
<td>Molluscs &amp; Crustaceans</td>
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<td>0</td>
<td>0.2</td>
<td>0</td>
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<td>0.2</td>
</tr>
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<td>Eggs</td>
<td>1.1</td>
<td>0.1</td>
<td>2.6</td>
<td>0.7</td>
<td>0</td>
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NA: Not applicable (no occurrence of food item) / NA1: Cannot calculate confidence intervals with bootstrap method because only one value of VOp
Table 2: Linear models used to test for statistical significance of differences in food items frequency of occurrence (FO) and volume (VO) in faeces of the small carnivore community, among regions and plantations: results of analysis of variance and goodness of fit test. Volumes are calculated either in overall diet, i.e. among all faeces (VOt), or only in faeces where the food item is present (VOp). The symbol * indicates the significance level associated to the p-value: * for $P \leq 0.05$, ** for $P \leq 0.01$ and *** for $P \leq 0.001$. See material and methods section for Adjusted $R^2$ or Pseudo $R^2$ calculation.

<table>
<thead>
<tr>
<th>Model retained</th>
<th>Response Variable</th>
<th>Covariates</th>
<th>Random effect</th>
<th>Adjusted $R^2$ or Pseudo $R^2$</th>
<th>Analysis of variance</th>
<th>Difference tested</th>
<th>p-value</th>
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<td>Conditional $R^2$</td>
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<td>Small mammals</td>
<td>FO</td>
<td>Region</td>
<td>Plantation</td>
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<td>0.159</td>
<td>Riau versus Bangka</td>
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<td>Region</td>
<td>Plantation</td>
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<td>Plantation</td>
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<td>0.279</td>
<td>Riau versus Bangka</td>
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<td>0.042</td>
<td></td>
<td></td>
<td>0.022 *</td>
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<td></td>
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<td>Riau_1 versus Riau_2</td>
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<td>Bangka_1 versus Bangka_2</td>
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<td>Riau_2 versus Bangka_1</td>
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<td>Riau_1 versus Bangka_1</td>
<td>0.014 *</td>
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<td></td>
<td>Riau_1 versus Bangka_2</td>
<td>0.685</td>
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Appendix 7: Variograms to assess spatial autocorrelation for small carnivore observations

Variograms plotted semivariance against distance between observations (in meter). Variograms were initially plotted with no maximum distance between observations. Sometimes, over a certain distance between observations (“the threshold”), data were not representative anymore (too little observations). When it was the case, a variogram was plotted once again, but with this threshold used as the maximum distance between observations (max. distance): i.e. when distance between observations was over this threshold, they were ignored.

Faeces counts - Small carnivores

![Variogram plots for Riau_1, Riau_2, Bangka_1, and Bangka_2]

- **Riau_1**
  - With no max.distance
  - With no max.distance

- **Riau_2**
  - With no max.distance
  - With max.distance: 1200 m

- **Bangka_1**
  - With no max.distance

- **Bangka_2**
  - With no max.distance

={$\Rightarrow$} no spatial autocorrelation suspected
Spotlight counts - Small carnivores

**Riau_1**

With no max.distance

**Riau_2**

With no max.distance

With max.distance: 12000 m

**Bangka_1**

With no max.distance

**Bangka_2**

With no max.distance

氕 no spatial autocorrelation suspected
Spotlight counts - Wild small carnivores

Riau_1

With no max.distance

With max.distance: 5000 m

⇒ no spatial autocorrelation suspected

Riau_2

With no max.distance

With max.distance: 11 km

With max.distance: 2000 m

⇒ a point laid out the random variogram at 2000 m, but if we take into account only short distances between observations (below 2000 m) no spatial autocorrelation is suspected

Bangka_1

With no max.distance

With max.distance: 11 km

⇒ no spatial autocorrelation suspected
Spotlight counts - Wild small carnivores

Bangka_2

With no max.distance

With max.distance: 11 km

Spotlight counts - Leopard cat

Riau_1

Riau_2

With no max.distance

no strong spatial autocorrelation suspected
Spotlight counts - Common palm civet

Riau_1

With no max.distance

Riau_2

With no max.distance

Bangka_1

With no max.distance

Bangka_2

With no max.distance

⇒ no spatial autocorrelation suspected

Spotlight counts - Small-toothed palm civet

Bangka_1

⇒ no spatial autocorrelation suspected in Bangka_1
No small-toothed palm civet on Riau_2 nor in Bangka_2, and only one small-toothed palm civet on Riau_1:
no variogram computed

With no max.distance
Spotlight counts - Malay civet

⇒ No variograms were computed as there was only one or two observation per plantation

Spotlight counts - Domestic and feral cat

Riau_1

With no max.distance

Riau_2

With no max.distance

Bangka_1

With no max.distance

Bangka_2

With no max.distance

⇒ no spatial autocorrelation suspected
Appendix 8: Additional recommendations about management of HCV areas within oil palm landscapes

Control hunting/harvesting practices within the plantation

As reported by Azhar et al. (2013a), illegal hunting or poaching activities committed within oil palm plantations are posing an additional substantial threat to transient or resident species within oil palm landscapes. Apart from wild boars, civets and reptiles are the main targets of hunters/poachers in oil palm plantations (see section III.2.1.). Common palm civet, monitor lizard and pythons are preferentially harvested, mainly for their high commercial value in the illicit wildlife market (Shine et al., 1999b; Kasterine, 2012; Azhar et al., 2013a; Luskin et al., 2014). Leopard cats are also targeted, since they were found to be the second most numerous mammal species (after the common palm civet) sold on wildlife market in Jakarta (Shepherd, 2012). This ranking corresponds to what we have heard (through interviews) or opportunistically observed during field surveys on our study sites: within rat predators, the common palm civet and other civets were highly hunted, followed by snakes harvesting (mainly pythons); moreover, hunters/poachers encountered were either plantation workers or people from local communities, and their captures were mainly intended for selling in wildlife market.

By law or by international convention such as CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), hunting and commercial trade of most of those species are forbidden or restricted, so much of those activities are illegal. However, most poachers, even plantation workers themselves, are not aware of local laws regarding wildlife (personal observations, confirmed by Azhar et al. (2013a) for others plantations), and enforcement by plantation management is poor, be it voluntarily or not.

Banning of such activities is difficult in practices, notably because:
- Road network and traffic is intense within plantations, and human presence within the plantation is quasi permanent, may it be plantation workers or local people passing through. Consequently, hunting/poaching opportunities are numerous and thus harder to control. To be noted that plantation workers often represent a serious hunting/poaching threat (Azhar et al., 2013a).

54 According to Sherperd (2012), the leopard cat is protected under Indonesian law, and other species that are not protected may only be traded domestically or internationally following a harvest and export quota system. This is the case for the common palm civet, for which the quota is below 300 individuals and specifies that the animals are to be sold only alive as pets. But the author reported that those quotas are largely ignored by hunters and traders, and not enforced by authorities.

Wildlife species trade is monitored and regulated by governments via the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). International trade of species threatened with extinction and affected by trade (species listed in CITES Appendix I) are authorized in exceptional circumstances. For species listed in Appendix II (species not necessarily now threatened with extinction, but may become so unless trade is regulated), international commercial trade is allowed under certain circumstances ensuring to avoid over-exploitation incompatible with their survival. For species listed in Appendix III (species that are protected in at least one country, which has asked other CITES Parties for assistance in controlling the trade), species may be imported or exported only if the appropriate document has been obtained. The common palm civet is listed on Appendix III, the leopard cat, the pythons species mentioned, and most monitor lizard species are included in appendix II; almost all wild small or medium sized felids are classified under appendix I. (CITES, 2015b, a).
- Many people are struggling with poverty; for those, bushmeat is a substantial source of protein and hunting/poaching is a way to increase their income.
- Many smallholding enclaves may lie within the oil palm plantation, like in Bangka. These enclaves are not « owned » by the company, so the company has no right on these lands, and cannot enforce any hunting restrictions. And yet, those pockets of forest like habitat (most enclaves in Bangka plantations are complex rubber agroforests) may harbour wildlife, notably small carnivores; so banning hunting of rat predators within those enclaves would very probably enhance the persistence of these species in oil palm landscape.
- Hunting is often encouraged by plantation managers, to control pests such as rodents or wild boar (Azhar et al., 2013a; Luskin et al., 2014); this was confirmed by our interviews.

We recommended that, within the oil palm plantations, commercial trade at a large scale should be banned for any species, and only subsistence hunting (harvesting levels limited by consumption needs and not profit-driven) should be allowed, excluding rat predator species and species protected by law or ratified conventions (such as rare, threatened or endangered species). But on what criteria to decide what fall under subsistence? Another option would be to permit hunting within oil palm landscapes only for widespread agricultural pest species such as wild boars. Luskin et al. (2014) suggested that, if sustainably managed, hunting wild boars in oil palm plantations may reduce crop damage while satisfying cultural practices and provide meat and income to local people.

Human and financial resources are needed for control and enforcement, as tackle next.

**Put in place a dedicated team for biodiversity and conservation issues**

It is to remember that, according to RSPO Principles and Criteria (RSPO, 2013), identifying, managing and enhancing High Conservation Values (HCVs) within the oil palm concession is under the responsibility of the oil palm producer (see Principle 5: “Environmental responsibility and conservation of natural resources and biodiversity” and Principle 7: “Responsible development of new plantings”).

Environmental Impact Assessment (EIA) and High Conservation Value (HCV) assessment should be carried out, and the results incorporated in land use planning, management and operations (RSPO, 2013). As soon as the results of these assessments are available, and before land clearing, a dedicated team in the local management organigram should be responsible for biodiversity and conservation issues, in close collaboration with the agricultural department. Practical handbooks and other guidelines documents are available for capacity building of such teams within oil palm company, to assist the company in implementing management interventions (including: Bakewell et al. (2012); Lim et al. (2012); ZSL (2012, 2013); RSPO (2013)).

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55 See notably criteria 5.2: “The status of rare, threatened or endangered species and other High Conservation Value habitats, if any, that could exist in the plantation or that could be affected by plantation or mill management, shall be identified and operations managed to best ensure that they are maintained and/or enhanced”.

56 The ideal would be that this company team is associated to the external consultant team carrying out the EIA and HCV assessment. And that they actively participate in land-use and management planning for the coming development.
Encroachment of HCV areas set aside, as well as illegal logging and hunting/poaching are the main threats for rat predators, but also the main challenge for the company. Information and sensitization among workers and local communities living within and around the oil palm plantation is a first step. In complement, monitoring and enforcement (within oil palm blocks and HCV areas) should be put in place.

However, enforcement may be difficult to implement, because of reasons mentioned above in hunting section (which also applied for many other conservation issues), but also because of the legitimacy of oil palm management for enforcement (what kind of collaboration with local police should be put in place for arrest and prosecution?), and of the risk of corruption.

The cost of such actions, may it be for sensitization, monitoring or enforcement may also repel or restrain some companies. Some often argue that such costs -of conservation- should not be bared only by the oil palm industry, and advocate the need of incentive for large private landowners to conserve biodiversity (Bateman et al., 2015). But most of all, companies must accept sustainability as a business model and not as an add-on burden (Paoli et al., 2010).