



Evolution de la migration à longue distance chez les oiseaux

Paul Dufour

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THÈSE

Pour obtenir le grade de

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Présentée par

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LECA de Grenoble

préparée au sein du **Laboratoire d'Ecologie Alpine**
dans l'**École Doctorale de Chimie et Sciences du Vivant**

**Evolution de la migration à longue
distance chez les oiseaux**

**Evolution of long distance migration in
birds**

Thèse soutenue publiquement le **26 mars 2021**, devant le jury
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LISTE DES ARTICLES

Article 1.

Dufour P., Descamps S., Chantepie S., Renaud J., Guéguen M., Schiffers K., Thuiller W. & Lavergne S. (2020) Reconstructing the geographic and climatic origins of long distance bird migrations. *Journal of Biogeography*, 47(1): 155– 166.

Article 2.

Dufour P., Crochet P.-A., Condamine L.F. & Lavergne S. How the evolution of geographic migration shaped an atypical latitudinal diversity gradient of shorebirds ? En cours de révision dans *Systematic Biology*

Article 3.

Dufour P., Guerra Carande J., Renaud J., Renoult J.P., Lavergne S. & Crochet P.-A. (2020) Plumage colouration in gulls responds to their non-breeding climatic niche. *Global Ecology and Biogeography*, 29(10): 1704–1715.

Article 4.

Dufour P., Wojczulanis-Jakubas K., Renaud J., Jakubas D., Lavergne S. & Descamps S. A two- fold migration distance does not have breeding consequences in a long-distance migratory seabird with high flight costs. Sous presse, *Marine Ecology Progress Series*.

Article 5.

Dufour P., de Franceschi C., Guéguen M., Doniol-Valcroze P., Jiguet F., Crochet, P.-A.* & Lavergne S.* Evolution of a new migratory route in an Asian passerine. En préparation. (co-dernier auteurs)

Article 6.

Dufour P., de Franceschi C., Hellström M., Illa M., Doniol-Valcroze P., Tillo S., Fair Isle Bird Observatory, VRS Castricum, Lavergne, S. & Crochet, P.-A. Siberian bird vagrants occurring in Europe may have become regular migrants. En préparation.

EN ANNEXES

Bliard L., Paquet M., Robert A., **Dufour P.**, Renoult J.P., Grégoire A., Crochet P.-A. Covas, R. & Doutrelant C. (2020) Examining the link between relaxed predation and bird colouration on islands. *Biology Letters*, 16 : 20200002.

Barnagaud, J.-Y., Mossion, R., Brockerhoff, E., **Dufour, P.**, Pavoine, S., Deconchat, M. and Barbaro, L. Ecological traits mediate habitat partitioning of alien and native species of bird assemblages in New Zealand landscapes. En cours de révision dans *Diversity and Distributions*.

AVANT-PROPOS

C'est le naturalisme et plus particulièrement l'ornithologie qui m'ont mené à la recherche en biologie évolutive. En tant qu'ornithologue de terrain, j'ai toujours été très intéressé par les questions de systématique, d'identification et d'estimation de l'âge chez les espèces cryptiques. J'ai donc pris beaucoup de plaisir à pouvoir continuer à observer les oiseaux en dehors de la thèse par le biais des voyages ou des sessions de terrain car ce fut le moyen d'une part de décrocher de l'ordinateur, et d'autre part de confronter les connaissances scientifiques accumulées à la réalité du terrain. J'ai ainsi alloué une partie de mon temps de thèse à l'écriture de quelques articles naturalistes qui ont été publiés dans des revues non indexées et dont la liste est donnée en bas de page. Ces publications résultent soit d'observations fortuites, soit de l'approfondissement des critères d'identification sur des groupes que j'affectionne particulièrement, soit de publications de la Commission de l'Avifaune Française (CAF). Ces dernières sont pour moi le moyen d'essayer de concilier les connaissances apportées par le monde scientifique académique et le milieu naturaliste qui, s'ils étaient proche par le passé, semble aujourd'hui commencer à s'éloigner. J'espère parvenir à continuer de trouver le temps d'écrire ce genre d'articles dans le futur.

Dufour P., Gernigon J. & Crochet P.-A. Identification and occurrence of Elegant x Sandwich tern hybrids in Europe. Sous presse, *Dutch Birding*

Dufour P. & Crochet P.-A. (2020) Orange-billed terns – ID PHOTO GUIDE. *Birdwatch*, 6 : 32-37.

Dufour P., Dubois P.-J., Jiguet F., Pons J.-M., Veyrunes F., Wroza S. & Crochet, P.-A. (2020) Décisions prises par la Commission de l'Avifaune Française (2016-2019) – 15e rapport de la CAF. *Ornithos*, 27(3) : 154-169.

Dufour P., Sallé L., Morisot A., de Franceschi C. & Delahaie B. (2020) Are Red-rumped Swallows starting to overwinter in the Western Palearctic? *Dutch Birding*, 42 : 111-113.

Dufour P. & Crochet P.-A. (2020) Identification of African and American Royal Terns (*Sterna albididorsalis* and *S. maxima*) based on photographic evidence and sound recordings. *Dutch Birding*, 42 : 1-24.

Dufour P., Veyrunes F. & la CAF (2019). Inscription du Pélican frisé *Pelecanus crispus* en catégorie A de la Liste des oiseaux de France. *Ornithos*, 26(6) : 298-307.

Crochet P.-A., Arnaud A., Béchet A., [...] & **Dufour P.** (2019). Le Flamant nain *Phoeniconaias minor* admis en catégorie A de la Liste des oiseaux de France. *Ornithos*, 26(6) : 292-297.

INTRODUCTION GENERALE

1 – Préambule : Evolution de la perception et des théories de la migration

Je m'intéresserai dans cette thèse à la migration définie comme l'ensemble des déplacements périodiques intervenant au cours du cycle annuel d'une espèce, entre son aire de reproduction et une autre aire en dehors de sa période de reproduction. De nombreux animaux effectuent des mouvements migratoires, parmi eux les oiseaux nous offrent l'une des plus spectaculaires : plusieurs milliards d'individus passent deux fois par an d'un hémisphère à l'autre et certaines espèces sont capables de réaliser des vols de plus de 10 000 km sans s'arrêter (Moreau 1972, Gil et al. 2009).

C'est donc d'abord parce qu'elle fascine les humains que la migration des oiseaux est la plus étudiée depuis toujours. Aujourd'hui la migration des oiseaux figure comme l'un des sujets les plus étudiés par la communauté scientifique, et cette passion de l'Homme pour comprendre ce phénomène de la migration remonte jusqu'à l'Antiquité. Ce sont ainsi de nombreuses théories qui ont été proposées depuis plusieurs siècles pour tenter d'expliquer ces disparitions et réapparitions d'oiseaux au fil des saisons et ce n'est que relativement récemment dans son histoire que l'Homme a compris où disparaissaient les oiseaux migrateurs (voir même très récemment chez certaines espèces, Smith et al. 2014).

Avant d'aborder la question de l'évolution de ce comportement, nous allons rapidement revenir sur l'évolution de la perception de la migration saisonnière (voir définitions dans l'Encadré 1) par l'Homme. En effet, si comprendre comment a évolué la migration dans l'histoire géologique de la Terre figure aujourd'hui comme l'une des grandes pièces manquantes au complexe puzzle de la migration, il est également intéressant de se rendre compte du chemin parcouru par les nombreux scientifiques au cours des siècles précédents. De façon surprenante, nous allons voir comment ces considérations passées ont également façonné notre vision de l'évolution de la migration.

C'est dans les notes de terrain d'Aristote, philosophe grec de l'Antiquité, qu'on retrouve les premières références à la migration des oiseaux (Stresemann 1951). Il développe notamment le mythe que les oiseaux migrateurs hibernent pour passer l'hiver. Ce mythe a très longtemps persisté comme le suggère une gravure sur bois du 16^e siècle montrant des pêcheurs scandinaves remontant un filet d'hirondelles hibernantes du fond d'un lac (Olaus Magnus in Fisher & Higgens 1996 ; Figure 1a). Encore au 18^e siècle, Linné (naturaliste

suédois) pensait que les hirondelles disparaissaient pour hiberner dans les marécages à l'automne avant de réapparaître au printemps (Schüz 1971).

Aristote croyait également que certaines espèces se transformaient en d'autres espèces à l'automne. Ainsi il pensait que les rougequeue à front blanc (*Phoenicurus phoenicurus*) se transformaient en rougegorges familier (*Erithacus rubecula*) lorsque l'hiver approchait, ce qui coïncidait avec le départ de l'un pour ses quartiers d'hivernage africains et l'arrivée de l'autre depuis ses aires de reproduction d'Europe du Nord et centrale. Au 12^e siècle, l'évêque Giraud le Cambrien relate le mythe que les bernaches nonnettes (*Branta leucopsis*) hivernant par milliers en Irlande naissaient vraisemblablement à partir d'arbres situés à proximité de la mer (voir Gerald of Wales 1893). Il explique dans ses écrits, que personne n'ayant jamais vu ces oiseaux se reproduire (elles nichent au Groenland où aucun navigateur ne s'était rendu à cette époque), la seule explication possible à leur arrivée massive au-dessus des mers irlandaises à l'automne était qu'elles naissaient là, directement dans l'océan. Ainsi, on a longtemps pensé que les pouces-pieds avec leur forme conique surmontée d'un « cou », qui s'accrochent à proximité du rivage étaient en réalité des fruits qui donnaient naissances aux bernaches à l'automne (Figure 1b-c). L'oiseau a donc été nommé '*Barnacle goose*' et les pouces-pieds '*Goose barnacles*'. Même s'il ne faisait pas l'unanimité (Albert le Grand le qualifiait de complètement absurde au 15^e siècle), ce mythe s'est tout de même perpétué au fil des siècles jusqu'à ce qu'un naturaliste britannique, John Hill, publie en 1751 (Hill 1751) une critique à la Royal Society of London attribuant le mythe à un groupe de pêcheurs ignorants ayant pris pour des plumes les filaments qui dépassent de ces crustacés. Il apporte également la preuve que des navigateurs hollandais ont observé ces oiseaux en nombres considérables dans les terres arctiques en train de couvrir leurs œufs, exactement comme le font les autres oies. La disparition saisonnière de certaines espèces d'oiseaux est donc largement expliquée par des phénomènes de métamorphose entre espèces, mythe central au sein des croyances antiques et médiévales concernant le monde vivant (Gouyon et al. 1997).

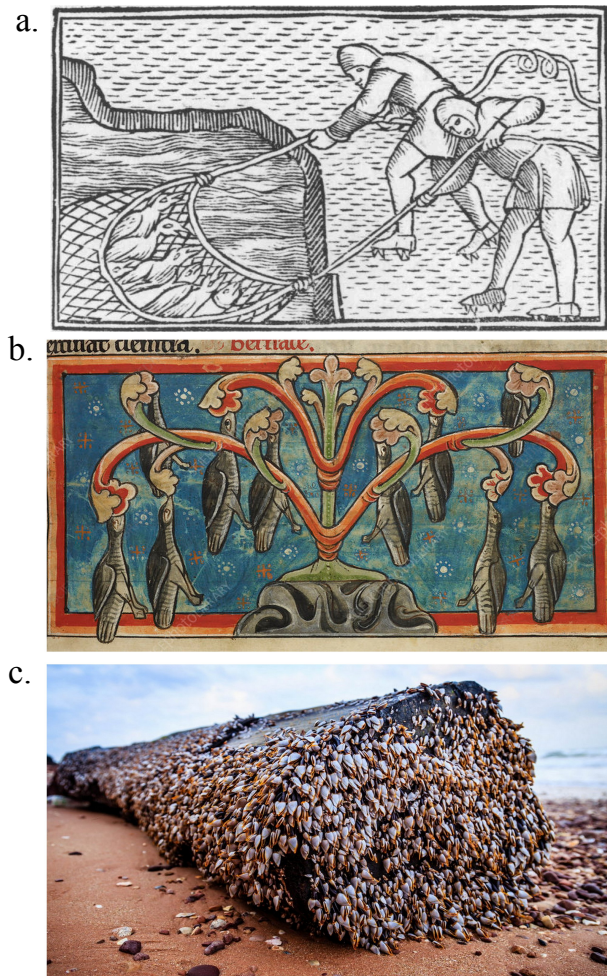


Figure 1. (a) Cette gravure sur bois du 16^e siècle représente des pêcheurs remontant un filet plein d'hirondelles en hibernation au fond d'un lac (Olaus Magnus in Fisher & Higgens 1996). (b) Représentation de « l'arbre à Bernaches nonettes » (*Barnacle Goose* en anglais ; tiré de British Library Harley). (c) Photographie des Pouces-pieds (*Goose barnacle* en anglais ; tiré de Patiparn46/Shutterstock.com). Ces deux dernières images illustrent le mythe de la naissance des Bernaches nonettes pour expliquer leur arrivée par milliers sur leurs quartiers d'hivernages irlandais.

Les premières interprétations sur le comportement migratoire, toujours valides aujourd'hui, sont à attribuer à l'Empereur Frédéric II (Empereur du Saint-Empire Romain-Germanique, 12^e siècle). Il est le premier à ainsi proposer le rôle du froid et du manque de nourriture comme cause du départ des oiseaux migrateurs et explique ainsi leur retour progressif le printemps venu (Stresemann 1951). Il suppose également en étudiant les vols en 'V' des grues cendrées (*Grus grus*) que l'oiseau en tête doit régulièrement être remplacé pour optimiser le partage de dépense énergétique. Il faudra attendre 1702 et Von Pernau (ornithologie autrichien) pour voir apparaître l'idée que la migration pourrait être un comportement prédéterminé. Il réalise que les migrateurs ne partent pas exclusivement à cause du froid et du manque de nourriture mais aussi à cause d'un « comportement naturel caché » (Berthold 2001). Johann Andreas Naumann (ornithologue allemand du 18^e siècle) fait la première description de l'agitation nocturne des oiseaux migrateurs et propose l'idée d'un programme inné de la migration (Berthold 2001). L'étude de la migration s'est ensuite intensifiée à partir du 19^e siècle, époque durant laquelle Farner (1955) distingue deux périodes : une période d'*observations* de 1825 à 1925 où Brehm, Palmen et Wallace notamment relatent une série d'observations, d'idées et de théories qui se sont avérées plus ou moins vraies, puis le début de la période d'*expérimentations* à partir de 1925. Rowan (1925) réalise ainsi les premières expérimentations sur des juncos ardoisés (*Junco hyemalis*) au Canada en exposant notamment les oiseaux à des durées de jour variable à différentes périodes de l'année. En montrant une reprise du chant et du développement des gonades, il suggère que la migration est aussi influencée par les hormones sexuelles (Rowan 1925).

Parallèlement à ça, le début du 20^e siècle a été marqué par le développement de la technique du baguage pour mettre en évidence le déplacement des oiseaux entre deux points donnés et par la création de plusieurs observatoires (ex. sur Heligoland en Allemagne) qui ont permis de mieux connaître les routes migratoires empruntées par de nombreuses espèces (Berthold 2001). Depuis, de très nombreuses stations de baguage ont été mises en place dans le monde et une quantité impressionnante de données biométriques et de recaptures ont été collectées. Ces informations ont majoritairement contribué à notre compréhension des mouvements migratoires. L'utilisation des nouvelles technologies depuis la fin du 20^e siècle, permet désormais de suivre les mouvements d'individus sur l'ensemble de leur cycle annuel (Bridge et al. 2011) ou en très grandes quantités (radars météorologiques ; voir Rosenberg et al. 2019), elles fournissent une nouvelle source de données pour aller encore plus dans l'étude du mouvement migratoire.

ENCADRE 1. La migration saisonnière et les différents mouvements qu'effectuent les oiseaux

On appelle migrateur, une espèce qui effectue un mouvement de **migration saisonnière**. Ce comportement peut être défini comme l'ensemble des déplacements périodiques intervenant au cours du cycle annuel d'un animal, entre une aire de reproduction et une aire où il séjourne un temps plus ou moins long, en dehors de la période de reproduction (Dorst 1962). Les aires de reproduction et d'hivernage fréquentées sont généralement les mêmes au cours de la vie d'un individu.

Ces mouvements ne doivent pas être confondus avec les mouvements de **migration irruptive** qui interviennent de manière périodique. Fréquent chez les espèces migratrices et souvent de grandes ampleurs, ils ont pour cause principale la raréfaction de ressources alimentaires dans certaines zones habituelles d'hivernages. De même, la **migration altitudinale** concerne des mouvements, aléatoires selon les années, vers les basses altitudes pour fuir des conditions devenues trop difficiles localement.

On notera également les **mouvements d'erraticisme** qui concernent généralement, dans les latitudes tempérées, de jeunes oiseaux qui effectuent des déplacements de prospection aléatoire à la recherche de territoire ou de nourriture. Les causes de ces types de mouvements restent encore peu connues aujourd'hui (voir PARTIE 3.B et la DISCUSSION).

Enfin, il ne faut pas confondre migration saisonnière et les mouvements de **dispersion**, effectués par toutes les espèces sans exception. On distingue généralement la **dispersion juvénile** qui représente la distance entre le lieu de naissance et le lieu de première reproduction et la **dispersion de reproduction** qui représente la distance entre deux lieux de reproduction successifs. Bien qu'un individu qui voyage sur des distances importantes semble plus susceptible de coloniser de nouveaux territoires, les liens entre dispersion et migration ne sont pas pour autant évidents (voir PARTIE 3.B). En effet, de nombreux oiseaux migrants sont **philopatriques**, ce qui veut dire qu'ils ont tendance à instinctivement revenir à l'endroit où ils sont nés, pour se reproduire

Au cours de cette thèse, nous utiliserons le terme de **stratégie de migration** pour définir les différents degrés de migration saisonnière. On distinguera notamment les *migrateurs stricts* pour lesquels toutes les populations migrent vers une aire d'hivernage en dehors de la saison de reproduction ; les *migrateurs partiels* où l'espèce se divise en une fraction de populations migratrices et une fraction de populations résidentes ; en opposition aux *résidents* qui en dehors des mouvements de dispersion au sein de leur aire de distribution, sont présents tout au long de l'année dans leur zone de reproduction (Rappole 2013).

Au sein des espèces migratrices, nous distinguerons généralement trois classes de **distance de migration**. Ainsi les espèces effectuant des **migrations de longues distances** seront considérées comme celles voyageant entre l'aire de reproduction et d'hivernage sur plus de 2000 kilomètres. À l'inverse des *espèces migratrices sur de courtes distances* qui voyagent sur moins de 2000 kilomètres et des *espèces à distances de migration variables* pour lesquelles certaines populations voyagent sur plus de 2000 kilomètres tandis que d'autres ne parcourent que de faibles distances (Rappole 2013).

2 – L'évolution biogéographique de la migration saisonnière

a) *Pourquoi, et depuis quand, les oiseaux migrent-ils ?*

Avant de répondre à la question de « depuis quand existent les oiseaux migrateurs ? », il s'agit dans un premier temps de répondre à la question de pourquoi migrent les oiseaux.

La migration saisonnière est aujourd'hui majoritairement perçue comme une adaptation permettant l'utilisation récurrente d'un environnement saisonnier, au même titre par exemple que l'hibernation (Winger et al. 2019, voir aussi Bell 2000, Alerstam et al. 2003). Cette perception du comportement migratoire est assez récente et elle a été longtemps mise de côté, possiblement à cause du caractère absurde des premières hypothèses historiques. En effet, l'hypothèse d'Aristote selon laquelle les oiseaux migrateurs hibernaient pour passer l'hiver a été radicalement oubliée dès lors qu'il a été observé que les oiseaux migrateurs parcouraient en réalité des milliers de kilomètres pour aller passer l'hiver dans des contrées lointaines. Ainsi en rejetant cette hypothèse, les premiers scientifiques ont vraisemblablement favorisé une vision de la migration comme un mécanisme permettant de tirer profit de l'abondance des ressources disponibles et d'une faible compétition (i.e. moins d'espèces) dans les zones saisonnières (tempérées) par rapport aux zones tropicales (Cox 1968, Rappole & Jones 2002) et cette vision a longtemps perduré, façonnant notre vision de l'évolution de la migration (voir paragraphe suivant et Winger et al. 2019). Pourtant l'hypothèse d'Aristote, aussi fausse soit-elle, indiquait déjà une vision de la migration comme adaptation pour survivre aux conditions environnementales de la saison hivernale. Et il a d'ailleurs été montré qu'une espèce d'oiseau, l'engoulevent de Nuttall (*Phalaenoptilus nuttallii*) pouvait occasionnellement hiberner (Jaeger 1948, Brigham 1992), tout comme d'autres adaptations hypothermiques (ex. Douglas et al. 2017), physiologiques (ex. Swanson & Garland 2009) ou comportementales (ex. Heinrich 2003) ont été mises en évidence chez de nombreuses espèces (voir Swanson & Garland 2009). Ainsi, si cette perception de la migration comme adaptation à la saisonnalité a été largement renforcée par les études globales montrant la corrélation positive du nombre d'espèces migratrices avec la saisonnalité (Somveille et al. 2013), ces diverses adaptations observées chez les espèces persistant toute l'année dans les environnements saisonniers (ex Heinrich 2003 ; Swanson & Garland 2009) l'ont fait tout autant.

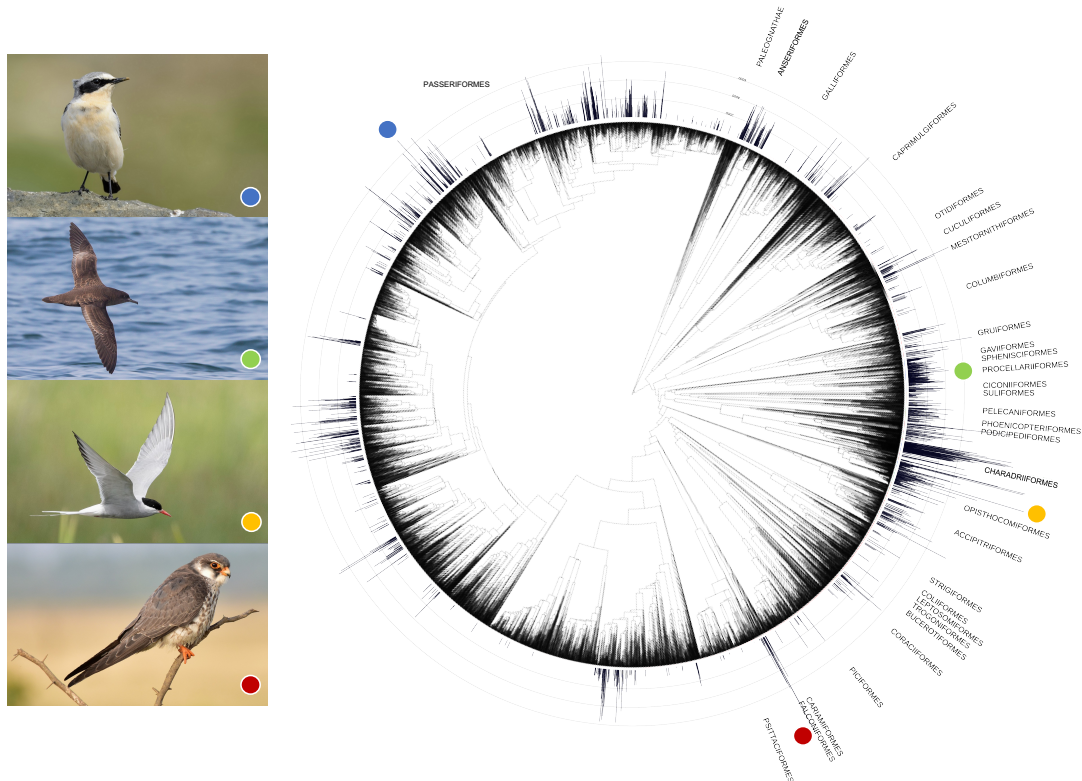
Tandis qu'il est intuitif de penser que l'augmentation de la survie puisse inciter un animal à quitter un territoire lorsque les conditions environnementales ne sont plus favorables et que les ressources viennent à manquer (et ce malgré le coût de la migration ; Norris 2005), il est plus difficile de concevoir pourquoi il va revenir le printemps suivant. Il a été longuement

proposé que cette décision de retour avait une base génétique au même titre que la décision de migrer ou la direction de la migration peuvent l'être (Berthold 1999). Aucune hypothèse satisfaisante n'a été proposée pour expliquer ce contrôle génétique. Plus récemment, Winger et al. (2019) ont suggéré que c'est l'augmentation du succès de reproduction permis par un retour sur des sites de reproduction efficaces qui sous-tendrait le contrôle endogène de la migration saisonnière comme un aller-retour.

Dans cette perspective où la saisonnalité est un aspect fondamental de la migration (Alerstam et al. 2003), on peut supposer que la migration est apparue en même temps que les saisons elles-mêmes. En effet, le climat terrestre n'a pas toujours été celui que nous connaissons aujourd'hui et les oiseaux modernes probablement apparus au Crétacé entre 70 et 100 millions d'années (Jetz et al. 2012, Prum et al. 2015), ont dû faire face à de profonds bouleversements terrestres avant d'occuper leurs distributions actuelles. Ainsi, le climat terrestre s'est particulièrement refroidi depuis le milieu de l'Eocène (autour de 34 millions d'années - Ma), entraînant l'apparition des premiers cycles saisonniers (Mosbrugger et al. 2005). Ce refroidissement s'est accompagné d'un retrait progressif des biomes tropicaux, qui occupaient autrefois les hautes latitudes, vers les latitudes que nous connaissons aujourd'hui (ex. Pound et al. 2012, Pound & Salzmann 2017). Cette contraction de l'habitat tropical coïncide également avec l'expansion des biomes ouverts : steppes, prairies, toundra et, dans une moindre mesure, taïga. Ces profondes modifications de la distribution des habitats ont eu des répercussions sur la distribution des espèces (Mayr 2009), comme le prouve la présence de fossiles d'espèces aujourd'hui tropicales à de hautes latitudes, mais elles ont vraisemblablement aussi eu des répercussions sur l'émergence du comportement migratoire. Si la migration saisonnière a évolué comme une stratégie prépondérante chez les oiseaux pour palier l'augmentation de la saisonnalité et probablement grâce à leur capacité de vol, on ne sait toujours pas pourquoi la migration et de surcroît la migration à longue distance ont évolué plus fréquemment dans certaines lignées évolutives plutôt que d'autres (voir Encadré 2).

ENCADRE 2. Aperçu de la distribution phylogénétique des espèces migratrices sur de longues distances

Les espèces migratrices et notamment celles migrant sur des distances importantes (> 2000 kilomètres) se retrouvent en de nombreux endroits de l'arbre phylogénétique des oiseaux. Cela suggère que ce comportement est un trait labile, qui est apparu (et disparu) à de nombreuses reprises au cours de l'histoire évolutive des oiseaux. Une mesure du signal phylogénétique de la distribution des espèces migratrices sur de longues distances indique néanmoins une distribution non-aléatoire sur la phylogénie (λ de Pagel = 0.63; Pagel 1999 ; $\lambda=0$ indiquant une absence de signal phylogénétique, $\lambda=1$ indiquant que le trait a évolué tel que la topologie originale de la phylogénie le suggérait). En effet, certains ordres comptent une proportion plus grande d'espèces migratrices et notamment sur de longues distances. Parmi ceux-ci, les Charadriiformes (369 espèces ; Jetz et al. 2012) sont majoritairement migrateurs (migrateurs strict et partiel ; 66%) et 54% d'entre eux migrent sur des distances importantes. Les Ansériformes (160 espèces) comptent 50% d'espèces migratrices dont 20% dont les aires de reproduction et d'hivernage se situent à plus de 2000 km. Enfin, les Procellariiformes (128 espèces) sont majoritairement migrateurs (99%) mais leurs mouvements en dehors de la période de reproduction sont encore trop peu connus pour affirmer qu'il s'agit d'une migration saisonnière comme définie dans l'ENCADRE 1.



Arbre phylogénétique des oiseaux et distribution des espèces migratrices. L'arbre phylogénétique est issu de la combinaison du squelette phylogénétique ('backbone') de Prum et al. (2015) avec l'arbre de 9993 espèces de Jetz et al. (2012). Les noms indiquent 35 des 39 ordres d'oiseaux reconnus (les Struthioniformes, Tinamiformes, Rheiformes, Apterygiformes et les Casuariiformes sont rassemblés sous le nom Palaeognathae). Les barres noires verticales représentent une estimation de la distance de migration parcourue par chaque espèce (elle est considérée comme nulle pour les espèces résidentes). Les cercles extérieurs représentent les limites de 2000, 4000 et 6000 kilomètres. Les espèces souvent considérées comme migratrices sur de longue distance voyagent sur des distances supérieures à 2000 kilomètres. Les photographies illustrent quelques-uns des plus emblématiques des grands migrateurs, de haut en bas : *Oenanthe oenanthe* (© Arda Dönerkayalı), *Ardenna grisea* (© Paul Jones), *Sterna paradisaea* (© Bryan Calk), *Falco amurensis* (© TheNatureTrust).

b) Retracer l'histoire biogéographique pour comprendre l'évolution de la migration ?

La géographie très complexe de la migration saisonnière a suscité de nombreux débats sur la manière de concilier les explications mécanistes sur les origines de la migration des oiseaux avec l'histoire biogéographique des lignées migratoires (Salewski & Bruderer 2007, Winger et al. 2014, Winger et al. 2019). Plusieurs théories historiques ont été développées et ont eu une influence persistante sur notre compréhension de l'évolution de la migration. Parmi celles-ci : (1) la *Southern-home theory* (SHT), proposant que la migration soit apparue à partir d'oiseaux tropicaux sédentaires ayant tiré profit des ressources abondantes et d'une compétition plus faible dans les latitudes supérieures, tout en revenant passer l'hiver dans les latitudes tropicales, et (2) la *Northern-home theory* (NHT), stipulant que la migration ait évolué à partir d'oiseaux sédentaires en zones tempérées pour éviter la rigueur hivernale et le manque de ressource (voir les schémas de l'Encadré 3 et aussi Gauthreaux 1982, Louchart 2009).

Ainsi les scientifiques ont longtemps cherché à trouver une réponse universelle à l'évolution géographique de la migration (notamment à l'aide des hypothèses NHT et SHT ; Encadré 3). Des résultats très différents suivant les clades et l'échelle considérée ont été trouvés (Outlaw et al. 2003, Winger et al. 2012, Winger et al. 2014) et même si les avancées méthodologiques ont permis d'aborder cette question sur de plus larges échelles (chez les *Emberizoidea*, 823 espèces ; Winger et al. 2014), en reconstruisant en simultanée l'évolution passée des aires de reproduction et d'hivernage (Winger et al. 2014), l'universalité d'une telle réponse à l'évolution de la migration est apparue peu probable.

Afin de comprendre comment la migration est apparue et a évolué, les scientifiques reconstruisent généralement l'évolution d'un caractère ancestral, ici la stratégie de migration (migrateur strict, partiel ou résident), à partir de l'histoire phylogénétique de la lignée (voir par ex. Rolland et al. 2014). Cette reconstruction d'états ancestraux s'appuie sur un modèle statistique d'évolution, généralement proche des modèles utilisés en phylogénétique pour déterminer le chemin évolutif le plus probable entre différents caractères (Brooks 1999, Pupko et al. 2000, Pagel et al. 2004, O'Meara 2012). D'autre part, ils peuvent également utiliser les distributions saisonnières des espèces (Matzke 2014), qui représentent plus ou moins indirectement les stratégies de migration, pour estimer l'origine et les mouvements géographiques passés afin d'inférer l'émergence et l'évolution de la migration. La reconstruction de ces mouvements biogéographiques peut être contrainte par différentes probabilités de passage entre deux aires géographiques (plus ou moins proches au cours de

l'histoire géologique de la Terre) et en calibrant certains points à l'aide des distributions de données fossiles.

Par contre, la reconstruction de l'origine géographique des lignées avec la dualité historique (NHT versus SHT) proposée pour expliquer l'apparition de la migration a longtemps engendré des confusions sur l'origine de la migration. Tout comme notre compréhension des origines biogéographiques des lignées migratrices a été obscurcie par la biogéographie complexe inhérente à la migration saisonnière. La région géographique d'où la migration a évolué a ainsi souvent été confondue à tort avec l'origine géographique de la lignée (Salewski & Bruderer 2007). Si nous prenons l'exemple des Tyrannidae, ils sont originaires d'Amérique du Sud et se sont largement diversifiés dans les tropiques (Ericson et al. 2002) et plusieurs espèces migratrices se reproduisent en Amérique du Nord et hivernent dans les forêts tropicales d'Amérique du Sud. Or puisque les ancêtres de ces espèces migratrices sont d'origine tropicale, les scientifiques ont longtemps suggéré que la migration ait de fait évolué à partir des tropiques selon l'hypothèse SHT (ex. Outlaw et al. 2003, Licona-Vera & Ornelas 2017). Pourtant la migration a pu également apparaître en Amérique du Nord selon l'hypothèse NHT, chez des espèces sédentaires qui avaient déjà colonisées ces latitudes (à la suite de mouvements de dispersion).

Afin de mieux séparer origine géographique et origine de la migration, Salewski et Bruderer (2007 ; Encadré 3) puis Winger et al. (2019), ont proposé une théorie de l'évolution de la migration indépendante du cadre géographique. Ils ont ainsi proposé de distinguer les comportements de migration et de dispersion (voir Figure 2 et Encadré 1). Par exemple, une espèce tropicale sédentaire peut étendre son aire de répartition dans des zones plus tempérées par des mouvements de dispersion progressive, et ce faisant, la sélection peut amener la population à devenir migratrice dans les parties de son aire de répartition qui sont les plus saisonnières (voir Figure 2). De cette façon, la migration saisonnière peut évoluer au sein d'une lignée d'origine tropicale à mesure que celle-ci étend son aire de répartition vers le pôle. En d'autres termes, la migration et l'aire de répartition géographique évoluent conjointement, de sorte qu'une lignée ne persistera pas dans les régions à forte saisonnalité à moins qu'elle ne s'adapte en devenant migratrice (voir aussi Figure 2). Les pressions de sélection qui déterminent l'évolution de la migration lorsque les populations étendent leur aire de répartition dans l'espace sont les mêmes que celles qui déterminent l'évolution de la migration lorsque la saisonnalité change au fil du temps. Ainsi Winger et al. (2019) suggèrent que la migration évolue par les mêmes mécanismes quelle que soit l'origine biogéographique (tempérée ou tropicale) de la lignée (voir aussi Bruderer & Salewski 2008).

Si la perception de Winger et al. (2019) de la migration, comme une adaptation qui facilite la persistance dans des environnements saisonniers, permet de découpler les origines biogéographiques des lignées migratoires et le mécanisme par lequel la migration évolue, retracer l'histoire biogéographique des lignées reste indispensable pour comprendre quand et comment les lignées se sont mises à occuper un environnement saisonnier. Elles peuvent en effet avoir des origines biogéographiques largement différentes. Par exemple, sur le continent Américain, les Tyrannidae sont vraisemblablement originaire de l'hémisphère sud (à partir du continent Gondwana) tandis que les Passerida (Parulines, Bruants, etc...) ont colonisé l'hémisphère nord (par le détroit de Bering) et tous deux présentent aujourd'hui des lignées avec des migrants longue distances utilisant le même système de migration néarctique-néotropical (Ericson et al. 2002, Winger et al. 2012, Winger et al. 2014). Retracer et dater l'histoire biogéographique peut permettre d'une part de retracer l'origine d'une lignée mais aussi d'autre part de savoir si la lignée a colonisé un environnement avant que celui ne devienne saisonnier ou à posteriori en adoptant un comportement de migration saisonnière. Enfin, cela permet également de suivre l'évolution des distributions saisonnières et l'évolution conjointe des aires de reproduction et d'hivernage. Par exemple, dans le cas d'une lignée d'origine tropicale, il est possible d'estimer si les mouvements de transitions latitudinales des zones de reproduction vers les pôles se sont aussi accompagnés d'une disparition des zones de reproduction des zones tropicales ancestrales.

Ces reconstructions biogéographiques suggèrent une complémentarité de ces deux théories historiques si on veille à ne pas confondre origine géographique de la lignée et de la migration. En effet, ces deux théories offrent un cadre théorique géographique pour conceptualiser les mouvements latitudinaux qui ont pu permettre la colonisation de milieux saisonniers, ou qui sont devenus saisonniers, et ainsi engendré l'évolution de la migration. Conserver ce cadre géographique semble donc indispensable pour étudier l'évolution de l'aire de répartition géographique des lignées contenant des espèces migratrices et des mécanismes par lesquels des aires d'hivernage et de reproduction disjointes apparaissent et se maintiennent dans le temps. Nous testerons le rôle respectif de ces deux théories dans l'évolution de la migration dans le CHAPITRE 1 de cette thèse et nous reviendrons sur ce cadre théorique et son application chez les Charadriiformes dans le CHAPITRE 2.

A: Evolution de la migration suite à la dispersion dans un environnement saisonnier

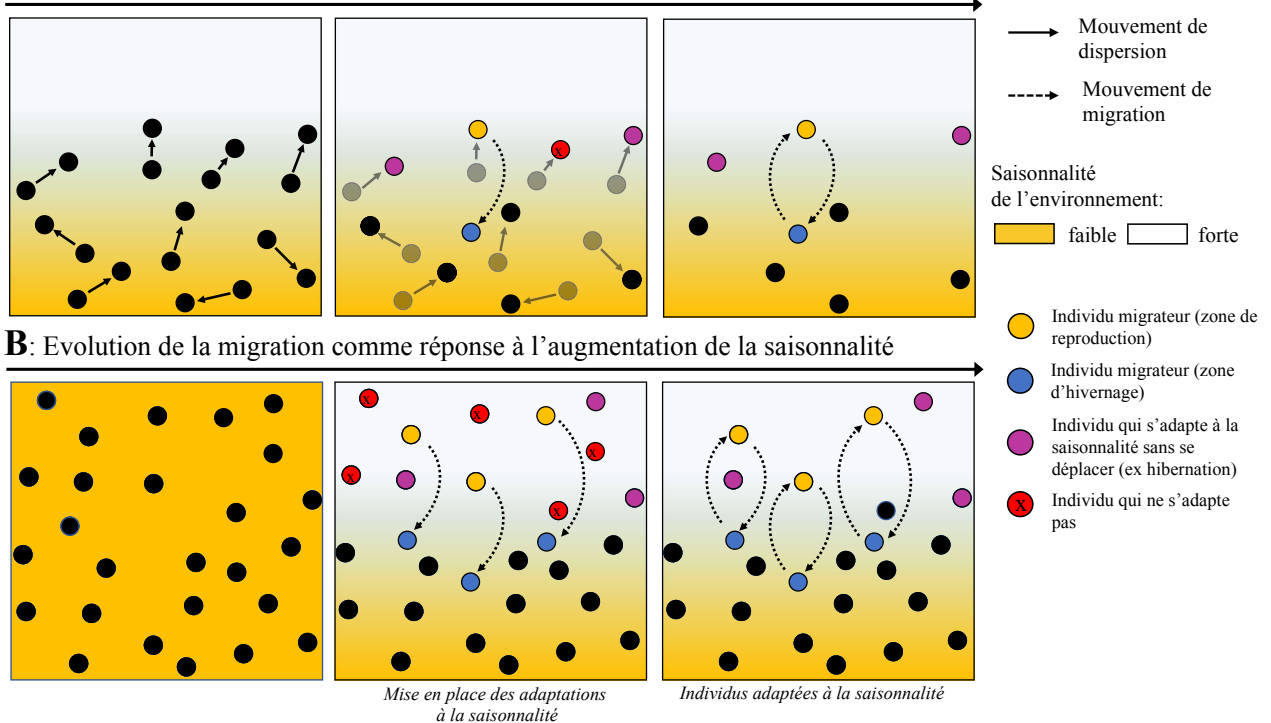


Figure 2. Evolution de la migration saisonnière comme réponse à la saisonnalité et quelle que soit l'origine biogéographique. Figure tirée et modifiée de Winger et al. (2019), elle-même inspirée de Salewski & Bruderer (2007). La couleur de fond indique la saisonnalité du milieu : blanc indique une forte saisonnalité tandis que jaune indique une faible saisonnalité. En (A), la migration évolue à la suite d'évènements de dispersion (plus ou moins orientés ; flèches pleines) vers un environnement saisonnier. Certains individus (orange) se déplacent en dehors de la période de reproduction (flèche pointillée) vers un environnement moins saisonnier (bleu). Ces individus peuvent avoir de meilleures chances de survie et la sélection devrait favoriser les individus qui retournent vers les sites de reproduction précédemment occupés. Ainsi la migration sera sélectionnée. Par ailleurs, certains individus s'adaptent à la saisonnalité sans entreprendre de mouvement (ex, l'hibernation - rose). Ils peuvent également survivre et se reproduire à nouveau près de leur lieu de reproduction précédent. Cependant, les individus qui ne présentent aucune modification physiologique ou comportementale pour une saisonnalité accrue ne survivront pas ou ne devraient pas être sélectionnés à long terme (rouge). En (B), la situation est la même sauf que les individus se trouvent dans un environnement qui n'est pas saisonnier à l'origine. L'apparition de la saisonnalité nécessite la mise en place d'adaptations (migration ou hibernation).

ENCADRE 3. Scénarios biogéographiques de l'évolution de la migration

L'évolution de la migration des oiseaux a souvent été présentée à travers l'opposition des théories 'southern-home' versus 'northern-home', généralisables sous les termes 'd'origine tropicale' ou 'd'origine tempérée' de la migration.

La **théorie 'southern-home'** a notamment été développée par Cox (1968), argumentant que la migration saisonnière a évolué chez les oiseaux tropicaux sédentaires qui ont tiré profit des ressources abondantes et d'une compétition plus faible dans les latitudes supérieures (Rappole & Jones 2002). Des mouvements hors des zones tropicales pour coloniser de nouvelles zones de reproduction dans les zones tempérées auraient donc eu lieu, nécessitant cependant le retour dans les tropiques en dehors de la période de reproduction pour pallier les hivers rigoureux et pauvres en ressource. Cox considère ainsi que le manque de ressources en hiver est moins important pour l'évolution de la migration que l'abondance de ressources et l'absence de concurrents pendant les étés sous les latitudes tempérées. Cette théorie a été de surcroît soutenue en relation avec l'évolution des connaissances sur l'écologie des espèces tropicales. La mise en évidence de nombreux mouvements de déplacements altitudinaux chez les espèces tropicales (Jahn et al. 2004) tout comme l'étroite relation observée entre espèces migratrices et tropicales en dehors de la saison de reproduction (Holmes et al. 1989) ont accru le soutien de cette théorie (voir Levey & Stiles 1992).

Bien que la saisonnalité a clairement été reconnue comme un aspect important de la migration (Alerstam et al. 2003), la **théorie 'northern-home'**, stipulant que la migration a évolué pour éviter la rigueur hivernale et le manque de ressource des environnements saisonniers a reçu une attention plus limitée, bien que défendue par plusieurs auteurs (Bell 2000, Salewski & Bruderer 2007).

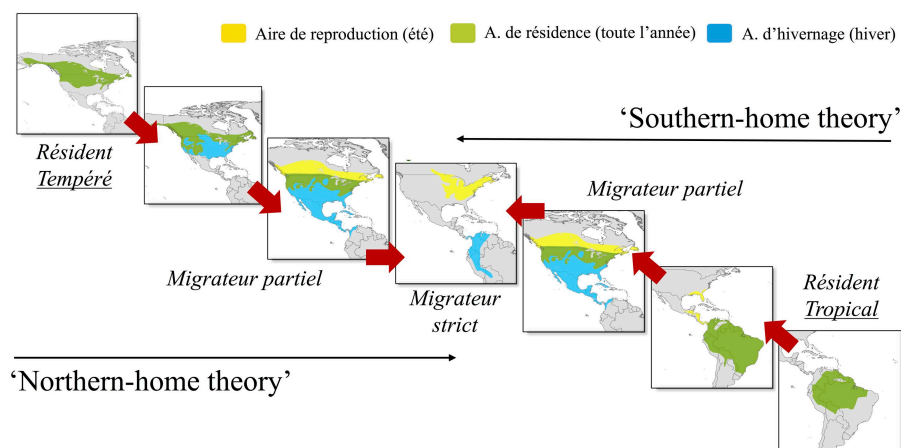


Schéma des deux théories biogéographiques 'Northern-home' et 'Southern-home'. Cette figure illustre le passage d'un état de résident (tempéré ou tropical) à un état de migrateur strict au fil du temps, en passant par l'état de migrateur partiel, à partir de cartes de distribution.

Salewski & Bruderer (2007) ont proposé une théorie plus intégrative tentant de réconcilier l'évolution de la migration et origine géographique des lignées (voir Winger et al. 2018). Ils argumentent notamment que les concepts de migration et de dispersion sont souvent confondus dans les deux théories précédentes (voir ENCADRE 1 et PARTIE 3.B). Ils proposent ainsi une théorie indépendante de la géographie et utilisant ces deux concepts : la **théorie de 'dispersion-migration'**. Cette théorie stipule qu'une dispersion régulière des zones moins saisonnières vers des zones plus saisonnières, indépendamment de l'orientation géographique, précède et facilite l'évolution du comportement migratoire. Lorsque des individus d'une population sédentaire se dispersent loin du territoire où ils sont nés, ils peuvent coloniser des zones qui sont plus saisonnières que leur région ancestrale. La sélection naturelle favoriserait alors l'évolution (voir Berthold 1999) de la migration dans la région nouvellement colonisée comme stratégie d'évasion pour éviter la saison plus rude et plus pauvre en ressources (voir ensuite la PARTIE 2.B).

3 – Les conséquences évolutives de la migration à longue distance

a) Migrer sur de longues distances : homogénéiser versus isoler les populations

On a longtemps pensé que la migration pouvait avoir un effet négatif sur la spéciation, le processus par lequel une espèce évolue en deux. Intuitivement, on pourrait en effet s'attendre à ce que les mouvements annuels entrepris entre les aires de reproduction et d'hivernage augmentent le brassage entre les individus d'une population. Ainsi Helbig (2003) et Claramunt et al. (2012) ont montré que la différenciation génétique était réduite chez les espèces migratrices sur de longues distances, respectivement au sein des Phylloscopidae et des Parulidae. Et il a été montré de façon plus générale que l'échelle spatiale de la spéciation dépend de la distance de dispersion (voir Kisel & Barraclough 2010).

Belliure et al. (2000) ont également montré une relation négative entre la distance de dispersion (juvénile et de reproduction, voir Clobert et al. 2009) et la diversité génétique (mesurée grossièrement par le nombre de sous-espèces décrites au sein de chaque espèce). Or il a souvent été proposé un lien étroit entre capacité de dispersion et distance de migration, supposant qu'un individu qui migre sur des milliers de kilomètres a plus de chance de montrer une dispersion juvénile (distance entre le lieu de naissance et le lieu de première reproduction, voir Encadré 1) plus importante qu'un individu sédentaire. En estimant la dispersion à partir des données de baguage de 75 espèces d'oiseaux terrestres, Paradis et al. (1998) ont testés les relations entre la capacité de dispersion et diverses variables géographiques et traits d'histoires de vie. Ils ont notamment montré que les espèces migratrices dispersent plus loin que les espèces résidentes et ce indépendamment de leurs tailles corporelles (Paradis et al. 1998). Pourtant, de nombreuses espèces migratrices (surtout en dehors des Passeriformes) sont philopatrices (i.e. certains individus ont tendance à rester ou à instinctivement revenir à l'endroit où ils sont nés pour se reproduire) et tendent à avoir des distances de dispersion très faibles. Ainsi cette relation entre distance de migration et capacité de dispersion est loin d'être évidente et n'a, à ma connaissance, jamais été testée à grande échelle en considérant l'ensemble des espèces migratrices (Passeriformes / non-Passeriformes, migrateurs marins / terrestres / côtiers).

Aujourd'hui, on observe une accumulation de preuves qui suggère que la migration pourrait jouer un rôle important dans l'émergence de nouvelles espèces. Dans un récent chapitre, Liedvogel & Delmore (2018) ont suggéré que les différences dans les routes migratoires empruntées par les oiseaux migrateurs peuvent contribuer à maintenir les barrières reproductives entre les populations de deux manières principales : 1) en amenant les

populations à arriver sur leurs lieux de reproduction à des moments différents et 2) car les oiseaux issus de l'hybridation entre des populations qui effectuent des trajets différents tendent à avoir une plus faible valeur sélective (voir Delmore & Irwin 2014). Cette première hypothèse s'appuie sur le fait que si les populations, utilisant des trajets différents, montrent des calendriers de migration différents (retour différé sur les sites de reproduction) et qu'elles s'accouplent selon ces dates, cela contribuera à maintenir les frontières entre les populations et à postériori les espèces (Irwin & Irwin 2005). Bearhop et al. (2005) a ainsi montré chez des fauvettes à tête noire (*Sylvia atricapilla*) allemandes, qui migrent soit vers le nord-ouest pour passer l'hiver au Royaume-Uni soit vers le sud-ouest pour passer l'hiver en Espagne et au Portugal, que les oiseaux allant au Royaume-Uni arrivaient plus tôt sur les sites de reproduction et s'accouplaient de manière préférentielle avec des partenaires issus des mêmes sites d'hivernage. De même, Friesen et al. (2007) ont montré chez l'océanite de Castro (*Oceanodroma castro*) que les temps d'arrivée sur les colonies (été versus hiver sur les îles Canaries) jouaient dans le maintien des frontières entre les espèces. Dans ce cas, la migration est considérée comme une barrière pré-accouplement où les deux populations se reproduisent à des temps différents (voir aussi Bolton et al. 2008). La seconde hypothèse s'appuie sur le fait que les routes migratoires sont largement déterminées génétiquement chez les oiseaux migrateurs (Berthold & Terrill 1991, Delmore et al. 2016, Toews et al. 2019). Ces routes migratoires sont souvent optimisées pour contourner de grandes barrières écologiques (comme de larges étendues désertiques, marines ou montagneuses) et peuvent être radicalement opposées. C'est le cas des *migratory divide* qui représente la frontière entre deux groupes de population adjacents dont la migration les emmène dans des directions différentes (par exemple, passer par Gibraltar versus passer par le Bosphore pour rejoindre l'Afrique en venant du nord de l'Europe). Il a été proposé que (1) des oiseaux issus de l'hybridation d'individus de ces deux populations utiliseraient une route migratoire intermédiaire car étant hétérozygotes pour les gènes d'orientations de ces deux groupes, et (2) que cette route intermédiaire conduirait probablement les oiseaux vers des zones inadaptées (sélection contre les hétérozygotes, Helbig 1991, Irwin & Irwin 2005). Cela a été montré chez les mêmes fauvettes à tête noire en Europe (Helbig 1991, Helbig et al. 1996), chez les grivettes à dos olive (*Catharus ustulatus*) en Amérique du Nord (Delmore & Irwin 2014), et chez les aigles criard, pomarin et leurs hybrides (*Clanga clanga*, *C. pomarina*) à l'aide de géo-localisateurs (Väli et al. 2018). Tandis que les grivettes nichant dans la chaîne Côtière du Canada migrent soit le long de la côte Ouest de l'Amérique du Nord jusqu'au Mexique soit à travers le centre-est de l'Amérique du Nord jusqu'en Colombie, les oiseaux hybrident traversent plusieurs

zones moins hospitalières tels que les déserts du sud-ouest des États-Unis et les montagnes Rocheuses (Delmore & Irwin 2014). Il a également montré que les densités de populations sont plus faibles au centre des zones hybrides confortant l'idée que ces voies intermédiaires réduisent la valeur sélective des hybrides et aident à maintenir les limites de ces *migratory divide*.

Ainsi, il semble que les *migratory divide* jouent un rôle important dans les processus de spéciation et il semblerait aussi que ce phénomène puisse être particulièrement important chez les oiseaux où de nombreux exemples sont aujourd'hui découverts grâce aux technologies de suivi individuel (voir Irwin & Irwin 2005, Turbek et al. 2019). Ces exemples pourraient permettre de trouver de nouveaux modèles afin d'étudier les traits impliqués dans la spéciation et de corroborer les résultats sur le déterminisme génétique de l'orientation (Delmore & Irwin 2014). Nous reviendrons sur cette question dans le CHAPITRE 5 de la thèse.

b) *La migration comme moteur de diversification ?*

Tous les travaux dont nous avons parlé jusqu'à présent, montrant que de façon générale la migration saisonnière a un rôle positif sur la différenciation des populations et la spéciation (Turbek et al. 2019), ont été menés une espèce à la fois (ex. fauvette à tête noire, grivette à dos olive). Ainsi peu d'études ont examiné le rôle que joue la migration dans la spéciation à des échelles taxonomiques plus larges et sur les processus de diversification (i.e. spéciation – extinction ; voir Encadré 4, mais voir Claramunt et al. 2012, Rolland et al. 2014).

Au-delà de la spéciation, on suppose également que la migration saisonnière affecte les taux d'extinction. Au cours des derniers cycles glaciaires, les espèces migratrices avaient vraisemblablement plus de chance d'échapper aux importants changements climatiques que les espèces sédentaires (voir Taberlet et al. 1998). Lorsque les calottes glaciaires s'étendaient vers des latitudes plus basses (ex. au cours du dernier maximum glaciaire, il y environ 20 000 ans), la labilité du comportement migratoire et ses changements progressifs de distance de migration ont probablement permis aux oiseaux migrateurs d'ajuster leurs distributions. Ces ajustements correspondaient vraisemblablement à un décalage des aires de reproduction vers le sud tout en restant migrateur (comme suggéré par Somveille et al. 2020) ou à un retour évolutif vers un l'état sédentaire dans les zones tropicales (comme suggéré par Zink & Gardner 2017). Dans cette perspective, il a aussi été montré que les espèces migratrices avaient eu une plus grande capacité à recoloniser les habitats arctiques très productifs après le retrait des glaciers (Milà et al. 2006, Ruegg et al. 2006), et que certaines colonies d'oiseaux de l'Antarctique ont été utilisées de manière plus ou moins continue pendant des dizaines de

milliers d'années (Thor & Low 2011). D'autre part, les individus qui se déplacent sur de longues distances sont exposés à des niveaux de stress plus élevés que les individus sédentaires, ce qui tend à augmenter les fluctuations démographiques (Møller et al. 2008) et peut entraîner des taux d'extinction globalement plus élevés.

Étant donné les effets opposés que peut avoir la migration saisonnière sur la spéciation et l'extinction, son effet net sur la diversification n'est pas évident de façon intuitive. Claramunt et al. (2012) ont par exemple étudié l'effet du comportement migratoire sur les taux de spéciation et d'extinction chez les Parulidae et n'ont trouvé aucun effet significatif. À l'inverse, Rolland et al. (2014) ont recherché ce même effet à l'échelle globale des oiseaux et chez les plus grands ordres d'oiseaux présentant des proportions d'espèces migratrices variées (14% chez les Passeriformes, 9% Apodiformes, 3% Piciformes, 4% Psittaciformes et 67% Charadriiformes ; Rolland et al. 2014). De façon générale, ils ont trouvé un taux de spéciation plus important et un taux d'extinction plus faible chez les espèces migratrices par rapport aux espèces sédentaires, indiquant un effet positif de la migration sur la diversification. Les auteurs ont estimé que les taux de spéciation sont globalement plus élevés chez les oiseaux migrateurs du fait que la divergence des espèces migratrices en une espèce fille migratrice et une espèce fille sédentaire est plus fréquente que la divergence des espèces sédentaires en une espèce migratrice et une espèce fille sédentaire. Chez les Charadriiformes (67% d'espèces migratrices), ils ont par contre trouvé un taux de spéciation symétrique plus élevé, alors que le taux de spéciation asymétrique est plus faible pour les espèces migratrices que pour les espèces sédentaires, suggérant que peu d'espèces soient repasser à un état sédentaire.

Il semble donc que chez les Charadriiformes (environ 380 espèces ; voir la description dans l'Encadré 5), le comportement migratoire ait un effet particulier sur les processus de diversification (voir Bridge et al. 2005). En comparant avec les résultats obtenus par Claramunt et al. (2012), on peut supposer que l'influence de la migration dans les processus de diversification soit dépendante du contexte évolutif, de la biogéographie mais aussi de l'écologie du clade. Nous tenterons de répondre à cette question en utilisant l'exemple des Charadriiformes dans le CHAPITRE 2.

c) *Se perdre pour mieux coloniser de nouvelles régions*

De par les trajets qu'elles effectuent deux fois par an, les espèces migratrices tendent à s'égarer plus régulièrement que les espèces sédentaires. On nomme *vagrancy*, le comportement d'apparition d'individus perdus loin de leurs aires normales de reproduction, de migration ou d'hivernage et il concerne généralement de jeunes oiseaux au départ de leur

première migration (voir Veit & Lewis 1996, Joseph et al. 2003, Outlaw et al. 2003). On sait encore peu de choses sur la part de déterminisme éventuelle dans ce comportement et plusieurs hypothèses ont été proposées. Parmi celles-ci, l'hypothèse d'une mutation génétique sur les gènes impliqués dans le déterminisme de l'orientation. Ce comportement a toujours été considéré comme une mal-adaptation et les oiseaux égarés comme des anomalies ayant peu ou pas de signification biologique (ex. Bock 1979). Comme cela concerne généralement un faible nombre d'individus avec une faible probabilité de se reproduire (en trouvant de nouveau territoire de reproduction ou en parvenant à revenir sur son lieu de naissance), le rôle de la *vagrancy* dans la colonisation de nouveaux territoires de reproduction et d'hivernage a été très peu considéré.

Des exemples de colonisation de nouveaux territoires à partir d'individus naturellement égarés, se référant alors à la notion d'invasion écologique, ont pourtant été documentés. Par exemple, chez les Ciconiiformes, le héron garde-bœuf (*Bulbulcus ibis*) s'est étendu dans toute l'Amérique du Sud à la suite de l'arrivée de plusieurs oiseaux sur le continent (voir Massa et al. 2014). Chez les Charadriiformes, la sterne élégante (*Thalasseus elegans*) niche actuellement en très petit nombre en Europe alors que son aire de répartition normale se situe sur la côte pacifique de l'Amérique (Dufour et al. 2017). Il a également été suggéré que l'augmentation des effectifs de plusieurs espèces de passereaux sibériens s'égarant généralement en Europe en automne, pourrait s'expliquer par l'établissement d'une nouvelle voie de migration en direction de cette région, loin des aires d'hivernages historiques en Asie du Sud-Est (Gilroy & Lees 2003).

Dans cette perspective, on peut donc supposer que dans de rares cas, ce comportement permet la découverte 1) de nouvelles zones de reproduction (au même titre que la dispersion mais sur la base de déplacements géographiques nettement plus grands, voir par exemple Barlein et al. 2012) et 2) de nouvelles zones d'hivernages. Dans le premier cas, les populations étant isolées géographiquement au moment de la reproduction, cela pourrait aboutir sur le long terme à une divergence évolutive à moins qu'elles ne reçoivent l'apport de nouveaux individus égarés de façon régulière. Dans le second, en suggérant que les individus utilisant une nouvelle zone d'hivernage occupent toujours la même zone de nidification tout en utilisant de nouvelles voies de migration, on peut alors supposer comme expliqué plus haut que les individus issus de l'hybridation d'oiseaux utilisant ces deux directions de migration seront contre-sélectionnés et que la phénologie de migration pourra induire une barrière pré-zygotique. Nous aborderons cette question du rôle potentiel de la *vagrancy* à travers l'étude de deux espèces d'origine sibérienne dans le CHAPITRE 5.

ENCADRE 4. Principe et limites des méthodes phylogénétiques pour étudier la diversification

L'étude de la diversification consiste à estimer les taux de spéciation, d'extinction et de diversification (spéciation – extinction). Ces trois taux représentent les probabilités qu'un événement (spéciation, extinction et diversification) se reproduise par unité de temps et sont par définitions des vitesses. Ce processus évolutif est un prédicteur indispensable pour comprendre 1) la répartition de l'abondance des espèces, 2) pourquoi la richesse des espèces augmente dans une zone géographique donnée et 3) pourquoi la similarité des communautés est étroitement liée à la distance géographique (Rosenzweig 1995). Par conséquent, le taux de diversification est devenu l'un des paramètres les plus importants dans les approches de macroévolution.

Devant le manque de données fossiles pour estimer correctement la diversification, il a fallu trouver de nouvelles méthodes. Les reconstructions phylogénétiques, représentant l'histoire évolutive des espèces, et les méthodes phylogénétiques pour étudier la diversification sont rapidement devenues une approche incontournable depuis les premiers développements dans les années 1990 (Hey 1992, Nee et al. 1992, 1994a,b).

Ces approches consistent par exemple à estimer les taux de spéciation selon un taux d'extinction relatif en connaissant l'âge du groupe-couronne (*crown group*) ou l'âge du groupe-tronc (*stem group*) et le nombre d'espèces actuelles (Figure a, Magallon & Sanderson). Comme le processus *birth-death* est exponentiel, le nombre d'espèces dans un clade avec un taux de diversification constant va donc croître de manière exponentielle avec le temps : $N(t) = N_0 \cdot \exp((b-d) \cdot t)$. Cela revient à considérer le $\log(N(t)/N_0)/t$ pour estimer le taux de diversification moyen ($b-d$).

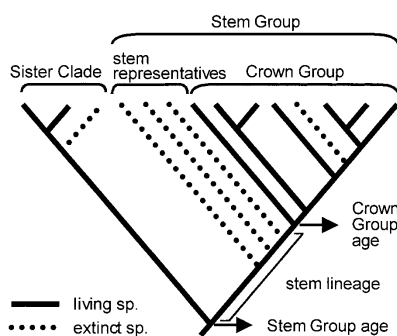


Figure a. Le *crown group* est défini comme le plus petit clade contenant un ensemble donné d'espèces actuelles, alors que le *stem group* prend également en compte les espèces éteintes (La figure est tirée de Magallon & Sanderson 2001).

Modèles de diversification

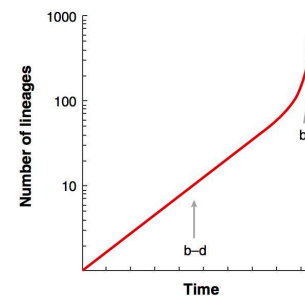
De nombreux modèles ont été développés pour estimer et comprendre la diversification. Ils reposent sur un principe commun qui consiste à comparer des reconstructions phylogénétiques empiriques à des reconstructions phylogénétiques obtenues par divers modèles de diversification. Plusieurs dizaines de modèles ont été développés (Morlon 2014) et je ne présenterai ici que quelques modèles qui ont été utilisés au cours de cette thèse.

- Diversification homogène dans la phylogénie et constante dans le temps : Ce modèle le plus simple est modélisé suivant le processus *birth-death* où chaque espèce donne naissance à deux nouvelles espèces (taux de spéciation - λ) ou s'éteint (taux d'extinction - μ) avec des taux constants. Dans ce cas, λ est généralement plus grand que μ avec une augmentation du nombre de lignées de façon exponentielle en fonction du temps.
- Diversification dépendante du temps : On peut facilement imaginer que le taux de diversification puisse varier au cours de l'histoire évolutive du clade, à cause de changements d'environnements et/ou d'effets de diversité-équilibre. Dans ce cas, le modèle assume une dépendance de λ et μ en fonction du temps (qui peut être linéaire, exponentielle, etc... ; ex. Nee et al. 1994, Rabosky & Lovette 2008).
- Diversification dépendante de l'environnement : Les modifications environnementales abiotiques semblent responsables des principales variations du taux de diversification pour certains groupes taxonomiques. Si on dispose de données paléo-environnementales (ex.

paléo-température), on peut tester l'effet de cette variation environnementale sur les taux de diversification en supposant une dépendance de λ et μ par rapport à l'état d'une variable environnementale au cours du temps (qui peut aussi être dépendante du temps, ex. Condamine et al. 2013).

- Diversification dépendante de la diversité : Ce type de modèle s'inspire du modèle de biogéographie insulaire de MacArthur & Wilson (1963) pour lequel le taux de d'immigration décroît et le taux d'extinction augmente si le nombre d'espèce sur l'île augmente. Dans ce cas, λ et μ sont dépendants du nombre d'espèces existantes à un temps donné (ex. Etienne et al. 2012).
- Diversification dépendante de la valeur d'un trait : Ce type de modèle est utilisé lorsqu'on fait l'hypothèse qu'un trait (d'histoire de vie, morphologique, géographique) puisse influencer la diversification. On réalise alors une reconstruction des états ancestraux du trait et une estimation des taux de diversification en fonction de cette valeur de trait ; λ et μ sont alors dépendants de la valeur du trait à chaque pas de temps (Maddison et al. 2007). Suspectant que des facteurs, non pris en compte dans ces modèles, puissent avoir un impact important sur le taux de diversification, de nouveaux modèles ont été récemment proposé afin de modéliser l'évolution parallèle d'un état "caché" ayant des taux de transition potentiellement distincts de ceux des états observés pris isolément (Beaulieu & O'Meara 2016).

Figure b. Les *lineage-through-time* plots permettent de visualiser efficacement les patterns de diversification en fonction du temps. On observe ici l'inflexion positive du nombre de lignée ('pull-of-the-present') pour une phylogénie moléculaire théorique qui suit un processus *birth-death* (La figure est tirée de Nee 2006).



Limites de ces approches

Du fait de la connaissance très incomplète du registre fossile, la limite évidente de ces modèles réside dans l'estimation du taux d'extinction et cette problématique a fait couler beaucoup d'encre dans la littérature scientifique. En 1994, Nee et al. publient un article intitulé 'Extinction rates can be estimated from molecular phylogenies' auquel font suite 'Can extinction rates be estimated without fossils?' (Paradis 2004) puis 'Extinction rates should not be estimated from molecular phylogenies' (Rabosky 2010). Enfin en 2020, Louca & Pennell ont publié "Extant timetrees are consistent with a myriad of diversification histories". Il semble donc que les limites de ces approches résident à la fois dans l'estimation et la datation des arbres phylogénétiques et dans la puissance des modèles eux-mêmes.

Dans son travail de synthèse, Morlon (2014) propose plusieurs arguments qui montrent la possibilité d'estimer l'extinction à l'aide d'une reconstruction phylogénétique :

- L'auteure indique que les temps de divergence estimés avec un *birth-death process* sont nettement différents de ceux estimés avec un *pure-birth process*. Ceci se visualise sur un *lineage-through-time* plot où un *birth-death process* montre une nette incurvation positive en présence d'extinction ('pull-of-the-present' voir Figure b ci-dessus ; Nee et al. 1994 a,b). Les taux d'extinctions peuvent ainsi être estimés à l'aide de cette 'incurvation' de la courbe (Ricklefs 2007).
- Partant du constat que le registre fossile montre des épisodes d'extinctions fréquents et que les taux d'extinctions estimés à partir d'approches de vraisemblance sont souvent proches de zéro, l'auteure indique que plusieurs modèles ne tiennent pas compte de l'hypothèse de taux d'extinction homogène et qu'une meilleure estimation de ce taux réside aussi dans le choix des priors des modèles.
- Dans le cas où des taux d'extinctions hétérogènes entre lignées sont suspectés (Morlon et al. 2011), il peut aussi convenir de paramétrer des dynamiques de diversité différentes pour les sous-clades de la phylogénie afin de mieux estimer les taux d'extinctions.

4 – Les contraintes écologiques imposées par la distance parcourue

a) *Le cycle de vie particulier des oiseaux migrateurs*

Chez les vertébrés, le cycle annuel s'organise en une série de périodes de reproduction et de non-reproduction successives qui varient en durée et en lieu mais qui sont liées biologiquement (Marra et al. 2015). Chez les animaux migrateurs et notamment chez les oiseaux, ce cycle annuel est complexifié par des périodes de transit entre les sites de reproduction et de non-reproduction, qui peuvent elles-mêmes être entrecoupées de périodes de mue variables en durée et en lieu (voir la Figure 3).

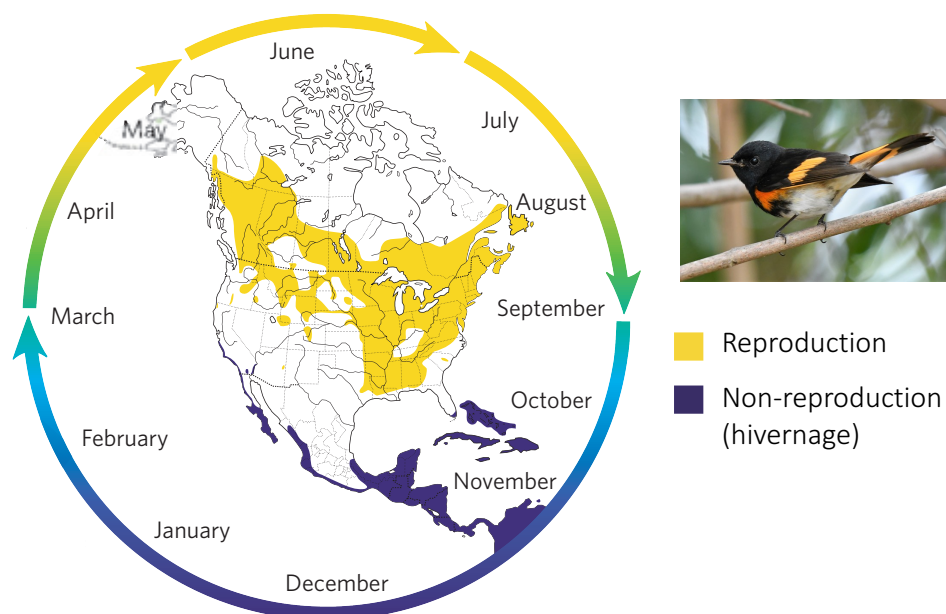


Figure 3. Exemple de cycle annuel d'un oiseau migrateur sur de longues distances : la paruline flamboyante *Setophaga ruticilla*. Ce cycle annuel illustre la phénologie de la migration saisonnière entre les zones de reproduction et de non-reproduction. Figure tirée et modifiée de Small-Lorenz et al. (2013) et photo de Christopher Johnson.

En 2015, Marra et al. ont montré que la recherche en écologie présentait un biais important vers l'étude de la saison de reproduction, en sous estimant les interactions et l'importance des autres périodes du cycle annuel. Même s'il semble logique que les animaux soient soumis à de nombreuses pressions de sélection durant cette période de reproduction, celle-ci reste relativement courte en comparaison du temps passé en dehors de la période de reproduction. Ainsi les oiseaux migrateurs passent la majeure partie de leur cycle annuel sur

les sites de non-reproduction (hivernage) où en transit entre ces sites d'hivernage et les sites de reproduction (Figure 3). Par conséquent, ils subissent de nombreuses pressions de sélection en dehors de la période de reproduction qui sont souvent sous-estimées ou négligées. Une illustration de ce biais se retrouve par exemple dans l'étude des fonctions de la coloration des oiseaux. Notre compréhension des multiples fonctions de la coloration des oiseaux et de leurs variations en fonction des conditions climatiques saisonnières reste limitée. Les études récentes ont abordé la question de la répartition de la coloration en fonction des conditions environnementales rencontrées dans les aires de reproduction : soit toute l'année (par exemple, Delhey et al. 2019), soit uniquement pendant la période de reproduction (Galván et al. 2018). La première option serait raisonnable pour les espèces sédentaires qui ne changent pas de plumage au cours de l'année et la seconde serait appropriée pour les espèces présentant un changement de couleur saisonnier (voir McQueen et al. 2019). Toutefois, pour les espèces qui ne présentent pas de changement de couleur saisonnier, la prise en compte des conditions rencontrées uniquement pendant la période de reproduction (pour les espèces sédentaires) ou uniquement dans les zones de reproduction (pour les espèces migratrices) conduira probablement à négliger une partie des pressions de sélection qui peuvent être exercées sur la coloration du plumage. En choisissant un clade d'oiseaux migrants, particulièrement approprié pour étudier les pressions de sélection sur la coloration du plumage, nous aborderons cette question dans le CHAPITRE 3.

b) Les conséquences énergétiques de la distance parcourue

Nous avons vu précédemment (Partie 2) que la migration saisonnière a probablement évolué en étroite relation avec l'apparition de la saisonnalité. Nous avons également noté que le comportement migratoire était largement répandu chez les oiseaux et qu'il présentait une remarquable diversité interspécifique notamment pour la distance parcourue entre les aires de reproduction et d'hivernage (voir Encadré 2). Cependant, pourquoi deux espèces proches d'un point de vue évolutif présentent des distances de migration très différentes reste encore mal compris.

La contrainte énergétique du vol peut expliquer en partie cette variation interspécifique. Watanabe (2016) s'est par exemple intéressé à l'importance du type de vol migratoire dans l'expression des mouvements entrepris. En effet, certains oiseaux utilisent le vol battu tandis que d'autres utilisent le vol plané pour réaliser la majeure partie de leurs trajets migratoires. Le vol battu, utilisé par la plupart des passereaux et des « petits » oiseaux migrants, est une forme de locomotion coûteuse qui nécessite de 5 à 19 fois la puissance (la dépense

énergétique par unité de temps) du taux métabolique au repos (Videler 2006). À l'inverse, le vol plané utilisé par de nombreux rapaces et oiseaux marins nécessite seulement environ deux fois la puissance de repos (Sapir et al. 2010). Cette dernière étude a ainsi démontré que les oiseaux utilisant le vol battu voient leurs distances de migration diminuer en fonction de leur masse corporelle, suggérant des coûts de vol qui augmentent rapidement avec l'augmentation de la masse corporelle. À l'inverse, chez les oiseaux utilisant le vol plané, les distances de migration sont indépendantes de la masse et plus grandes que celles des oiseaux utilisant le vol battu, ce qui suggère un coût de vol plus faible et indépendant de leur masse corporelle.

Il a également été proposé que la variabilité des distances parcourues puisse s'expliquer par la conséquence indirecte de ces mouvements sur les autres événements du cycle annuel. Les *carry-over effects* ont ainsi été définis comme des événements qui se produisent au cours d'une saison mais qui influencent la valeur sélective des individus la saison suivante (voir Norris 2005). Chez les animaux migrateurs et notamment les oiseaux, il a ainsi été montré que la distance entre sites d'hivernage et de nidification peut avoir des conséquences importantes sur la survie (Alerstam & Hedenstrom 1998, Reneerkens et al. 2019) et/ou sur les succès de reproduction des années suivantes (Alves et al. 2013) à travers ces *carry-over effects* (Norris 2005, Gunnarsson et al. 2005, Norris & Marra 2007, Harrison et al. 2010, Bogdanova et al. 2017).

Cependant les conséquences de la distance de migration parcourue sur la valeur sélective des individus semblent très variables selon les espèces, les sites et les systèmes migratoires étudiés. Si pour de nombreuses espèces les coûts énergétiques élevés engendrés par de longs vols migratoires peuvent avoir des conséquences sur la valeur sélective des individus (voir par exemple Hotker 2002, Bearhop et al. 2004, Bregnballe et al. 2006), migrer sur de plus longues distances peut n'avoir aucun effet sur la reproduction chez certaines espèces (Kentie et al. 2017, Reneerkens et al. 2019) ou peut même être bénéfique pour la reproduction et la survie (par exemple, Alves et al. 2013). Les individus effectuant les distances les plus importantes peuvent en effet compenser ces coûts de vol supplémentaires en profitant de meilleures conditions d'hivernage (meilleure disponibilité des ressources, plus faible compétition ou prédation ; Alves et al. 2012, 2013, Conklin et al. 2017).

A titre d'exemple, Alves et al. (2013, mais voir aussi Alves et al. 2012) ont suivi les mouvements migratoires, la phénologie et les paramètres de reproduction d'une population de barges à queue noire islandaises (*Limosa limosa islandica*). De façon contre intuitive, ils ont ainsi montré que les oiseaux qui hivernaient sur le site le plus loin du site de nidification (i.e. au Portugal) bénéficiaient de meilleures conditions d'hivernages que ceux hivernant plus près

(en Irlande et en Angleterre), migraient plus vite et pouvaient ainsi accéder aux meilleurs sites de reproduction. De nombreuses études suggèrent ainsi que les *carry-over effects* peuvent jouer un rôle important dans la dynamique des populations migratoires (voir Norris 2005, Alves et al. 2013) et par conséquent dans la variabilité des mouvements que nous observons.

D'autres facteurs, comme le rôle de l'histoire évolutive des espèces et des populations dans l'évolution des destinations d'hivernages restent jusque-là peu explorés. Or pour certaines espèces, il semble que l'histoire phylogéographique des populations puisse influencer le choix des destinations d'hivernages en lien étroit avec la façon dont l'orientation de la route migratoire est codée génétiquement. Même si peu d'études se sont intéressées à cette question (Outlaw et al. 2003), elles ne font que renforcer la difficulté de trouver une réponse générale au coût énergétique de la migration. La variabilité des distances de migration à l'échelle inter- et intra-spécifique pourraient être le résultat de l'intervention de multiples facteurs évolutifs, écologiques, dont l'importance respective varie selon les espèces considérées, les systèmes migratoires ou l'évolution des sites fréquentés. Nous chercherons à répondre à cette question dans le CHAPITRE 4 de cette thèse.

5 – Organisation de la thèse

a) Une approche multi-échelles autour de trois axes majeurs

Afin d'aborder de la meilleure manière possible le sujet de l'évolution de la migration longue distance chez les oiseaux, j'ai organisé cette thèse autour de trois axes majeurs (Figure 4a). Ces axes traitent :

1) de l'évolution biogéographique de la migration : comment les mouvements migratoires apparaissent et qu'est-ce que cela implique sur la répartition de ces espèces migratrices dans leurs milieux écologiques,

2) des contraintes écologiques imposées par l'action de migrer entre une zone de reproduction et une zone de non-reproduction : comment les pressions de sélection changent au cours du cycle annuel et quelles conséquences cela peut avoir sur le phénotype des espèces migratrices, et

3) du rôle de la migration comme facteur de diversification et de différenciation des populations : la migration favorise-t-elle l'isolement des populations et si c'est le cas, de quelle(s) manière(s).

Les différents projets réalisés au cours de cette thèse s'inscrivent dans ces axes ou à l'interface entre plusieurs d'entre eux. De plus, afin de pouvoir utiliser différentes approches

et de tester les mêmes hypothèses sur différents modèles biologiques, les projets abordés au cours de cette thèse couvrent différents niveaux hiérarchiques de la classification taxonomique (Figure 4b). Par exemple, j'ai d'abord étudié l'évolution de la migration pour l'ensemble de la classe Aves (tous les oiseaux du monde, 9993 espèces ; Jetz et al. 2012), puis je me suis intéressé à un grand ordre d'oiseaux migrateurs avec l'ordre des Charadriiformes (376 espèces), puis au sein de cet ordre à la famille des Laridae (97 espèces) pour enfin m'intéresser au cas d'une espèce de Charadriiformes migratrice, le mergule nain.

L'étude de ces trois axes et de ces différents modèles biologiques m'a permis d'utiliser une grande variété d'approches analytiques. J'ai d'abord utilisé des approches macro-évolutives et macro-écologiques qui correspondent à l'étude des grandes théories évolutives et écologiques au-dessus du rang de l'espèce. Si ces approches globales nécessitent une simplification de la complexité du comportement migratoire, elles n'en restent pas moins extrêmement utiles pour proposer des réponses générales et examiner des hypothèses profondément ancrées dans la littérature classique sur la migration des oiseaux. Ces approches permettent également d'identifier les lignées qui semblent les plus intéressantes pour poursuivre l'étude de ces hypothèses à des échelles taxonomiques plus fines. Ces échelles plus fines (ordre, famille, espèce) permettent quant à elles d'aborder la complexité des mécanismes, plus faciles à appréhender sur des échelles temporelles et taxonomiques fines. Elles permettent également d'affiner les modèles et les hypothèses établies aux rangs supérieurs. Enfin, les études de cas précises faisant intervenir une espèce sur un site donné semblent indispensables pour compléter l'étude des mouvements migratoires. Si ces études sont souvent couteuses en temps et en moyens, elles permettent d'une part de se confronter à la réalité du terrain et d'autre part de mieux appréhender la diversité des réponses possibles. En effet, l'hétérogénéité des réponses observée au sein d'un même clade (voir les liens entre fitness et stratégies de migration dans le paragraphe 4-b) montre la nécessité de répéter ce type d'étude pour aboutir à un résultat complet. De plus, elles permettent aussi d'envisager de nouveaux modèles explicatifs, que le cadre théorique de la discipline avait jusque-là négligé ou sous-estimé.

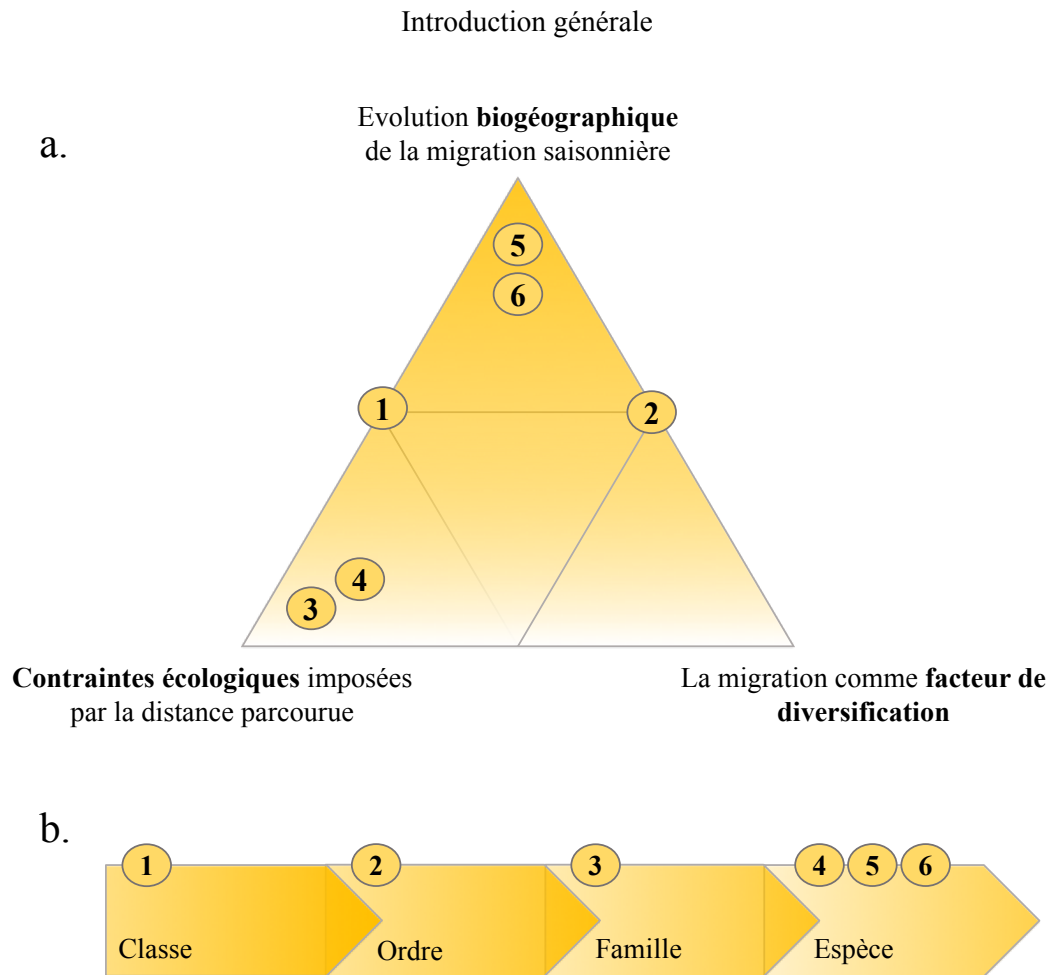


Figure 4. Organisation schématique de la thèse et place des différents projets. La figure a. indique la place des projets au sein ou à l'interface des trois axes abordés au cours de cette thèse. La figure b. montre la place des projets au sein des différents niveaux hiérarchiques de la classification taxonomique. Les projets, numérotés de 1 à 6 correspondent aux différents manuscrits de cette thèse (voir la liste précise des articles).

b) Données et méthodes utilisées au cours de cette thèse

Les approches de macro-évolution et macro-écologie, ainsi qu'une partie des études de cas (ex. modélisation de niches), ont été réalisées avec des données librement accessibles. Il s'agit d'une part des données environnementales mise à disposition par la NASA Earth Observations (<https://neo.sci.gsfc.nasa.gov/>), le NOAA Physical Sciences Laboratory (<https://psl.noaa.gov/data/index.html>), le site WordClim (Fick & Hijmans 2017) et Chelsa-Climate (Karger et al. 2017). D'autre part, les cartes de distribution de toutes les espèces d'oiseaux ont été obtenues sur demande auprès de BirdLife International and Handbook of the Birds of the World (HBW ; 2018). Les données phylogénétiques ont été obtenues directement auprès des auteurs des études (Prum et al. 2015), sur le site associé à ces études (Jetz et al. 2012, <http://birdtree.org/>) ou construites à partir des séquences d'ADN disponibles sur le site

du National Center for Biotechnology Information (NCBI). Les données sur les mouvements de toutes les espèces d'oiseaux du monde ont été collectées sur le sites du Handbooks of the Birds of the World alive (devenu maintenant le Birds of the World, piloté par le Cornell Lab of Ornithology). D'autres données d'occurrences et de phénotypes (couleur du plumage) ont été collectées sur des bases de photos en ligne et sur le site du projet Global Biodiversity Information Facility (GBIF). Finalement, la réalisation des études de cas a été permise par le suivi d'individus directement sur le terrain grâce à l'aide de nombreux observateurs locaux, d'aides bagueurs et de responsables des collectivités territoriales en matière d'environnement.

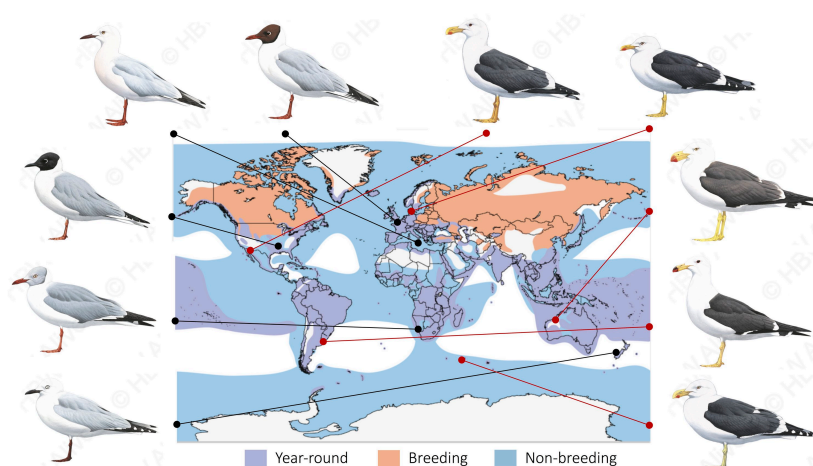
L'ensemble des approches évolutives utilisées au cours de cette thèse se rapportent aux méthodes comparatives phylogénétiques. Ces méthodes se basent sur le principe de non indépendance des données du fait de l'apparentement évolutif des lignées entre elles. Si ces méthodes utilisent majoritairement les données (phénotypique, distribution) disponibles sur les organismes existants, il est possible d'incorporer les données disponibles pour les taxons éteints (i.e. données fossiles) pour améliorer la robustesse des résultats. J'ai utilisé d'une part des méthodes comparatives pour estimer les caractères ancestraux à travers la phylogénie (ex. stratégie de migration) mais aussi pour mesurer les taux de diversification. L'utilisation de ces méthodes nécessite donc de disposer de la phylogénie de la lignée à étudier. Cette estimation phylogénétique est désormais réalisée à partir des données moléculaires pour estimer les relations entre les lignées et la longueur des branches qui les séparent. Le registre fossile est utilisé à posteriori pour estimer les temps de divergence entre ces différentes lignées.

Pour une partie des approches écologiques, j'ai notamment utilisé à plusieurs reprises une méthode de modélisation de distribution géographique pour comparer les niches des espèces où des populations entre elles. Cette méthode repose sur une définition classique de la niche de Hutchinson ou des facteurs abiotiques et biotiques conditionnent l'existence de populations d'une espèce à un endroit donné. Pour la partie modélisation et projection, j'ai notamment suivi la procédure décrite dans le package *Biomod* implémenté dans R (Thuiller, 2003 ; Thuiller et al. 2009). J'ai également bénéficié pour cette tâche de l'aide Maya Guéguen (ingénieur d'étude, UGA) et Julien Renaud (ingénieur d'étude, CNRS).

ENCADRE 5. Aperçu de quelques espèces et clades étudiés au cours de cette thèse.

L'ordre des **Charadriiformes** comptent environ 380 espèces réparties en 3 sous-ordres (Lari, Charadri et Scolopaci) et 19 familles, parmi lesquelles trois familles particulièrement diversifiées : les Scolopacidae (i.e. barges, bécasseaux, chevaliers – 96 espèces), les Charadriidae (i.e. vanneaux, gravelots, pluviers – 67 espèces) et les Laridae (i.e. mouettes, goélands, sternes – 97 espèces). Tandis que les Scolopacidae ont la particularité d'avoir des becs de formes très variables et réalisent des vols nuptiaux complexes (Winkler et al. 2020), les Charadriidae se distinguent par des plumages aux motifs très variés. Les Laridae sont par contre relativement peu variables d'un point de vue phénotypique (mais voir ci-après) mais se distribuent très largement. La plupart de ces espèces fréquentent le milieu aquatique pendant au moins une partie de leur cycle annuel et cet ordre à la particularité de présenter une proportion d'espèces migratrices très importante avec plusieurs clades migrateurs très diversifiés. Représentant ainsi un bon modèle pour aborder les questions de biogéographie et de diversification, il sera étudié à de plusieurs reprises au cours de cette thèse : dans son ensemble dans les CHAPITRES 1 et 2 et à l'échelle des Laridae et intra-spécifique dans les CHAPITRES 3 et 4.

Chez les **Laridae**, je me suis intéressé aux espèces et aux sous-espèces de la sous-famille des *Larinae*, correspondant à l'ensemble des mouettes et goélands (del Hoyo & Collar 2014). Cette sous-famille contient 80 sous-espèces pour 52 espèces et figure comme un excellent modèle pour étudier les pressions de sélection subies par les espèces migratrices. En particulier, nous avons étudié comment ces variations de pressions de sélection au cours du cycle annuel peuvent influencer le déterminisme et la distribution de la coloration du plumage au sein de ce groupe. Les mouettes et les goélands sont en effet pour la grande majorité des espèces migratrices et présentent des plumages très similaires à l'âge adulte qui diffèrent notamment par la couleur du manteau (plumes du dos et des ailes) et la proportion de noir au bout de l'aile. L'absence de dimorphisme sexuel et de variation saisonnière suggère que ces traits ne sont pas soumis à la sélection sexuelle (Skékely et al. 2004) tout comme la position de ces espèces en haut des chaînes trophiques suggère que ces traits ne sont pas soumis à des pressions de sélection pour échapper aux prédateurs (comme c'est pourtant le cas de nombreuses autres espèces d'oiseaux). Enfin, toutes ces espèces occupent les mêmes milieux, ouverts et à proximité de l'eau. Ainsi, les grandes variations de coloration associées à un nombre limité de fonctions supposées du plumage en font un bon modèle d'étude pour comprendre l'influence du climat dans la distribution de la coloration animale en contexte saisonnier (voir CHAPITRE 3).



Distribution saisonnière des Laridae et illustration de quelques phénotypes de mouettes et goélands. De gauche à droite : *Chroicocephalus bulleri*, *cirrocephalus*, *philadelphia*, *genei* & *ridibundus*, puis *Larus livens*, *fuscus*, *pacificus*, *atlanticus* & *dominicanus*. Ce schéma illustre la distribution cosmopolite de ce clade et les grandes similitudes phénotypiques entre plusieurs taxons. La carte est tirée du site Birds of the World (2020) et les illustrations sont de Ian Lewington (© HBW Alive/Lynx Edicions).

Le **mergule nain** (*Alle alle*) représente l'espèce d'oiseau la plus abondante de l'Arctique. Il niche en colonies denses notamment sur les côtes du Groenland, de l'archipel de Spitzberg (Norvège) et en Russie. En dehors de la période de reproduction, cette espèce occupe majoritairement les eaux situées autour de l'Islande, au large du Groenland et de Terre-Neuve (Canada ; Fort et al. 2013). Comme les autres alcidés (ex. macareux moine, guillemot de Troïl), le mergule plonge pour capturer ses proies. L'évolution a ainsi permis un compromis entre la nage et le vol (Thaxter et al. 2010, Elliot et al. 2013) impliquant une dépense énergétique supérieure à d'autres espèces lorsque le mergule se déplace en vol (Sakshaug et al. 2009). La variation des zones d'hivernage fréquentées et les distances parcourues, en lien avec le coût de vol élevé chez cette espèce en font un bon modèle d'étude pour 1) examiner les contraintes énergétiques liées au fait de migrer sur de longues distances, 2) identifier les facteurs qui pourraient les compenser et 3) étudier l'évolution de ces stratégies migratoires (CHAPITRE 4).



Mergule nain photographié sur la colonie de Bjørndalen (Svalbard – P. Dufour).

Avec plus de 6200 espèces, l'ordre des **Passeriformes** représentent l'une des radiations évolutives les plus remarquables du règne animal (Fjeldså et al. 2020). Les études récentes ont radicalement changé notre compréhension de l'histoire évolutive de cet ordre (Oliveros et al. 2019). Elles estiment que les passereaux sont apparus au début de la radiation des oiseaux modernes sur les continent Gondwana, après la crise Crétacé-Tertiaire (-66 Ma) impliquant la disparition des grands dinosaures et de certains groupes basaux de la classe Aves. De façon intéressante, seul un petit nombre de familles se sont largement diversifiées sur l'ensemble des continents (sauf l'Antarctique). Il est possible que l'apparition de la migration ait joué un rôle important dans l'histoire évolutive de ce clade, permettant de grandes expansions géographiques et la colonisation des milieux de hautes latitudes. Nous étudierons ce clade en particulier dans le CHAPITRE 1 et à l'échelle intra-spécifique dans le CHAPITRE 5.

Le **pouillot à grands sourcils** (*Phylloscopus inornatus*) et le **pipit de Richard** (*Anthus richardi*) sont deux passereaux migrateurs qui nichent respectivement en Sibérie et dans les steppes d'Asie centrale et orientale. Ils hivernent tous deux dans le sud-est de l'Asie (Alström & Mild 2003). Ces deux espèces ont toujours été notées de façon occasionnelle en Europe (*vagrants*, Gilroy & Lees 2003) au cours du 20^e siècle. Mais l'augmentation rapide des effectifs au cours des dernières décennies laisse suggérer que nous pourrions également observer des migrateurs qui utilisent une nouvelle voie migratoire les menant à l'opposé de leurs quartiers d'hivernages ancestraux (CHAPITRE 5).



Pipit de Richard et Pouillot à grands sourcils photographiés en plaine de Crau (France – P. Dufour) et à Ottenby (Suède – M. Hellström).

7 – Bibliographie de l'introduction

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CHAPITRE 1

Reconstruire l'origine géographique et climatique des migrations longues distances chez les oiseaux

Résumé du chapitre : La migration saisonnière des oiseaux figure comme l'un des phénomènes écologiques les plus fascinants du règne animal. Pourtant, les scénarios biogéographiques et les facteurs climatiques qui ont conduit des espèces ou des lignées entières à évoluer vers un comportement de migration saisonnière restent mal compris. Dans cette étude, nous avons exploré le contexte biogéographique et climatique de l'émergence de la migration saisonnière chez tous les oiseaux du monde (9993 espèces).

Pour cela, nous avons utilisé la phylogénie mondiale de tous les oiseaux, que nous avons mis à jour avec un nouveau squelette phylogénétique, pour tester le lien entre la distance de migration des oiseaux (courte, variable, longue) et la stratégie (résident, migrateur partiel et strict) avec quatre mesures différentes décrivant les niches climatiques des espèces dans leurs aires de reproduction et d'hivernage. En parallèle, nous avons reconstitué les événements passés d'apparition et de perte de comportement migratoire, ainsi que les scénarios biogéographiques qui ont conduit à l'émergence de la migration saisonnière chez plusieurs grands ordres d'oiseaux migrants.

Nous avons montré que les espèces migratrices, et de surcroît les migrants sur de longues distances, font l'expérience d'un climat plus chaud dans leur aire d'hivernage que dans leur aire de reproduction, bien qu'il existe des exceptions notables. Nous avons également constaté que la migration saisonnière est apparue à différentes époques, par des voies biogéographiques variées (à la fois à partir d'ancêtres tempérés et tropicaux) et que le comportement migratoire est probablement apparu très tôt dans l'histoire évolutive des Passeriformes (suivi de plusieurs épisodes de perte de celui-ci).

Cette étude rapporte une corrélation évolutive entre la migration à longue distance et la tendance des oiseaux à rechercher des climats plus chauds pendant leur période de non-reproduction, par rapport aux migrants à courte distance. Nous mettons également en évidence que l'évolution de la migration saisonnière a été extrêmement labile au cours de l'histoire évolutive des oiseaux avec plusieurs lignées qui semblent s'être adaptées à de nouvelles opportunités écologiques en retournant à un état résident. Ces résultats constituent la

première étude à grande échelle des origines biogéographiques et climatiques de la migration des oiseaux dans le monde.

[Etats ancestraux, scénarios biogéographiques, migration des oiseaux, conservatisme des niches, distance de migration, méthodes phylogénétiques comparatives]

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RESEARCH PAPER



Reconstructing the geographic and climatic origins of long-distance bird migrations

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Abstract

Aim: Seasonal bird migration is one of the most fascinating global ecological phenomena. Yet, the biogeographic scenarios and climatic drivers that led single species or entire lineages to evolve seasonal migration between disjunct breeding and wintering ranges remain unclear. Based on distribution and phylogenetic data for all birds worldwide, we explored the biogeographic and climatic context of the evolutionary emergence of seasonal geographic migration in birds.

Location: Global.

Taxon: The Aves class (9,819 species).

Methods: We used the worldwide phylogeny of all birds, with a new backbone tree, to test the link between birds' migration distance (short, variable, long) and strategy (resident, mixed, strict migrant) with four different metrics depicting species' thermal niches in their breeding and wintering ranges. We also performed ancestral state reconstructions for the main migratory orders to reconstruct past events of appearance and loss of migration behaviour, and past biogeographic scenarios that led to the emergence of seasonal geographic migration.

Results: Migratory species generally experience warmer climates in their wintering range compared to their breeding one, although notable exceptions exist. This thermal niche change due to migration was found to be much larger for species travelling large distances. We also found that geographic migration emerged at different time periods through varied biogeographic paths (i.e. both from temperate and tropical ancestors) and that migration behaviour was likely ancestral to Passeriformes, with several subsequent episodes of loss of migration behaviour.

Main conclusions: We report an evolutionary correlation between long-distance migration and the tendency of birds to seek warmer climates during their non-breeding period, compared to short-distance migrants. Migration behaviour was likely ancestral to Passeriformes, and migratory lineages in general seem to have often adapted to novel ecological opportunities by returning to a resident state. Our results provide the first large-scale study of biogeographic and climatic origins of bird migration worldwide.

KEYWORDS

ancestral state reconstructions, biogeographic scenarios, bird migration, climatic niche conservatism, migration distance, phylogenetic comparative methods

1 | INTRODUCTION

Birds undertake some of the most spectacular annual migrations in the animal kingdom, with several billions of birds travelling twice a year, sometimes over tens of thousands of kilometres between their breeding and wintering grounds (e.g. Egevang et al., 2010). This phenomenon of geographic disjunction between the breeding and wintering ranges of certain species has long invited investigations regarding the physiology, behaviour and navigation of migratory birds (see Alerstam, Hedenström, & Åkesson, 2003; Gwinner & Helm, 2003; Newton, 2008; Pulido, 2007). Yet, the conditions that triggered the evolution of seasonal migration behaviour remain poorly understood, and seem to include both abiotic and biotic drivers, such as seasonal habitat quality and trophic resources, escape from predators, pathogens or competitor avoidance (Alerstam et al., 2003; O'Connor, Cornwallis, Hasselquist, Nilsson, & Westerdahl, 2018; Somveille, Rodrigues, & Manica, 2018).

A largely documented biogeographic pattern is the tendency of most migratory birds to breed in regions characterized by strongly seasonal environments (Somveille, Rodrigues, et al., 2015, 2018). A recent paper (Winger, Auteri, Pegan, & Weeks, 2019) reviewed the studies that attempted to integrate theories about the evolution of bird migration with the biogeographic history of migratory clades (Louchart, 2008; Salewski & Bruderer, 2007; Winger, Barker, & Ree, 2014; Zink, 2002) and stressed that the biogeographic origins of bird migration have rarely been considered in relation to the onset of climatic seasonality. They further called for a change of perspective towards viewing the evolution of bird seasonal migrations as an adaptation for long-term persistence in seasonal environments. Consequently, understanding the biogeographic and climatic drivers that triggered the emergence of bird migration requires an examination of the year-round climatic niches in their breeding and wintering ranges, in relation to different birds' migratory strategies. Considering a global scale and comparing major migratory bird clades can help shed additional light on this phenomenon.

Recent works suggested that the year-round climatic conditions experienced by migratory birds can show two distinct patterns, which have been termed 'niche tracking' and 'niche switching' strategies (e.g. Gomez, Tenorio, Montoya, & Cadena, 2016; Laube, Graham, & Boehning-Gaese, 2015; Zurell, Gallien, Graham, & Zimmermann, 2018). First, seasonal migration may allow birds to track similar climates through time ('niche tracking' hypothesis) due to relatively narrow environmental tolerances (Gomez et al., 2016; Zurell et al., 2018). Indeed, some migratory birds tend to exploit overlapping climatic niches in their breeding and wintering ranges (Somveille, Manica, & Rodrigues, 2018). Other migratory birds tend to spend winter in a different climate than that of their breeding range ('niche switching', e.g. Joseph & Stockwell, 2000; Laube et al., 2015; Nakazawa, Peterson, Martínez-Meyer, & Navarro-Sigüenza, 2004). This would be particularly expected when migrating towards a warmer environment is associated with a greater resource supply or lower pathogen avoidance (Alves et al., 2013, 2011), or more broadly when an adjustment of breeding ranges is favoured during evolution

(Martínez-Meyer, Peterson, & Navarro-Sigüenza, 2004). It remains unknown, however, which of the two patterns of niche tracking and switching generally applies, whether there are differences between clades and associations with particular features of migratory species, in particular migration distance. For example, a recent study suggests that bird species travelling intermediate distances would be the most likely to track their climatic niche (Somveille, Manica, et al., 2018).

Traditional paradigms to explain the emergence of bird migration are based on the geographic origin from which the migration evolved, although this region of origin does not need to be the same as the biogeographic origin of a lineage (Bruderer & Salewski, 2008; Salewski & Bruderer, 2007). The most widely accepted 'southern-home' theory (SHT hereafter) proposes that long-distance migrants evolved from resident tropical species through the poleward shift of their breeding ranges, in order to avoid competition and exploit summer resource peaks in temperate latitudes (Cox, 1968; Gauthreaux, 1982; Levey & Stiles, 1992; Rappole, 1995). Alternatively, the 'northern-home' theory (NHT hereafter) stipulates that migration evolved from resident temperate species at higher latitudes, shifting their wintering grounds to lower latitudes to escape adverse winters (Bell, 2000; Gauthreaux, 1982). The latter scenario assumes greater fitness benefits when migrating towards lower latitudes (as shown in Alves et al., 2013), but it does not necessarily imply tracking of the same climatic niche year-round. Thus far, no consensus has emerged to explain the biogeographic origins of seasonal bird migrations (see also Louchart, 2008; Salewski & Bruderer, 2007; Winger et al., 2019). We suggest that the support of either of these two hypotheses may mostly depend on the evolutionary history of the clades under consideration (see Winger et al., 2014 for *Emberizoidea*).

In this study, we explored the biogeographic and climatic context of the evolutionary emergence of seasonal geographic migration in birds worldwide. To do so, we merged two recent phylogenies of all extant bird species and characterized the geographic range information of all migratory birds. We tested whether species migration distances (short, variable, long) and strategies (resident, mixed, strict migrant) are linked to the seasonality of their breeding range and to their tendency to track their thermal niches through seasons ('niche tracking' vs. 'niche switching'). We also reconstructed the temporal and biogeographic scenario under which seasonal geographic migration evolved in major migratory bird orders (NHT vs. SHT), by retracing the biogeographic origin of the lineages that have developed migration behaviours. To identify general patterns, we first based our study on a global scale (9,819 species). Then, to confirm the generality of these patterns, we focused on three orders accounting for most of the world's migratory species, including the longest migrants (see Figure 1a): the orders of *Anseriformes* (160 species), *Charadriiformes* (368 species) and *Passeriformes* (5,895 species). We employed this hierarchical approach because the emergence of seasonal migration behaviour is likely a complex phenomenon influenced by the specific ecological and evolutionary context of the particular clade. Few studies have so far explored and test the evolutionary links between birds' climatic niches, geographic distributions

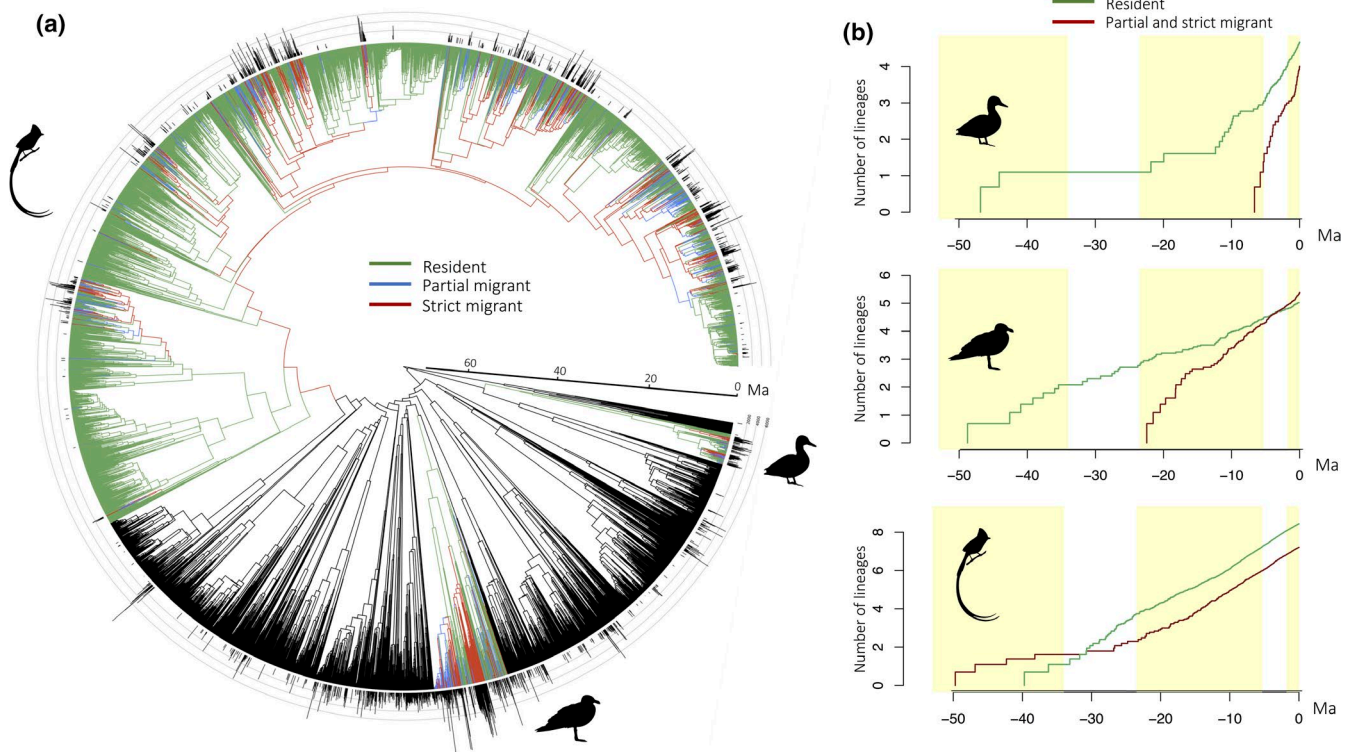


FIGURE 1 Reconstruction of ancestral migratory strategies and their temporal accumulation across the global bird phylogeny and the three study orders, Anseriformes, Charadriiformes and Passeriformes. (a) The phylogeny's edges are coloured based on the reconstructed ancestral migration strategies, as follows: green for *resident species*, blue for *partial migrants* and red for *strict migrants*. Edges from species not belonging to the three study orders are in black. Black lines in front of the tip labels depict a quantitative estimate of distance of geographic migration for each species (considered null for resident species). (b) Lineage-through-time plots depicting the temporal accumulation of migratory and resident species (red and green lines, respectively). *Partial and strict migrants* were grouped together. Ancestral migratory behaviours were assigned to each node based on the marginal likelihood values. Yellow and white shading highlights important geological eras, namely Eocene (–56/–34 Ma), Oligocene (–34/–23 Ma), Miocene (–23/–5.3 Ma), Pliocene (–5.3/–2.6 Ma) and Pleistocene–Holocene (–2.6 Ma to present) [Colour figure can be viewed at wileyonlinelibrary.com]

and different migratory characteristics, both at a global scale and within major orders of migratory birds.

2 | MATERIALS AND METHODS

2.1 | Species ranges, climatic niches, migration strategies and phylogeny

Breeding, resident, and wintering distribution ranges of all bird species were collected from Birdlife International and NatureServe (2017) and gridded at a 10-min resolution after substantial corrections and recoding for some bird groups (see Appendix S1). Such a high spatial resolution was necessary to depict the climatic niches of species having particularly narrow and fragmented breeding ranges, which is typical for many colonial migrants nesting in insular environments. As the climatic niche of a single cell may not reflect the climate experienced by narrow-ranging species, we removed species with distributional ranges smaller than the size of a grid cell (omitted species listed in Appendix S1). In total, we considered 9,819 species out of the 9,993 species recognized in Jetz, Thomas, Joy, Hartmann, and Mooers (2012). The mean temperature of each grid cell was

calculated for both boreal and austral location and for both winter and summer time periods, which we call temperatures of breeding and wintering ranges hereafter (Appendix S1). For reasons of data availability, we made the choice to assign northern summer to all breeding ranges above the equator (and vice versa for the Southern hemisphere) without considering the few species that may not fully follow this pattern.

Movement information was taken from standard reference handbooks (e.g. del Hoyo, Elliott, Sargatal, Christie, & Juana, 2018). To deviate from the oversimplified binary view of bird migration ('migrant' vs. 'non-migrant'), we distinguished three strategies: *strict migrants* (784 species), for which all individuals move to a wintering range geographically disjunct from the breeding one; *partial migrants* (813 species), for which the species consists of a strict migrant and resident fraction; and *residents* (8,222 species), for which all populations occur year-round within their breeding range (Rappole, 2013). Defining avian migration as a regular, endogenously controlled, seasonal return movement of birds between breeding and non-breeding areas (Salewski & Bruderer, 2007), we assumed that most tropical species fall into the *resident* category, even if facultative migration (Winger et al., 2019) and dispersal movements of these tropical

species may have implications on the evolution of migratory behaviour (see details in Appendix S1).

For migratory species (strict and partial), we defined three classes of migration distance from distribution maps and reference handbooks (del Hoyo et al., 2018). We defined (a) *short-distance* migrants as species travelling to a wintering site within 2,000 km; (b) *long-distance* migrants as species travelling more than 2,000 km; and (c) *variable-distance* migrants as species with some populations travelling less than 2,000 km and some more (Rappole, 2013). Overall, 620 species were classified as *short-distance* migrants, 576 species as *variable-distance* migrants and 401 species as *long-distance* migrants. A quantitative value of the distance of migration was calculated from range maps to support the categorization by testing whether our categorical and quantitative measurements of migration distance showed a consistent relationship (see details in Figure S2.2 in Appendix S1).

To base our study on the most up to date worldwide avian phylogeny, we merged two phylogenies by constructing a composite of the new phylogeny of birds recently established by Prum et al. (2015) and the maximum clade credibility (MCC) tree from Jetz et al. (2012), following the method described in Cooney et al. (2017; see details in Supporting Information). We also pruned all trees from the Prum MCC posterior distribution to generate trees for the three study orders (i.e. Anseriformes, Charadriiformes and Passeriformes).

2.2 | Climatic data

Monthly averages of mean air temperatures (from 1960 to 1990) were extracted from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a 10-min resolution (18.5 km at the equator). As the previous metric was not available for marine areas, monthly averages of mean sea surface temperatures (from 1971 to 2000) were extracted from the NOAA Physical Sciences Division (<http://www.esrl.noaa.gov/psd/>) and projected to the same grid. In grid cells of coastal areas, where both mean air temperature and mean sea surface temperature were available, we checked that the two measurements were correlated (see Figure S2.1 in Appendix S1). This allowed us to combine both temperature measurements (air and sea) to a single dataset of ocean and terrestrial monthly average temperatures. This is an important step to consider all migratory species in our analyses, including seabirds wintering at sea, which are usually excluded from analyses of climatic niches (e.g. Lavergne, Evans, Burfield, Jiguet, & Thuiller, 2013; Pearman et al., 2013). As a further variable, we extracted temperature seasonality from the databases, defined as the amount of temperature variation over a given year (or averaged years) based on the standard deviation of monthly temperature averages (Hijmans et al., 2005).

2.3 | Comparative analyses of climatic niches

We used four different metrics to characterize and compare species' thermal niches of breeding and wintering ranges (see Figure S2.3 in Appendix S1 for details).

1. First, we computed the mean temperature seasonality across each species' breeding range to test whether the experienced climate seasonality correlates with the species' migratory strategy and migration distance. Assuming that seasonality increases with increasing latitude, we also checked for a correlation between mean breeding latitude and migration strategies.
2. Second, to assess whether migratory species tend to track the same thermal conditions through the seasons, we computed the overlap between the temperature kernel density distributions of species' breeding and wintering ranges (Figure S2.3 in Appendix S1), based on the four summer and four winter months' temperatures of these two ranges respectively. This overlap was computed as the D-metric (Schoener, 1970), which ranges from zero (no overlap) to one (complete overlap).
3. Third, to quantify whether a species tends to spend the winter in a warmer or colder thermal niche, we calculated the difference between the 97.5 percentiles of the kernel density distribution of wintering and breeding temperatures. We used the 97.5 percentiles instead of an average value in order to characterize the maximum thermal niche, which may be the main driver of selection towards wintering under warmer climates.
4. Finally, we quantified how migration behaviour affects the experienced year-round thermal niche of each species by comparing the wintering ground and the hypothetical wintering on the breeding ground. To do so, we calculated the difference between the 97.5 (and 2.5) percentile of the density distributions of temperature values each species actually experiences in its breeding and wintering ranges all together (4 months in its breeding range + 4 months in its wintering range) and the 97.5 (and 2.5) percentile of temperature values it would hypothetically experience if it was wintering and breeding in the same range (8 months in its breeding range). We term this last metric 'thermal niche change' (TNC, Figure S2.3 in Appendix S1). A positive value indicates that the migration behaviour shifts the thermal niche of a species towards overall higher temperatures.

Phylogenetic generalized least squares regressions (PGLS) were used to test for the linear relationships between the above four metrics of climatic niches as explanatory variables and migration strategies and distances as response variables. PGLS avoid pseudo-replication due to the relatedness of species by applying a phylogenetic correction (R package PHYLOLM, Ho & Ane, 2014) through a lambda model of phylogenetic signal (Pagel, 1999). All models were fitted for all birds worldwide and then separately for the three focal orders Anseriformes, Charadriiformes and Passeriformes.

2.4 | Ancestral state reconstructions and inference of biogeographic scenarios

Due to the distinct evolutionary history of the different bird clades of the world, the lability of the traits characterizing migration behaviour and the so far shifting relationships between major avian orders (Jarvis et al., 2014; Jetz et al., 2012; Prum et al., 2015), we

did not perform an ancestral state reconstruction on all bird species but focused separately on the three focal orders Anseriformes, Charadriiformes and Passeriformes.

Ancestral state reconstructions of migratory strategies (*resident*, *partial migrant*, *strict migrant*) were performed using constant rate Markov Chain models (R package Diversitree, FitzJohn, 2012). We tested three different transition rate models: equal rates between all states (ER), different rates between all states (ARD) and different rates with the transition rate between *resident* and *strict migrant* constrained to zero (stepping-stone model, ST hereafter). The hypothesis underlying the ST model is that direct shifts from resident to strict migratory behaviour (and vice versa) are impossible, and lineages necessarily need to go through a state of partial migration containing both the *strict migrant* and *resident* fractions. The model yielding the lowest AIC value was selected and used for ancestral state reconstructions. Joint ancestral state reconstructions were used to assign the most likely migratory strategy to each internal node (FitzJohn, 2012). This allowed us to determine the most likely ancestral migration strategy of each study order. To quantify the accumulation of migratory lineages over time, we performed lineage-through-time plots for each order by assigning nodes to either a migratory strategy (*strict* and *partial migrants* combined) or a resident strategy.

To test whether one of the biogeographic scenarios (NHT and SHT) better explains the evolutionary emergence of migration within the three studied orders, we performed additional ancestral state reconstructions using a more detailed set of states depicting species ranges, as *residents*, *partial migrants* and *strict migrants*, with reference to their latitudes of occurrence (see Figure 2a). The rationale of our approach is that particular combinations of transitions between these states correspond to the alternative NHT and SHT. To do this, we used the package Diversitree (FitzJohn, 2012, see Table S3.2b in Appendix S1) to select the best model (lowest AIC) depicting the data for each study clade, and to perform a 10,000-generation MCMC Bayesian inference (FitzJohn, 2012) to compute the posterior probability of each transition rate. We then combined the posterior distributions of different parameters to compute the posterior probability of each biogeographic scenario, that is $q_{2.5} + (q_{2.3} \times q_{3.5})$ as an estimate of the probability of the NHT scenario, and $q_{1.5} + (q_{1.4} \times q_{4.5})$ as an estimate of the probability of the SHT scenario (as depicted in Figure 2a; $q_{i,j}$ is the transition parameter between states i and j). We estimated the difference between both scenario probabilities in each step of the MCMC chain to get the posterior distribution of credible values of the differences. We then assessed the statistical difference between scenario probabilities by checking whether the 95% credible interval of this distribution overlapped zero.

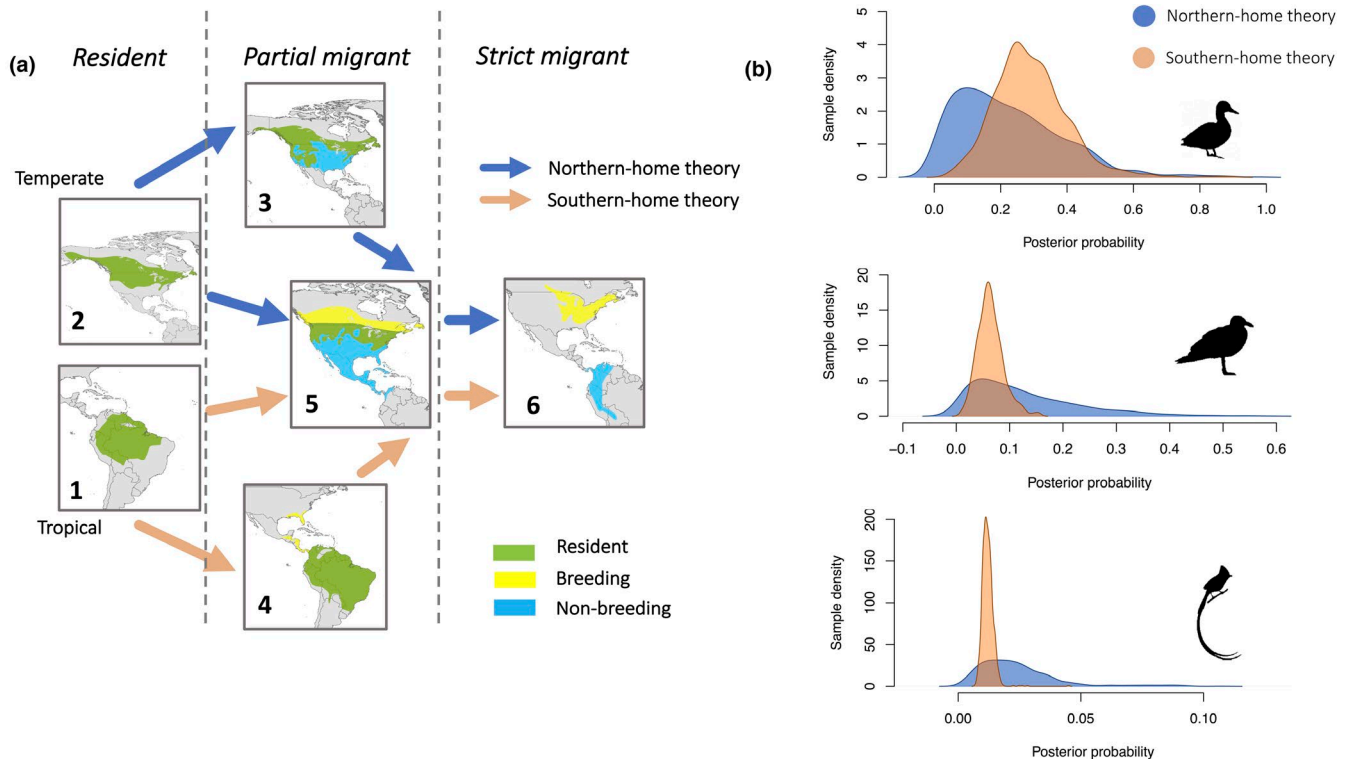


FIGURE 2 (a) Schematic modelling of the best Markov chain model explaining the evolution of migration behaviour under the biogeographic scenarios of NHT (blue arrows) or SHT (light red arrows). Different states of this model of evolution are pictured with distribution maps 1–6. Different ranges on maps are represented with standard bird handbook colours, that is, green for the distribution of sedentary birds, yellow for the breeding area and light blue for the wintering area of migratory birds. (b) Resulting posterior probabilities for NHT (blue) and SHT (light red) scenarios, based on the estimated transition rates of the best model, computed for Anseriformes, Charadriiformes and Passeriformes. Distribution kernels of posterior probabilities of NHT and SHT scenarios were calculated from 9,000 post-burnin MCMC samples of the best model [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Comparative analyses of climatic niches

Breeding range climatic seasonality was strongly associated with migratory strategies and distances (Figure 3). *Residents* experienced the lowest breeding range seasonality, while *partial migrants* bred under greater climatic seasonality and *strict migrants* under the highest seasonality. Within migratory species (partial and strict migrants), *long-distance* migrants had greater range seasonality than both *short-* and *variable-distance* migrants. As expected, similar patterns of correlation were found between strategy and distance of migration on the one hand and the mean breeding latitude on the other (Table S3.1 in Appendix S1 for statistical tests).

For both the global-scale analysis and for Passeriformes, we found that the thermal overlap between breeding and wintering ranges of *partial* and *strict migrants* was significantly lower than for *resident* species (Figure 4a, Table S3.1 in Appendix S1). We did not find any significant difference in the thermal niche overlap for Anseriformes and only between *residents* and *strict migrants* for Charadriiformes (Table S3.1 in Appendix S1), where the thermal overlap of *strict migrants* was significantly lower than for *resident* species. We also found an effect of the migration distance on the thermal niche overlap: both *short-* and *long-distance* migrants showed lower overlap values than *variable-distance* migrants at the global scale and for Charadriiformes and Passeriformes (Figure 4b, Table S3.1 in Appendix S1). However, for Anseriformes, *long-distance* migrants exhibited a higher thermal overlap than *variable-* and *short-distance* migrants.

The difference between the 97.5% quantiles of wintering and breeding temperatures showed that *long-distance* migrant species

tended to migrate towards warmer environments during their non-breeding period, when compared to their breeding temperatures (97.5% temperature difference: 3.74°C; Figure 4c). In contrast, both *variable-* and *short-distance* migrant species, tended to migrate towards temperatures colder than those they experience in their breeding quarters (97.5% temperature difference: -1.76 and -4.21°C, respectively; Figure 4c). The same results were consistently found for the three study orders (Table S3.1 in Appendix S1).

Within migratory species, the change in species' thermal niche due to migration shows that the results for the shifts of the 2.5% and 97.5% percentiles of the temperature values were similar (Table S3.1 in Appendix S1): *long-distance* migrants showed the largest thermal niche change during migration by increasing both their thermal minima and maxima, followed by *variable-distance* migrants and *short-distance* migrants (Figure 4d). This pattern was strikingly consistent between the three main study orders, which showed the exact same difference of thermal niche changes between classes of migration distance (Figure 4d, Table S3.1 in Appendix S1).

3.2 | Ancestral state reconstructions and biogeographic scenarios

Model selection for ancestral state reconstructions of migration strategies systematically rejected the equal rates model for the three studied bird orders (Table 1). For both Anseriformes and Charadriiformes, the stepping stone models were retained, with a root constrained to *resident* for Charadriiformes, and with no root constraint for Anseriformes (Table 1). Marginal likelihoods from models with an unconstrained root yielded a 0.76 and 0.34 posterior probability for a *resident* ancestor as an ancestor of Charadriiformes and Anseriformes respectively (see Figure 1a). For Passeriformes, the best model depicting the evolution of migration strategies was a model with all rates different and a root constrained to *strict migrant* (posterior probability of 0.62).

In Anseriformes, migratory behaviour seems to have first appeared around 6.6 Ma ago (Figure 1b), with the first node exhibiting migratory behaviour being the most recent common ancestor of the subfamily Anserinae (swans and true geese). This emergence was then followed by a rapid accumulation of migratory lineages during the Pleistocene. In Charadriiformes, ancestral state reconstructions suggested that the earliest appearance of migratory behaviour occurred around 22.5 Ma ago (Figure 1b). The emergence of most migrant lineages was estimated to mainly occur during the Pliocene. Surprisingly, the ancestor of Passeriformes was estimated most likely as a *strict migrant*. The first return to a sedentary strategy was estimated to occur around 39.7 Ma and *resident* lineages became the dominant strategy within Passeriformes from mid-Oligocene (Figure 1b).

The biogeographic model excluding transitions 3–6 and 4–6 (and vice versa) best fitted our data (Figure 2a), and this model structure was then used to run MCMC sampling to estimate the relative probability of the two biogeographic scenarios of the origins of migration (NHT or SHT; Table S3.2c in Appendix S1). For all three orders, we found no support for any of the two biogeographic scenarios

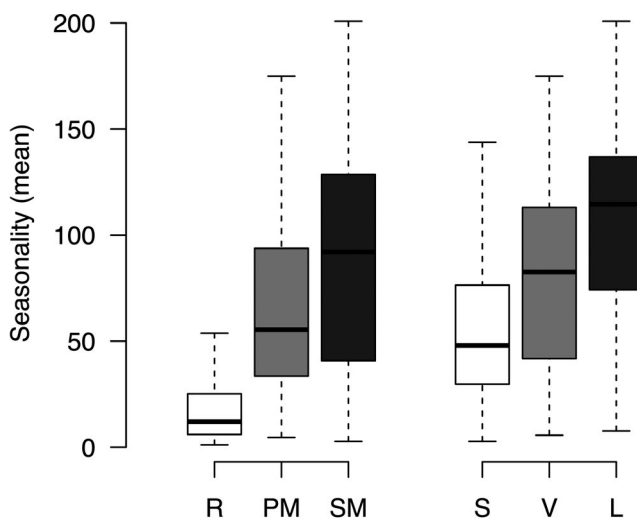


FIGURE 3 Relationships between the mean temperature seasonality (SD of monthly temperature averages) of species' breeding ranges and their migration characteristics. Migration strategy are resident (R), partial migrant (PM) and strict migrant (SM), and migration distance (right panel) are short distance (S), variable distance (V) and long distance (L)

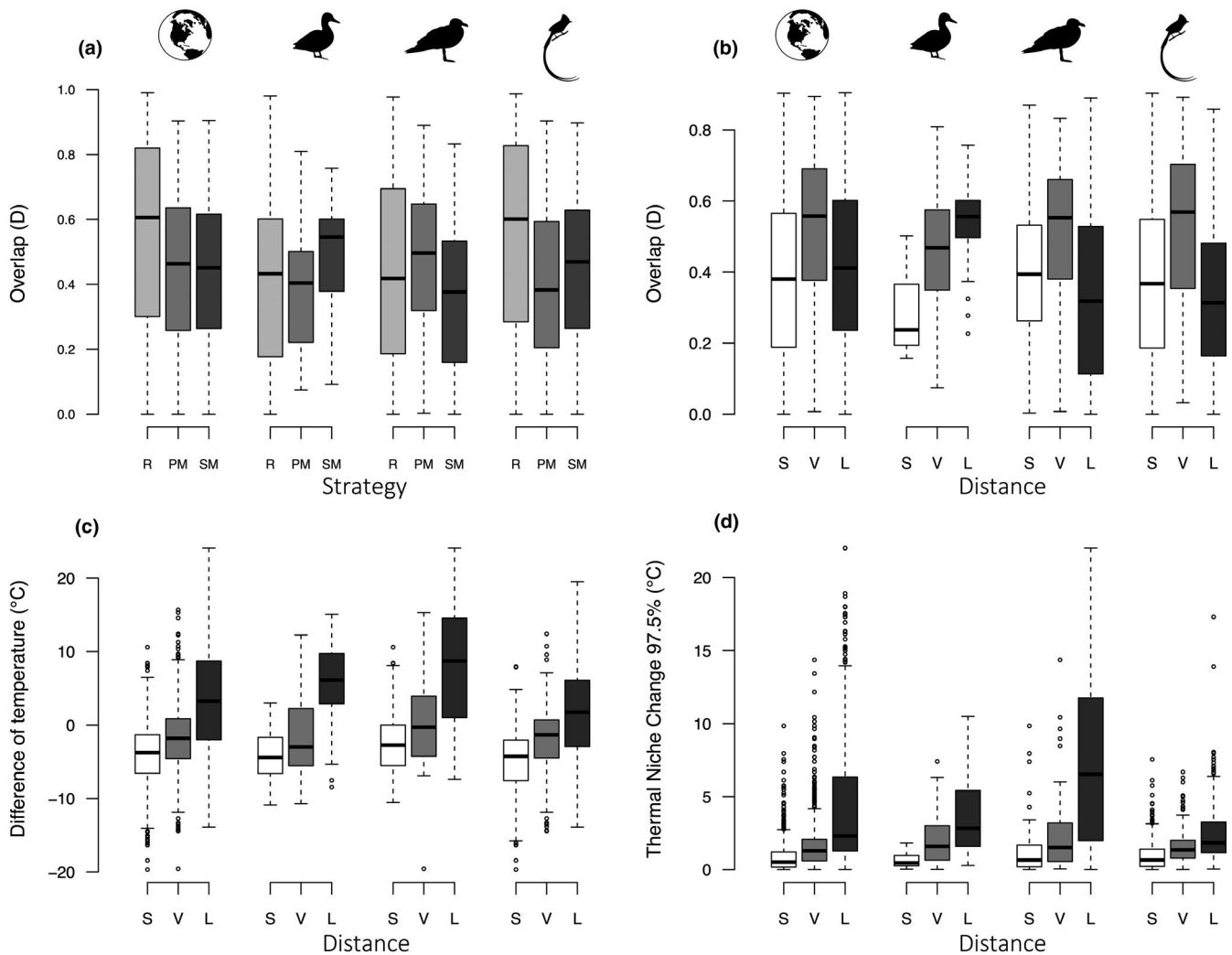


FIGURE 4 Boxplots showing (a) the overlap between temperatures of species' wintering and breeding ranges for each migration strategy; (b) the overlap between temperatures of species' wintering and breeding ranges for each class of migration distance; (c) the difference between the 97.5% temperature quantile in species' wintering and breeding ranges for each class of migration distance; and (d) the difference between the 97.5% percentile of temperature values experienced by a migratory species (in its breeding and wintering range) and the 97.5% percentile of temperatures it would hypothetically experience when staying year-round in its breeding range, for each class of migration distance. Each relationship is plotted for all bird species worldwide and for the three study orders, Anseriformes, Charadriiformes and Passeriformes

(Figure 2b). Indeed, while the modal value suggests emergences of migratory behaviour more frequently under a SHT scenario in Anseriformes (0.28 against 0.19 for NHT) and under a NHT scenario in Charadriiformes (0.1 against 0.06 for SHT), these differences in probabilities are not statistically supported (95% confidence interval for Charadriiformes: $-0.106:0.352$; Anseriformes: $-0.457:0.403$; Passeriformes: $-0.011:0.034$).

4 | DISCUSSION

Large-scale phylogenetic studies investigating the evolutionary origins of long-distance migration are very scarce (Winger et al., 2014).

Here we studied an almost unexplored area: the biogeographic and climatic context of the evolutionary emergence of long-distance bird migration worldwide (see Gomez et al., 2016).

While we think that case studies of particular clades with well-resolved phylogenies would provide more in-depth tests of the evolutionary origins of bird migration, large-scale analyses are equally important to provide generalization and to examine broad evolutionary hypotheses deeply rooted in the classical literature of bird migration. These hypotheses concern the link between migration and climatic seasonality, the different selection of climatic niches during breeding and non-breeding periods, as well as the past tempo and the geographic routes of emergence and loss of bird migration.

TABLE 1 Model selection for ancestral state reconstructions of migration strategies (resident, partial migrant, strict migrant) in large migratory orders of birds

Model	Nb parameters	Anseriformes			Charadriiformes			Passeriformes		
		Log-lik	AIC	ΔAIC	Log-lik	AIC	ΔAIC	Log-lik	AIC	ΔAIC
ARD	7	-152.1	318.2	5.1	-364.8	743.6	6.2	-2159.0	4,332.0	2.5
ARD.root1	6	-152.1	316.2	3.1	-364.6	741.2	3.8	-2160.5	4,332.9	3.5
ARD.root2	6	-152.1	316.2	3.1	-365.7	743.3	5.9	-2159.5	4,331.0	1.6
ARD.root3	6	-152.1	316.2	3.1	-367.8	747.7	10.3	-2158.7	4,329.4	0.0
ER	2	-169.1	342.2	29.1	-403.9	811.8	74.4	-2661.3	5,326.6	997.2
ER.root1	1	-169.1	340.2	27.1	-403.9	809.8	72.4	-2661.3	5,324.6	995.2
ER.root2	1	-169.1	340.2	27.1	-403.9	809.8	72.4	-2666.3	5,334.5	1,005.1
ER.root3	1	-169.1	340.2	27.1	-403.9	809.8	72.4	-2666.3	5,334.5	1,005.1
ST	5	-152.6	315.2	2.0	-364.9	739.8	2.4	-2171.9	4,353.9	24.5
ST.root1	4	-152.6	313.2	0.0	-364.7	737.4	0.0	-2173.4	4,354.8	25.3
ST.root2	4	-152.6	313.2	0.0	-365.7	739.5	2.1	-2172.4	4,352.8	23.4
ST.root3	4	-152.6	313.2	0.0	-367.9	743.8	6.4	-2171.7	4,351.3	21.9

For each study order, models were compared using Akaike information criterion (AIC) scores; model likelihood and delta AIC relative to the best model are also given. Three models were tested: equal transition rates between all states (ER), different transition rates between all states (ARD), and models without direct transition between resident and strict migrant states (stepping stone model; ST). For each model, four different root constraints were tested: no constraint, constrained to resident (root1), constrained to partial migrant (root2), or constrained to strict migrant (root3). Models in bold were considered the best models following Akaike information criterion (AIC) selection.

4.1 | Climatic seasonality has triggered the evolution of long-distance migration

A primary result of our study is that birds' geographic migration likely evolved, at least in part, as a response to the onset of seasonal environments on a geologic time-scale (see Somveille, Rodrigues, et al., 2018; Winger et al., 2019). Although the link between species migration and relatively high latitudes was known (Somveille, Manica, Butchart, & Rodrigues, 2013), this statistical link between long-distance migration and the strong climatic seasonality of birds' breeding ranges had never been regarded using phylogeny-based comparative analyses. In fact, despite the mostly temperate and Arctic latitudes of the breeding ranges of migratory species, this link between bird migration distances and the local climate of their breeding ranges is not trivial at all. For instance, the migration distances of species breeding in very seasonal local environments within temperate latitudes (between latitudes 50° and 30° and -30° and -50°) are as long as, and sometimes longer than, the migration distances of some species breeding in Arctic latitudes (results not shown). In addition, many species breeding in highly seasonal mountain environments could escape climatic seasonality by travelling much shorter distances than they actually do (but see Laube et al., 2015). These results support the idea that strong climatic seasonality has been an important factor in the evolution of long-distance bird migration (see Winger et al., 2019; Zink & Gardner, 2017). However, more in-depth studies are needed to confirm and understand the effect of different drivers on the evolution of long-distance migration, ideally by considering several environmental factors (see O'Connor et al., 2018; Somveille, Manica, et al., 2018) and by using clades with well-resolved phylogenies.

4.2 | Long-distance migrants seek warmer niches during winter

When considering all migratory species of the world, we found that *partial* and *strict migrant* species do not generally follow the same climatic niche year-round but rather spend winters in an environment warmer than that experienced in their breeding range ('niche switchers'). This result appears to somewhat contradict the results obtained by Somveille, Manica, et al. (2018), but are in agreement with the study by Laube et al. (2015) conducted on fewer species. Studies exploring the link between adaptive fitness costs or benefits and migration distances within a philopatric species of Charadriiformes (*Limosa limosa*) indeed show that wintering further south in Europe yields greater individual fitness (Alves et al., 2013) without any apparent flight cost (Kentie et al., 2017). These studies suggest that selection gradients may favour wintering areas in warmer areas in certain bird lineages. There are, however, notable exceptions to this general pattern of birds switching to warmer climates during their winter migration. These exceptions mainly concern Anseriformes, where *strict migrants* are more likely to be niche trackers than *partial migrants* and *residents*. These results call for complementary analyses testing whether the niche tracking or niche switching migration strategy could be linked to different life history traits such as parental care, reproductive investment, diet composition or foraging strategies.

Our results indicating that *strict migrants*, particularly Passeriformes, are mostly 'niche switchers' may seem odd in the light of two former studies conducted on smaller clades of Passeriformes and suggesting that migratory species are mostly 'niche trackers' between seasons (Gomez et al., 2016; Nakazawa et al., 2004). Here,



based on the 97.5% quantiles of wintering and breeding temperatures, we found that the best predictor of the strategy of niche switching is migration distance (Figure 4c,d). *Long-distance* migrants tend to spend winter in warmer climate niches than species migrating over shorter distances, and this pattern was strikingly consistent across global and order-centred analyses. This is corroborated by another recent study suggesting a lack of overlap between climatic niches of breeding and wintering ranges of long-distance migrants on a subset of migratory species (Zurell et al., 2018). Moreover, a recent study found that species travelling intermediate geographical distances (corresponding to our *variable-distance* class) tend to be relatively good at tracking thermal conditions closely throughout the year and having moderate gains in terms of access to resources (Somveille, Manica, et al., 2018). It was also demonstrated that *Sylvia* warblers did not compensate for the flight costs of a longer migratory journey by tracking their more nearby climatic and land cover niches (Laube et al., 2015). Our results and, at least partly, recent literature suggests an important phenomenon about bird migration: the evolution of long-distance migration could be linked to a behaviour of seeking warmer climates in which to spend the non-breeding period.

Such a large-scale study obviously comes with limitations. One limitation certainly lies in the fact that climatic variability of species niches was only quantified in terms of temperature variations. There is evidence suggesting that several environmental factors (precipitation, NDVI, etc.) are relevant to bird demography (Somveille, Manica, et al., 2018), but nevertheless temperature alone has been identified as an important driver of bird distributions (Fort, Beaugrand, Grémillet, & Phillips, 2012; Meehan, Jetz, & Brown, 2004; Root, 1988). It is important to note that the aim of our study was to include all long-distance migrants of the avian class, as these are often omitted from global analyses (e.g. Somveille et al., 2013; Zurell et al., 2018), due to their partially or strictly oceanic range. Considering only birds' thermal niches was thus the only way to include species whose distribution range include oceanic environments at some moment of their annual cycle. Another limitation could come from the fact that we have classified the migration characteristics of birds into discrete classes, assuming a relatively shorter migration distance for year-resident tropical species. Future analyses that would take into account a more detailed value of the migration distance would certainly detect tighter links between the evolution of birds' migration distance and tracking of their climatic niche.

Another limitation could come from the fact that we have classified the migration characteristics of birds into discrete classes, including the migration distance, which is actually complex than three classes. Future analyses that would take into account a more detailed value of the migration distance would certainly detect tighter links between the evolution of the migration distance and the tracking of the climate niche.

4.3 | Diverse biogeographic scenarios led to long-distance migration

Our estimation of a resident ancestor of Anseriformes and Charadriiformes converges with previous studies realized on clades

nested within these two orders. A study on the genus *Charadrius* (Charadriiformes) estimated a resident ancestor from South America (Joseph, Lessa, & Christidis, 1999), whereas a possible resident ancestor of the Anatidae family (Anseriformes) was estimated from Afrotropical or Neotropical areas (Gonzalez, Düttmann, & Wink, 2009). We did not find convincing statistical support to explain the emergence of a migratory behaviour indicating that migration did not evolve more often from tropical or temperate resident ancestors. However, our ancestral state reconstructions suggest that migration could have appeared in Anseriformes lineages more frequently from tropical locations, whereas migration could have appeared more frequently in Charadriiformes lineages from temperate areas. Nevertheless, the estimation of a resident ancestor and a tropical origin for the Anatidae family, to which most Anseriformes migratory species belong, may be consistent with a hypothetical *southern-home* appearance of migration behaviour. The lack of a clear delimitation between the NHT and SHT scenarios suggests that, as shown by Winger et al. (2014), this type of modelling approach from distribution maps shows interesting patterns in the evolution of bird migration but is probably more powerful for detecting recent scenarios of evolution. Recent changes in bird species' distributions and adjustments of their migration behaviour (see for example Able & Belthoff, 1998) may have masked signatures of biogeographic movements in deeper nodes of the phylogenetic trees of study orders.

While we highlighted the emergence of seasonal migration behaviour and its repeatability across time and space, we also found evidence for several episodes of loss of migration behaviour. This suggests that in the past migratory lineages may have adapted to novel ecological opportunities by returning to a resident state. This reasoning is supported by Kondo, Peters, Rosensteel, and Omland (2008) who demonstrated that sedentary and subtropical species may be secondary drop offs of temperate long-distance migrants (see also Bruderer & Salewski, 2008; Winger, Lovette, & Winkler, 2012). They indeed showed that the subtropical short-distance migrant, the black-backed oriole (*Icterus galbula*), diverged recently from the temperate breeding long-distance migrant, the Baltimore oriole (*Icterus abeillei*). They suggested that the latter maintained long-distance migration throughout the last glacial episodes, and that a founder population of the black-backed oriole reduced migratory distance by using an unoccupied niche (Kondo et al., 2008). More generally, this was suggested by the study of Rolland, Jiguet, Jönsson, Condamine, and Morlon (2014), which showed that migration triggered speciation when migratory lineages settled down to become resident. Moreover, the better fit of the stepping stone model and the low transition rates observed between *resident* and *strict migrant* states indicate that the *partial migrant* state is probably a necessary evolutionary step between strict residence and strict migration. Altogether this suggests a high flexibility in the proportions of migratory behaviour within populations over time (Bruderer & Salewski, 2008). It would be interesting to consider, in the future, the wide variety of non-breeding movements in resident species (especially in the tropics) and dispersal movements (natal and breeding dispersal; Campbell & Lack, 1985) to better understand the

gradual appearance of a *strict migratory* behaviour between seasonal habitats.

4.4 | Ancestral migratory strategies and timing of emergence

The possibility of an ancestral migratory behaviour (*strict migrant*) in Passeriformes is somewhat surprising considering the large number of resident species within this order (more than 85%), but the marginal likelihood of the unconstrained model clearly favoured a strict migrant strategy as an ancestral state. The lack of a well-resolved phylogeny for Passeriformes invites caution in the interpretation of this result. It is also important to note that considering migration strategies as discrete classes did not impact our results since we found an ancestral migratory behaviour despite the existence of a large number of tropical species that were all assumed to be sedentary in our analyses. Our finding of ancestral migratory behaviour in Passeriformes suggests that the large number of resident species observed today could result from repeated losses of migratory behaviour in the evolutionary history of this clade. It also makes sense in the light of the biogeographic history of the clade (see Bruderer & Salewski, 2008; Ericson et al., 2002): Claramunt and Cracraft (2015) showed that part of the Passeriformes (suborder *Tyranni*, currently ~1,000 species) probably diversified in South America, whereas the other part (suborder *Passeri*, currently ~5,000 species) probably diversified later in the east of the Gondwana continent (Australia and New Guinea). Thus, an ancestral migratory character would have favoured the spread of this order across the globe during its diversification, positing that migratory behaviour could have allowed the exploration of different continents and niches. In addition, it should be noted that among the first fossils of Passeriformes discovered in the Northern hemisphere and dating from the late Oligocene and early Miocene, only one of them could be assigned to an extant family: that of Alaudidae (Ballmann, 1972), which is currently composed of many migratory species. Similarly, the first fossils of the North American continent containing Passeriformes are species considered close relatives to families of migratory birds (i.e. Passerellidae; Steadman, 1981).

The emergence date of migration behaviour was estimated at different times between study orders: in the upper Miocene for Charadriiformes, in the lower Miocene for Anseriformes and in the middle Eocene for Passeriformes. The appearance of migration behaviour in the Miocene for Charadriiformes and Anseriformes is consistent with a marked decrease in global temperatures and a concomitant reduction in the area of tropical biomes (see Bruderer & Salewski, 2008). The estimated increase in the number of migratory species and the strong correlations observed between breeding seasonality and migration characteristics (strategy and distance) indicate that global cooling of the lower Oligocene had probably triggered the emergence of migratory species and lineages (see also Claramunt & Cracraft, 2015; Louchart, 2008). Under this new emerging global climate, it seems that migration had then become a successful life

history strategy for persistence under seasonal climates and may have allowed greater speciation rates (Rolland et al., 2014; Winger et al., 2012). Under such a biogeographic scenario, Passeriformes would have thus benefited from an early opportunity with ancestors already adapted to geographic migrations, allowing them to take advantage of the global cooling and fragmentation of tropical biomes to diversify into the many ecological niches left vacant.

5 | CONCLUSIONS AND PERSPECTIVES

Our results provide a large-scale test of how climatic niches and their year-round variability correlate with different aspects of bird migration, such as distance and the proportion of migrant and resident populations. We also report a correlation between long-distance migration and the tendency of birds to seek warmer climates during their non-breeding period, compared to short-distance migrants. Beyond that, we also infer an ancestral migratory behaviour in the deep evolutionary history of the Passeriformes order, which currently dominates the avian class. This result is consistent with an ancestral large diffusion of the clade around the globe (Ericson et al., 2002) and the fact that migration triggered speciation when migratory lineages settled down to be resident (Rolland et al., 2014). This leads to a prediction that would be interesting to test in the future: that long-distance migration behaviour not only allowed higher speciation rates but also faster rates of evolution of ecological niches.

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DATA AVAILABILITY STATEMENT

Some data are publicly available; bird range maps at www.birdlife.org, climate data at www.worldclim.org and <http://www.esrl.noaa.gov/psd> and bird phylogenetic data at www.birdtree.org. A table containing all species' migration characteristics is available in Supporting Information.

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BIOSKETCHES

Paul Dufour is an experienced field ornithologist, and PhD candidate with broad interests in the evolution of long-distance bird migration, at different taxonomic scales.

Co-authors are researchers with interests in population biology, macroecology and macroevolution of biodiversity.

Author contributions: S.L., K.S., S.D. and P.D. conceived the ideas. J.R. collected and gridded the distribution maps and the climatic data. S.L., K.S., S.C., S.D., W.T. and P.D. developed the methods. M.G. and P.D. ran the analyses. P.D. and S.L. wrote the first version of the paper and all authors contributed substantially to the revisions.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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SUPPORTING INFORMATION

Appendix 1 : Supplementary methods

Species data : geographic ranges

For almost 120 species, we found strong divergences between the online distribution ranges and the ranges in reference bird handbooks (del Hoyo et al. 2018). As it is likely that the online maps were incorrectly coded, we used the maps from the reference books and corrected the online maps. See below the list of species for which maps were corrected :

Acrocephalus dumetorum	Hymenops perspicillatus	Pterodroma baraui
Aphrodroma brevirostris	Luscinia pectoralis	Pterodroma brevipes
Ardenna bulleri	Macronectes giganteus	Pterodroma cahow
Ardenna carneipes	Macronectes halli	Pterodroma cervicalis
Ardenna creatopus	Morus bassanus	Pterodroma cookii
Ardenna gravis	Myiagra cyanoleuca	Pterodroma defilippiana
Ardenna grisea	Nesofregetta fuliginosa	Pterodroma externa
Ardenna pacifica	Oceanites gracilis	Pterodroma feae
Ardenna tenuirostris	Pachyptila belcheri	Pterodroma hasitata
Bulweria bulwerii	Pachyptila crassirostris	Pterodroma heraldica
Bulweria fallax	Pachyptila desolata	Pterodroma hypoleuca
Calonectris diomedea	Pachyptila salvini	Pterodroma incerta
Calonectris edwardsii	Pachyptila turtur	Pterodroma inexpectata
Calonectris leucomelas	Pachyptila vittata	Pterodroma lessonii
Carduelis uropygialis	Pagodroma nivea	Pterodroma leucoptera
Daption capense	Pelagodroma marina	Pterodroma longirostris
Diomedea amsterdamensis	Pelecanoides garnotii	Pterodroma macroptera
Diomedea antipodensis	Pelecanoides georgicus	Pterodroma madeira
Diomedea exulans	Pelecanoides magellani	Pterodroma magentae
Elaenia strepera	Pelecanoides urinatrix	Pterodroma mollis
Epthianura tricolor	Phalacrocorax chalconotus	Pterodroma neglecta
Fregata ariel	Phalacrocorax punctatus	Pterodroma nigripennis
Fregetta grallaria	Phoebastria albatrus	Pterodroma phaeopygia
Fregetta maoriana	Phoebastria immutabilis	Pterodroma pycrofti
Fulmarus glacialis	Phoebastria irrorata	Pterodroma sandwichensis
Fulmarus glacialoides	Phoebastria nigripes	Pterodroma solandri
Garrodia nereis	Phoebastria palpebrata	Pterodroma ultima
Geositta antarctica	Phylloscopus subviridis	Sula dactylatra
Halobaena caerulea	Procellaria aequinoctialis	Sula granti
Hippolais caligata	Procellaria cinerea	Sula neboxii
Hirundo spilodera	Procellaria conspicillata	Sula sula
Hydrobates castro	Procellaria parkinsoni	Sylvia deserticola
Hydrobates furcatus	Procellaria westlandica	Sylvia melanothorax
Hydrobates homochroa	Pseudobulweria aterrima	Thalassarche bulleri
Hydrobates leucorhous	Pseudobulweria beeki	Thalassarche cauta
Hydrobates markhami	Pseudobulweria	Thalassarche chrysostoma
Hydrobates microsoma	macgillivrayi	Thalassarche impavida
Hydrobates monorhis	Pseudobulweria rostrata	Thalassarche melanophris
Hydrobates montei	Pterodroma alba	Thalassarche steadi
Hydrobates pelagicus	Pterodroma arminjoniana	Thalassarche antarctica
Hydrobates tethys	Pterodroma atrata	Tyrannus albobularis
Hydrobates tristrami	Pterodroma axillaris	

Species data : species omitted

As the climatic niche of a single cell may not reflect the climate experienced by narrow-ranging species, we removed species with distributional range smaller than the size of a grid cell. We also removed species without wintering distribution and species considered as possibly extinct. In total, we considered 9819 species out of the 9993 species recognized in Jetz et al. (2012). See below the list of species omitted from the analysis :

Sporophila_caerulescens	Luscinia_ruficeps
Ramphocelus_icteronotus	Myadestes_lanaensis
Dacnis_egregia	Stizorhina_finschi
Hemispingus_ochraceus	Speculipastor_bicolor
Hemispingus_piurae	Onychognathus_neumanni
Hemispingus_auricularis	Troglodytes_tanneri
Camarhynchus_pauper	Malacocincla_perspicillata
Pinaroloxias_inornata	Zosterops_murphyi
Nesospiza_questi	Zosterops_albogularis
Nesospiza_wilkinsi	Zosterops_rotensis
Calyptophilus_tertius	Zosterops_nehrkorni
Piranga_lutea	Zosterops_tenuirostris
Piranga_hepatica	Rukia_ruki
Chlorothraupis_frenata	Zosterops_griseovirescens
Amaurospiza_carrizalensis	Apalis_argentea
Atlapetes_pallidiceps	Apalis_alticola
Spizella_pallida	Eremomela_canescens
Molothrus_armenti	Phyllastrephus_lorenzi
Cacicus_microrhynchus	Phylloscopus_amoenus
Cacicus_leucoramphus	Phylloscopus_emeiensis
Leucopeza_semperi	Phylloscopus_nitidus
Vermivora_bachmanii	Phylloscopus_proregulus
Melamprosops_phaeosoma	Phylloscopus_kansuensis
Carduelis_hornemanni	Phylloscopus_orientalis
Leucosticte_australis	Megalurulus_llanae
Psittirostra_psittacea	Acrocephalus_rehsei
Carpodacus_rodopeplus	Acrocephalus_rimatarae
Hemignathus_lucidus	Acrocephalus_familiaris
Loxops_caeruleirostris	Acrocephalus_baeticatus
Telespiza_ultima	Acrocephalus_sorghophilus
Paroreomyza_maculata	Acrocephalus_rodericanus
Anthus_longicaudatus	Hirundo_perdita
Lagonosticta_umbrinodorsalis	Hirundo_striolata
Pytilia_lineata	Progne_sinaloae
Estrilda_kandti	Progne_dominicensis
Estrilda_quartinia	Progne_cryptoleuca
Vidua_orientalis	Tachycineta_albiventer
Foudia_flavicans	Pseudochelidon_eurystomina
Nectarinia_tsavoensis	Eurochelidon_sirintarae
Nectarinia_stuhlmanni	Alauda_razae
Nectarinia_ludovicensis	Heteromirafra_sidamoensis
Dicaeum_quadricolor	Parus_teneriffae
Phoenicurus_caeruleocephala	Parus_carpi
Luscinia_obscura	Mayrornis_versicolor

Pomarea_nigra
 Pomarea_dimidiata
 Monarcha_boanensis
 Eutrichomyias_rowleyi
 Rhipidura_malaitae
 Corvus_hawaiiensis
 Pica_hudsonia
 Lanius_meridionalis
 Dicrurus_modestus
 Vireo_caribaeus
 Vireo_gracilirostris
 Oriolus_traillii
 Colluricincla_tenebrosa
 Colluricincla_sanghirensis
 Prionops_rufiventris
 Coracina_newtoni
 Xanthomyza_phrygia
 Philemon_kisserensis
 Myzomela_cineracea
 Myzomela_chermesina
 Gerygone_modesta
 Gerygone_hypoxantha
 Cinclodes_comechingonus
 Xenops_milleri
 Dendrocincla_turdina
 Deconychura_stictolaema
 Formicarius_moniliger
 Pithys_castaneus
 Herpsilochmus_parkeri
 Frederickena_unduligera
 Myrmotherula_fluminensis
 Nesotriccus_ridgwayi
 Elaenia_strepera
 Elaenia_ridleyana
 Pachyramphus_xanthogenys
 Cephalopterus_glabricollis
 Chamosyna_diadema
 Cyanoramphus_forbesi
 Cyanopsitta_spixii
 Rhynchopsitta_pachyrhyncha
 Campephilus_principalis
 Campephilus_imperialis
 Todoramphus_cinnamominus

Otus_moheliensis
 Otus_insularis
 Sterna_bernsteini
 Catharacta_maccormicki
 Numenius_borealis
 Lophornis_brachylophus
 Discosura_letitiae
 Eriocnemis_godini
 Collocalia_sawtelli
 Cypseloides_cherriei
 Aegotheles_savesi
 Caprimulgus_centralasicus
 Caprimulgus_maculosus
 Chordeiles_gundlachi
 Phalacrocorax_carunculatus
 Fregata_aquila
 Pseudobulweria_aterima
 Puffinus_huttoni
 Pseudobulweria_macgillivrayi
 Puffinus_bulleri
 Procellaria_westlandica
 Procellaria_conspicillata
 Pterodroma_caribbaea
 Pterodroma_incerta
 Oceanites_maorianus
 Oceanites_oceanicus
 Oceanites_gracilis
 Thalassarche_salvini
 Thalassarche_eremita
 Diomedea_amsterdamensis
 Diomedea_epomophora
 Oceanodroma_hornbyi
 Oceanodroma_monteiroi
 Megadyptes_antipodes
 Spheniscus_demersus
 Aptenodytes_forsteri
 Gallinula_silvestris
 Gallirallus_owstoni
 Coccozys_ferrugineus
 Ptilinopus_chalcurus
 Ducula_aurorae
 Zenaida_graysoni
 Mitu_mitu

Phylogenetic data

We merged two phylogenies by constructing a composite of the new phylogeny of birds recently established by Prum et al. (2015) and the maximum clade credibility (MCC) tree from Jetz et al. (2012), following the method described in Cooney et al. (2017). We grafted sub-clades (mostly family level) onto nodes in the phylogeny at positions where the two trees could be sensibly combined. We believe this new updated tree provides more reliable divergence times

and topology of the earliest branching events separating major non-passerine taxa than previously published phylogenies (see Thomas 2015).

Movement information

We defined austral summer as November through February, and boreal summer as May through August, and assumed that these are the main breeding and wintering periods for the focal species. The mean temperature of each grid cell was calculated for both time periods. The remaining four months were considered migration periods so that temperature data of these months were not used in our analyses. If a species' breeding distribution was completely or predominately in the Northern hemisphere, the boreal summer average temperature was taken for all cells in the breeding distribution, and the austral summer temperature average were taken for cells in the wintering distribution. The opposite averages were used for species breeding completely or predominately in the Southern hemisphere. We made this choice without considering the few species that they may not fully follow this pattern for reasons of data availability.

Movement information was taken from distribution maps and standard reference handbooks (e.g. del Hoyo et al., 2018). Distribution maps from Birdlife International & NatureServe (2017) were used first to translate visually the information. If the categorization of *strict migrants* was easy due to their wintering range geographically disjunct from the breeding one (see Figure SMa below), categorization of *partial migrants* and *residents* were sometimes more challenging. Indeed, in some cases, the distribution does not reflect the migratory status of the species. As example, if the distribution map of Eurasian Blackbird *Turdus merula* could indicate mostly a resident species (see Figure SMb), ringing recoveries showed that most of the populations are actually partial migrants (Collar & Christie, 2018). When a species presented *residents*, *partial migrants* and *strict migrants* populations without predominant migration strategy, we usually labelled the species as a *partial migrant* (see *Fringilla coelebs* in Figure SMc for example).

For migratory species (strict and partial), we defined three classes of migration distance from distribution maps and reference handbooks (del Hoyo et al., 2018). For the *strict migrant* distribution maps, we visually defined the migration distance from the distance between breeding and wintering areas. For partial migrants, the 'year-round' area may blur the population movements ('leap-frog' movements of northern populations for example ; Lundberg

& Alerstam, 1986). In such cases, distance was defined from information about movements in the text part of reference handbooks (del Hoyo et al. 2018). A quantitative value of the distance of migration was calculated from range maps to support our categorization.

For considering the migration distance as a quantitative trait, in addition to partial migratory species, we had to consider the problem of resident species. We would have considered most of the tropical species as 'resident'. However, considering a distance of 0km for the three quarters of Passeriformes as well as comparing, within the Charadriiformes, resident species with ones traveling nearly 20 000km, would not give a very convincing results and ancestral state reconstruction. Therefore, due to a great difficulty in considering the movements of resident species, we chose to keep our qualitative categorization and to use the quantitative measure to check it in return.

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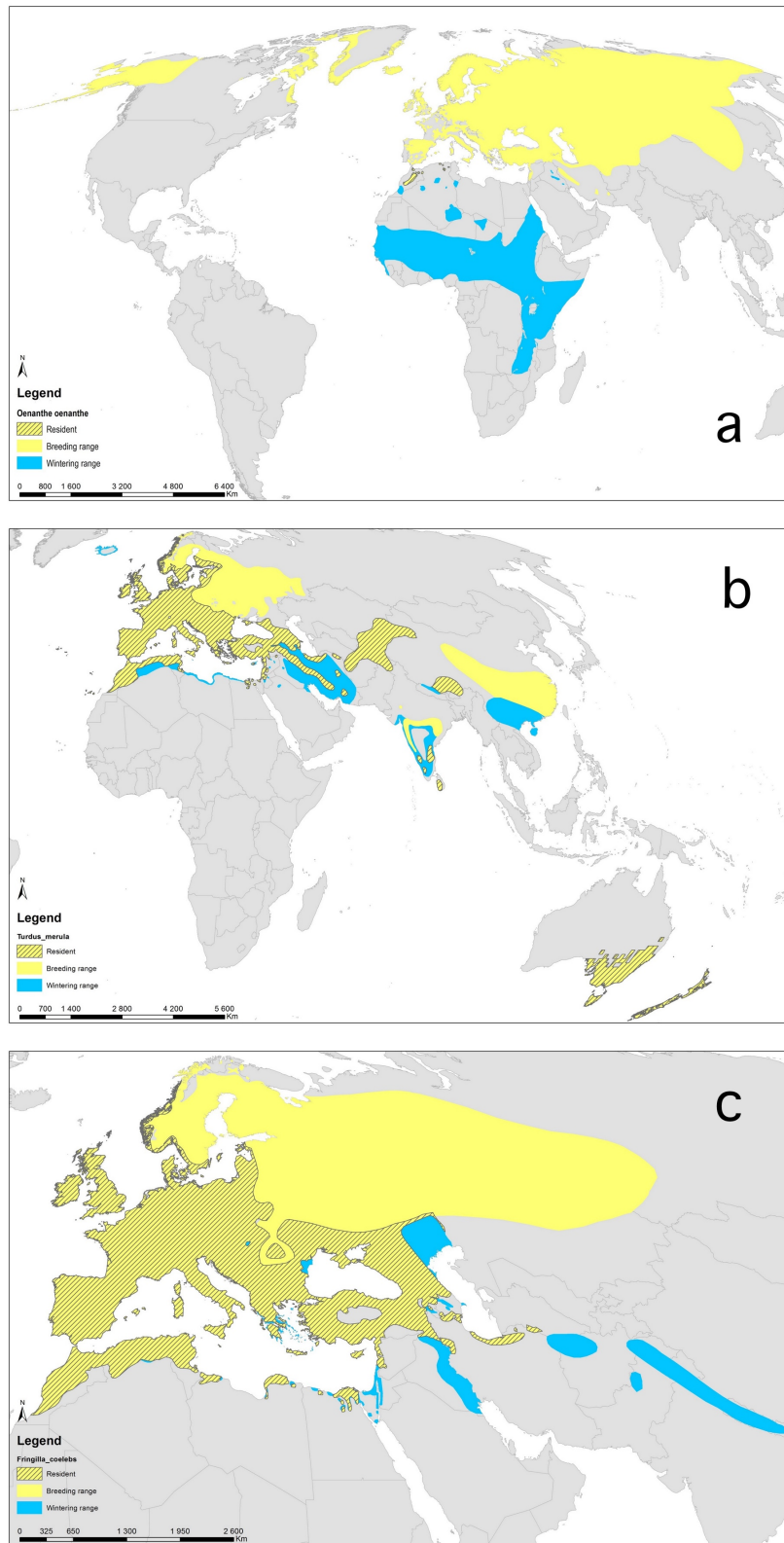


Figure SM Distributions maps of three species of Passeriformes : (a) *Oenanthe oenanthe*, (b) *Turdus merula* and (c) *Fringilla coelebs*. Maps were adapted from Birdlife International & NatureServe (2017).

Appendix 2 : Supplementary figures

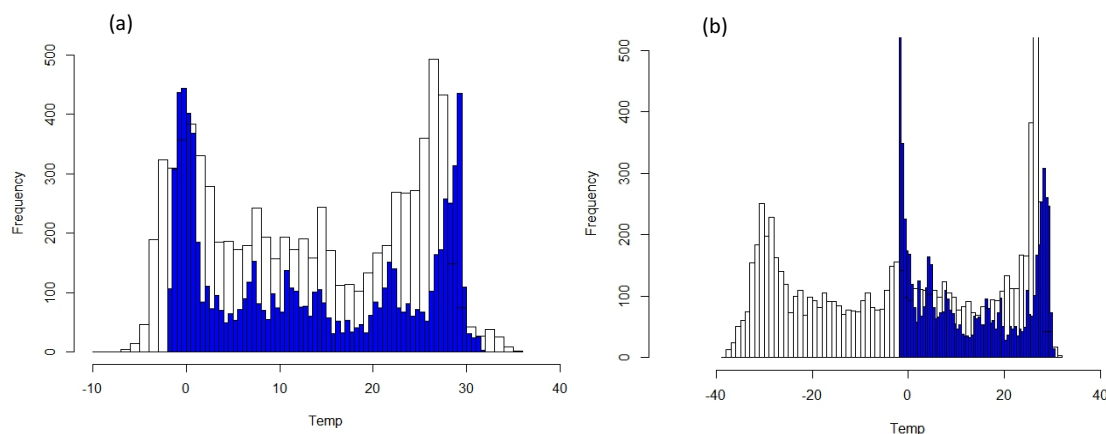


Figure S2.1 Histograms comparing mean sea surface temperature and mean air temperature in coastal grid cells at the global scale. (a) Similarity between the average sea surface temperatures (blue) and mean air temperatures (white) in coastal cells from May to August. (b) Comparison of the average sea surface temperatures (blue) and mean air temperatures (white) in coastal cells from November to February. The minimum sea surface temperature is -1.8°C , which corresponds with the known temperature of frozen ocean waters. The air temperature gets much colder.

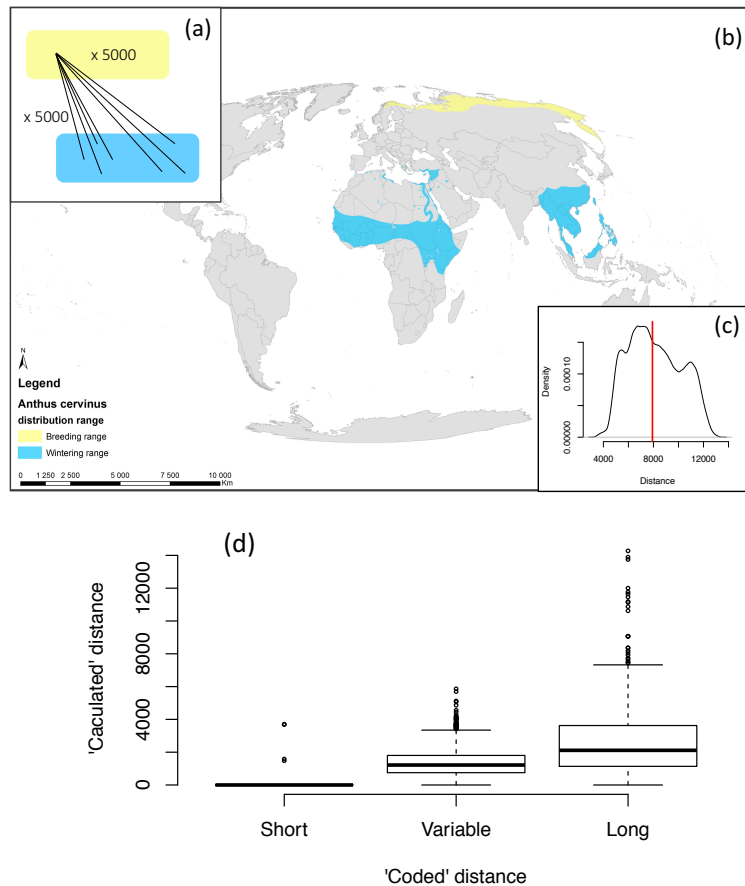


Figure S2.2 Quantitative estimation of species' migration distances from their distribution maps. (a) Schematic representation of the computation method : 5000 points were randomly chosen within the breeding and wintering ranges of each species, allowing to compute 5000x5000 distances between breeding and wintering locations. (b) An example of distribution map from BirdLife International, here the Red-throated Pipit' *Anthus cervinus* map. For worldwide distributed species only, the Nearctic migration system was separated to the rest of the world considered as an another migration system, and worldwide distributed species known for not following these systems were treated like the others (Newton, 2007) (c) From the obtained distribution of potential migrations distances, we computed the median value as an estimation of median distance of migration for each species (here 7922 kilometers for the Red-throated Pipit). (d) Boxplots comparing the calculated distance of migration with our manually coded distance classes (short, variable, long).

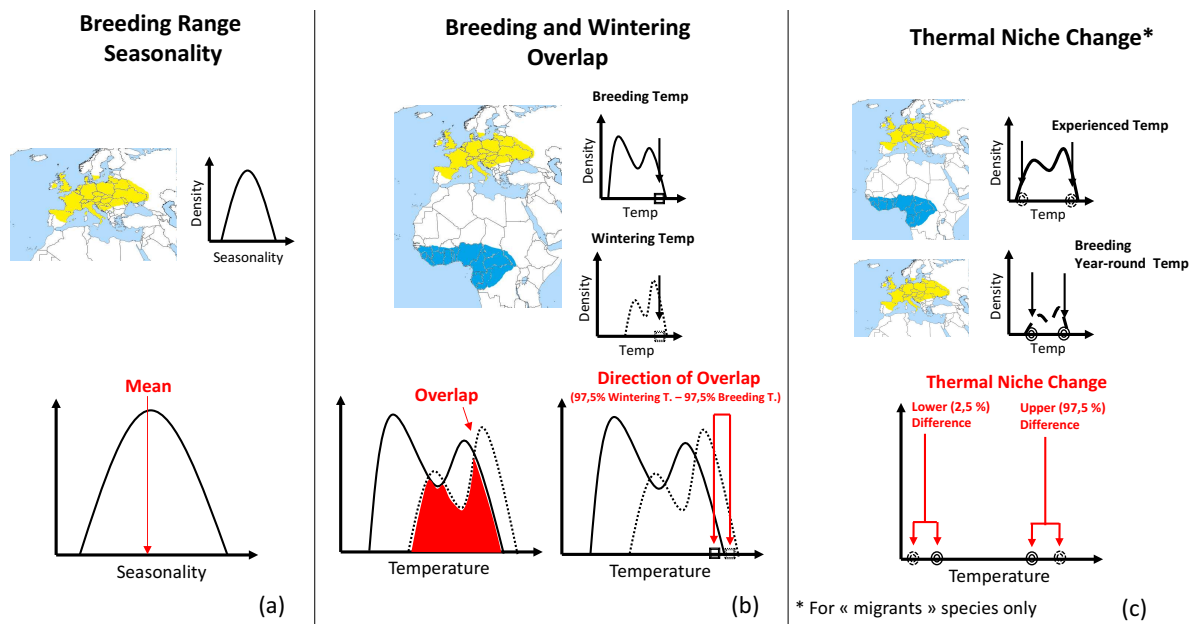


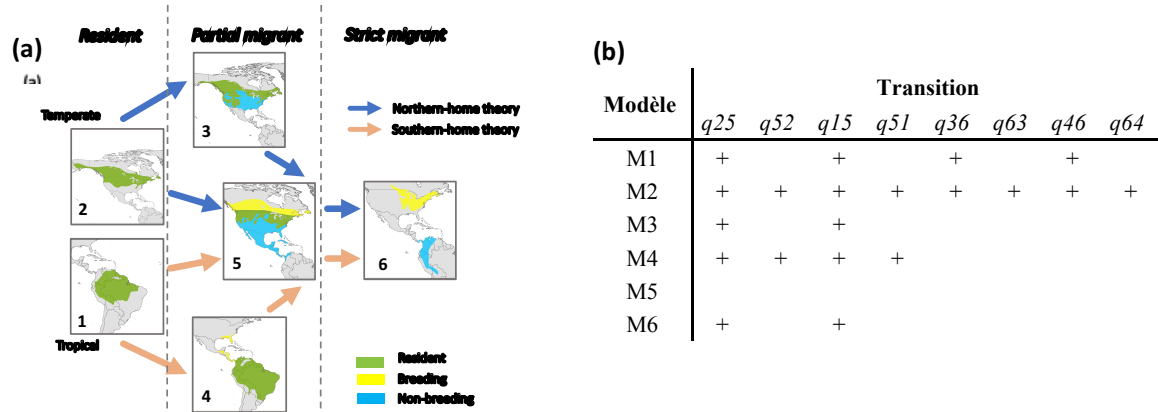
Figure S2.3 Diagrams illustrating the metrics to quantify and compare the breeding and non-breeding climatic niches of migratory birds. On insert maps, the yellow range represents an hypothetical species' breeding range while the blue range represents an hypothetical species' wintering range. (a) The breeding range seasonality was computed as the mean value of climate seasonality across the breeding range of each species. (b) The climatic overlap between the breeding and wintering ranges of each species was computed as the overlap between the kernel density distributions of temperatures in their breeding range and wintering range, during the four summer and four winter months, respectively. This overlap is displayed as the red intersection between the kernels of summer and winter temperature distributions. The direction of this climatic overlap was also calculated for each species as the difference between the upper 97.5 quantiles of temperatures experienced during the four summer months in its breeding range and using the four winter months of its non-breeding range. (c) For estimating thermal niche shift due to geographical migration, we compared the experienced temperature distribution by each migratory species (4 months in its breeding range + 4 months in its wintering range) with the temperatures experienced by the same species hypothetically remaining resident in its breeding range (8 months in the same breeding range). The difference in temperature values at the 2.5 and 97.5 distribution percentiles was calculated between these two distributions.

Appendix 3 :Supplementary tables

Strategy	Global			Anseriformes		
	model.fit	part. migrant vs res.	strict migrant vs res.	model.fit	part. migrant vs res.	strict migrant vs res.
Seasonality	4981.127 (2) ***	41.921 (0.870) ***	67.342 (0.946) ***	895.128 (2) ***	60.715 (5.452) ***	99.396 (5.186) ***
Latitude	1875.09 (2) ***	11.853 (0.961) ***	-19.289 (0.714) ***	121.876 (2) ***	31.046 (6.120) ***	-38.385 (5.403) ***
Overlap	130.361 (2) ***	-0.094 (0.011) ***	-0.097 (0.011) ***	5.702 (2)	-0.027 (0.044)	0.082 (0.042) °
Difference of temperature	895.129 (2) ***	-1.524 (0.134) ***	3.829 (0.145) ***	44.287 (2) ***	-0.196 (0.926)	5.814 (0.881) ***
Distance	model.fit	variable vs short	long vs short	model.fit	variable vs short	long vs short
	model.fit	variable vs short	long vs short	model.fit	variable vs short	long vs short
Seasonality	374.527 (2) ***	24.390 (2.063) ***	46.956 (2.305) ***	175.375 (2) ***	41.946 (10.517) ***	68.754 (11.461) ***
Latitude	163.598	15.306 (1.674) ***	23.913 (1.900) ***	19.941 (2) ***	32.147 (9.873) ***	50.544 (10.811) ***
Overlap	113.456 (2) ***	0.136 (0.013) ***	0.030 (0.014) *	19.518 (2) ***	0.166 (0.049) **	0.247 (0.054) ***
Difference of temperature	431.814 (2) ***	2.680 (0.308) ***	7.657 (0.341) ***	25.728 (2) ***	2.967 (1.789)	9.501 (1.950) ***
Thermal niche difference - 2.5%	709.064 (2) ***	9.048 (0.563) ***	18.638 (0.628) ***	36.454 (2) ***	12.587 (3.037) ***	21.977 (3.309) ***
Thermal niche difference - 97.5%	338.503 (2) ***	0.806 (0.147) ***	3.151 (0.164) ***	20.266 (2) ***	1.398 (0.649) *	3.200 (0.707) ***

Strategy	Charadriiformes			Passeriformes		
	model.fit	part. migrant vs res.	strict migrant vs res.	model.fit	part. migrant vs res.	strict migrant vs res.
Seasonality	44.287 (2) ***	32.778 (4.719) ***	78.724 (4.365) ***	176.371 (2) ***	46.692 (1.122) ***	76.643 (1.230) ***
Latitude	121.876 (2) ***	31.046 (6.120) ***	-38.385 (5.403) ***	1382.335 (2) ***	14.437 (1.263) ***	-20.824 (0.921) ***
Overlap	9.54 (2) *	0.049 (0.034)	-0.065 (0.031) *	69.730 (2) ***	-0.114 (0.015) ***	-0.083 (0.017) ***
Difference of temperature	176.370 (2) ***	0.860 (0.768)	10.655 (0.698) ***	212.383 (2) ***	-1.859 (0.181) ***	1.793 (0.199) ***
Distance	model.fit	variable vs short	long vs short	model.fit	variable vs short	long vs short
	model.fit	variable vs short	long vs short	model.fit	variable vs short	long vs short
Seasonality	25.726 (2) ***	18.380 (5.817) **	69.197 (5.523) ***	431.814 (2) ***	27.741 (2.602) ***	52.359 (3.288) ***
Latitude	66.481 (2) ***	21.366 (5.417) ***	46.227 (4.945) ***	128.125 (2) ***	15.619 (2.019) ***	28.451 (2.554) ***
Overlap	25.919 (2) ***	0.130 (0.039) **	-0.045 (0.036)	73.508 (2) ***	0.141 (0.019) ***	-0.033 (0.023)
Difference of temperature	79.474 (2) ***	2.598 (1.183) *	10.546 (1.080) ***	175.376 (2) ***	3.387 (0.388) ***	6.936 (0.485) ***
Thermal niche difference - 2.5%	189.825 (2) ***	5.914 (1.719) ***	24.615 (1.569) ***	402.221 (2) ***	10.481 (0.746) ***	20.985 (0.940) ***
Thermal niche difference - 97.5%	66.373 (2) ***	1.069 (0.750)	5.559 (0.701) ***	122.620 (2) ***	0.532 (0.122) ***	1.762 (0.153) ***

Table S3.1 The climatic PGLS models for all species and each clade studied. A Likelihood ratio-test is presented for each clade in model.fit, the number between brackets indicates the number of degrees of freedom. Estimates of comparison models against the first variable are indicated also for each clade, the number between brackets indicates the standard error. In both case, significant codes are : 0 ***, 0.001 **, 0.01 * and 0.05 °.



Modèle	Paramètres	Anseriformes			Charadriiformes			Passeriformes		
		Log-lik	AIC	ΔAIC	Log-lik	AIC	ΔAIC	Log-lik	AIC	ΔAIC
M1	13	-699,45	1 424,90	141,16	-1 871,92	3 769,85	232,85	-22 595,14	45 216,28	1 360,42
M2	22	-623,87	1 291,74	8,00	-1 749,38	3 542,76	5,76	-21 910,02	43 864,03	8,17
M3	11	-699,45	1 420,90	137,16	-1 883,15	3 788,29	251,29	-22 623,59	45 269,17	1 413,31
M4	18	-623,87	1 283,74	0,00	-1 750,50	3 537,00	0,00	-21 909,93	43 855,86	0,00
M5	9	-703,26	1 424,53	140,79	-1 892,02	3 802,04	265,04	-22 677,85	45 373,69	1 517,83
M6	14	-678,52	1 385,03	101,29	-1 762,81	3 553,61	16,61	-23 789,64	47 607,27	3 751,41

Table S3.2 (a) Schematic modelling of the best fitted model simulating apparition of migration behavior under NHT (blue arrows) or SHT (light red arrows) from distribution maps. *Resident* species were assigned to a tropical or temperate category depending on where their ranges occur in term of latitudes (states 1 and 2). Species were labelled as tropical residents for species living between the tropics and for species spanning both temperate and tropical areas, the area where most of their range occur was chosen. As possible intermediary states toward strict migratory species (state 6), states of partial migration (states 3-5) were coded depending on the relative position and overlap of breeding and wintering ranges. (b) Different models tested with consideration (+) or not () of transition rates. (c) Comparison of all transition rate models for ancestral state reconstructions for the three study clades. Bold values indicate the best model fit.

CHAPITRE 2

Rôle de la migration saisonnière dans l'évolution d'un gradient de diversité latitudinal inverse chez les Charadriiformes

Résumé du chapitre : Si l'évolution de la migration saisonnière a fait l'objet de nombreuses études, ses liens avec les mouvements biogéographiques passés et son potentiel rôle dans les processus de diversification ont été beaucoup moins étudiés. Nous avons exploré ce sujet chez les Charadriiformes (environ 380 espèces) : un clade d'oiseaux qui regroupent les limicoles, les laridés et diverses lignées parmi lesquelles les plus grands migrateurs connus. Ce clade a également la particularité de se distribuer selon un gradient de diversité latitudinale inverse, biaisé vers les latitudes tempérées et arctiques.

Pour étudier le rôle de la migration saisonnière dans l'évolution de la distribution de ce clade, nous avons d'abord estimé son histoire phylogénétique, afin de déduire l'origine biogéographique (tropicale ou tempérée) de celui-ci. Nous avons ensuite reconstruit l'évolution du comportement migratoire en relation avec les changements d'aires de répartition géographiques selon la latitude. Enfin, nous avons étudié comment les Charadriiformes ont pu bénéficier d'évènements de dispersion en dehors des tropiques pour se diversifier dans les hautes latitudes.

Nous avons découvert que l'ancêtre des Charadriiformes était probablement sédentaire en milieu tropical et que la répartition actuelle a été façonnée par plusieurs évènements de dispersion indépendants, en étroite relation avec l'émergence du comportement migratoire. Nous avons également constaté que plusieurs familles largement migratrices se sont diversifiées plus rapidement dans les zones tempérées et arctiques, contredisant ainsi l'idée générale selon laquelle les taux de spéciation sont plus élevés sous les tropiques. En outre, nous avons fourni des preuves suggérant une influence positive du comportement migratoire sur les taux de spéciation, soit en permettant la reproduction dans des zones très saisonnières, soit en permettant la colonisation de nouvelles zones de reproduction par des mouvements de migration longue distance.

Ces résultats montrent comment l'évolution du comportement migratoire a influencé la diversification et l'histoire biogéographique d'un grand clade d'oiseaux, façonnant un gradient de diversité latitudinale très atypique.

[Migration saisonnière, Charadriiformes, gradient de diversité, biogéographie, macro-évolution, phylogénie]

Note sur la participation : Ce travail constitue une partie importante de ma thèse et aussi la transition entre ma première étude globale et les approches taxonomiques plus fines. Il m'a permis notamment de mobiliser l'ensemble des connaissances acquises sur l'évolution biogéographique de la migration pour proposer et discuter d'un cadre conceptuel faisant le lien entre l'origine géographique des lignées et le rôle de la saisonnalité (voir Winger et al. 2018). Ce projet a été l'occasion de me former sur les méthodes de reconstructions phylogénétiques, d'apprendre à sélectionner des fossiles pour calibrer une phylogénie et de tester différentes méthodes pour estimer les taux de diversification. Il m'a aussi permis de collaborer avec Fabien Condamine et Pierre-André Crochet avec qui nous avons eu des discussions extrêmement enrichissantes, autant sur la méthodologie que sur les hypothèses biologiques. Ce papier est actuellement en cours de révision dans *Systematic Biology*.

Migratory behavior allowed the evolution of an inverse latitudinal diversity gradient in shorebirds

RUNNING TITLE: Migratory behavior and atypical diversity gradient

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ABSTRACT

While the evolution of seasonal migration has been the subject of numerous studies, its links with past biogeographic movements and influence on species diversification have been less examined. We explored this topic by conducting a phylogenetic study of the bird order Charadriiformes (shorebirds and allies), which includes the longest distance migratory species in the avian class and exhibits a puzzling inverse latitudinal diversity gradient. We studied the clade's biogeographic history using a newly reconstructed time-calibrated phylogeny to infer whether this clade had a tropical or temperate origin. We also performed estimations of ancestral migratory strategy to assess how this behavior evolved in relation to geographic range shifts along latitude. Finally, we studied how Charadriiformes may have benefited from transiting outside the tropics to diversify in higher latitudes. We found that the ancestor of Charadriiformes was likely a tropical year-round resident and that the current clade's distribution was mainly shaped by dispersal out of the tropics in relation to the emergence of migratory behavior. This was accompanied by equatorial extirpations of ancestral resident populations and poleward shifts of breeding ranges. We also found that some migratory families diversified faster in temperate and Arctic areas, which contradict the general expectation that speciation rates are higher in the tropics. Furthermore, we provided evidence suggesting a positive influence of migratory behavior on speciation rates, either by allowing the breeding into highly seasonal areas or by enabling the colonization of new areas through long-migration movements. Our results bring original insights into how the evolution of migratory behavior influenced the diversification and biogeographic history of a large bird clade, ultimately shaping a very atypical latitudinal diversity gradient.

[migration behavior, shorebirds, diversity gradient, biogeography, macroevolution, phylogeny]

INTRODUCTION

One of the most conspicuous biogeographic patterns on Earth is the latitudinal diversity gradient (LDG hereafter; Pianka 1966). Most groups of organisms are indeed more diverse in the tropics than elsewhere (e.g. Hillebrand 2004; Mannion et al. 2014), and the origins of this global diversity pattern have been the subject of much investigation and debate for nearly 50 years (e.g. Pianka 1966; Willig et al. 2003; Mittelbach et al. 2007; Jablonski et al. 2017). Most avian orders are no exception to this rule (Pulido-Santacruz and Weir 2016; Rabosky et al. 2015), as bird diversity mainly consists of year-round tropical resident species (see Somveille et al. 2013). However, some notable bird clades have evolved extreme strategies of seasonal migration: these species occupy the temperate latitudes during their breeding period but exhibit seasonal migration patterns towards tropical latitudes outside the breeding period. Several hypotheses have been proposed, and often debated, to explain the evolution of this type of migratory behavior (e.g. Louchart 2008; Salewski and Bruderer 2007; Winger et al. 2019). Among these hypotheses, two have long been promoted to explain the biogeographic origins of birds migration: (1) the most widely accepted ‘southern-home’ theory (SHT hereafter) which proposes that long-distance migrants evolved from resident tropical species through the poleward shift of their breeding ranges (Cox 1968; Gauthreaux 1982; Levey and Stiles 1992; Rappole 1995), and (2) the ‘northern-home’ theory (NHT hereafter) which stipulates that migration evolved from resident temperate species at higher latitudes, shifting their wintering grounds to lower latitudes (Bell 2000; Gauthreaux 1982). More recently, Salewski and Bruderer (2007) and Winger et al. (2019) rightfully insisted on the importance of examining separately the mechanisms of migration evolution from the biogeographic origin of migratory lineages (see also Zink 2002). The two possible mechanisms for the evolution of migration are (1) increased seasonality in geographically stable breeding areas and (2) breeding range shifts through dispersal into more seasonal environments (see Bruderer and Salewski 2008; Winger et al. 2019). In both cases migration evolves as a response to seasonality and these mechanisms make no assumption on the geographic origin of migratory lineages and thus migration.

While we wholeheartedly agree with the importance of examining separately the biogeography and the evolution of migration, we also note that an explicit association between mechanisms and biogeography can be expected because temperate latitudes have experienced a marked increase in seasonality linked to the global cooling since the middle Eocene (see Zachos et al. 2001; Mosbrugger et al. 2005; Meseguer and Condamine 2020), while thermally stable areas mostly remained associated with tropical latitudes (Wallace

1978). Dispersal into more seasonal habitats would have thus mainly occurred when tropical lineages shifted their range into higher latitude (hence following the SHT) while increased seasonality would have mostly affected temperate lineages (hence generating NHT). In this study, we will thus confront these two hypotheses as a general conceptual framework for tracing and dating the biogeographic history of migratory lineages without reference to the underlying intrinsic mechanisms. Indeed, both hypotheses seem to contribute to the evolution of seasonal migrations (Dufour et al. 2020) and the debate should move away from determining which one explains the evolution of avian seasonal migration towards identifying their relative contributions to the evolution of each avian migration system (Newton 2008).

In certain migration systems such as the Palearctic-African system, seasonal migration implies large annual latitudinal movements; the emergence of migration may thus have allowed the colonization of novel biogeographic regions, in turn opening new ecological opportunities and boosting diversification processes (see Liedvogel and Delmore 2018). The emergence of long-distance seasonal migration may thus have strongly impacted the LDG by shaping both the geographical distribution and the diversification dynamics of different clades. In addition, seasonal migration has been proposed as an important factor promoting population differentiation, especially in the case of migratory divides (e.g. Delmore et al. 2015). However, and despite the fact that the link between migration and dispersal is not straightforward (see Paradis et al. 1998), migration has also long been suspected to reduce genetic divergence between populations by increasing gene flows (Helbig 2003; Claramunt et al. 2012). Very few empirical studies have addressed this question, although Rolland et al. (2014a) found that migratory bird lineages had a higher net rate of species diversification than resident ones at a global scale, and Gómez-Bahamón et al. (2020) suggested that migration may increase speciation rates. The links between seasonal migration and diversification clearly remain elusive, and should thus be tackled in the context of the LDG.

The avian order Charadriiformes comprises ca. 380 species (BirdLife and HBW; del Hoyo and Collar 2014) including more than 75% of partial or strict migrants. Some of them undertake among the most spectacular seasonal migrations of the animal world, traveling over tens of thousands of kilometers every year, with sometimes over 7,000-kilometer non-stop flights (e.g. Arctic Tern *Sterna paradisaea*, Egevang et al. 2010; Bar-tailed Godwit *Limosa lapponica*, Gill et al. 2009). In addition, this group is the only avian clade to exhibit an inverse LDG, i.e. whose diversity is highest towards temperate zones (Fig. 1; Kindlmann et al. 2007; but see Pyron and Burbrink 2009; Rivadeneira et al 2011; Rabosky et al. 2018), because of many species breeding at exceptionally high latitudes (e.g. Winkler et al. 2020). Several

families (e.g. Scolopacidae) mostly composed of migratory species occupy the Arctic temperate zones during the breeding season and spend the winter in tropical latitudes. Fewer families (e.g. Burhinidae) mostly comprise resident species of tropical latitudes. In addition, some clades (e.g. Gallinaginae and Scolopacinae; genus *Catharacta*) present migratory species breeding in the northern hemisphere that are closely related to resident or migratory species of the southern hemisphere. The inverse LDG and the diversity of migration strategies of Charadriiformes suggest that the evolution of migration might have increased ecological opportunities by allowing the colonization of new biogeographic areas visited during the annual cycle, thus promoting speciation. Charadriiformes thus appear to be a prime model to explore the influence of migration on diversification processes and to better understand the mechanisms that have shaped a rare instance of inverse LDG.

A first hypothesis to explain the inverse LDG of Charadriiformes implies a temperate or Arctic origin for this clade followed by high *in situ* diversification and southward shifts of wintering ranges (i.e. the NHT scenario). Alternatively, a second hypothesis would propose a tropical origin implying that this LDG results either from a few events of breeding range shifts outside the tropics also followed by increased speciation or from repeated dispersal events outside the tropics at different time periods and in different biogeographic regions (i.e. the SHT scenario). It is important to note that the aforementioned scenarios involve contrasted roles of the emergence of seasonal migration. In the case of a temperate origin, migratory lineages may have evolved concomitantly with the global expansion of seasonal biomes (see Louchart 2008; Dufour et al. 2020), whereas in the case of a tropical origin, migratory behavior may have evolved as a consequence of dispersal events outside the tropics (see Salewski and Bruderer 2007; Winger et al. 2019). Hence, this raises the question of whether and how seasonal migration may have influenced species dispersal and diversification processes in temperate and Arctic areas compared to tropical areas.

In this study, we aim at understanding how the evolution of migration may have influenced the historical processes that shaped an inverse latitudinal gradient in Charadriiformes. To do so, we reconstructed a phylogeny of the order using available molecular data, and provided novel estimates of divergence times based on the latest fossil discoveries. First, we tested to what extent the colonization of high latitudes may have been allowed by the evolution of migratory behavior. This has been stated by Winger et al. (2019), but has rarely been empirically tested to our knowledge (see Winger et al. 2014). We used species latitudinal distributions during the breeding and the non-breeding seasons to determine the geographic origin (tropical or temperate) of Charadriiformes and to examine the

concordance between the colonization of seasonal environments and the emergence of migratory behavior. Based on modern species distribution of this avian order, we can expect to find either (1) a tropical origin and several tropical extirpation events followed by poleward shifts of breeding ranges, or (2) a temperate origin and several tropical colonizations followed by equator-ward shifts of wintering ranges. We think that Charadriiformes may have benefited from the appearance of seasonality and the retreat of tropical biomes (Louchart 2008), to rapidly colonize vacant habitats in high latitudes by means of the appearance of annual latitudinal migrations (Winger et al. 2019). Second, we tested whether the colonization of Arctic and temperate regions has enhanced the diversification of Charadriiformes using character-dependent diversification models with extant geographic distributions as species' characters (Goldberg and Igic 2012; Magnuson-Ford and Otto 2012). Because these models have well-known limitations (Davis et al. 2013; Beaulieu and O'Meara 2016), we also addressed this question with hidden state speciation and extinction models (Beaulieu and O'Meara 2016) by comparing Charadriiformes families with different distribution patterns and migration behavior.

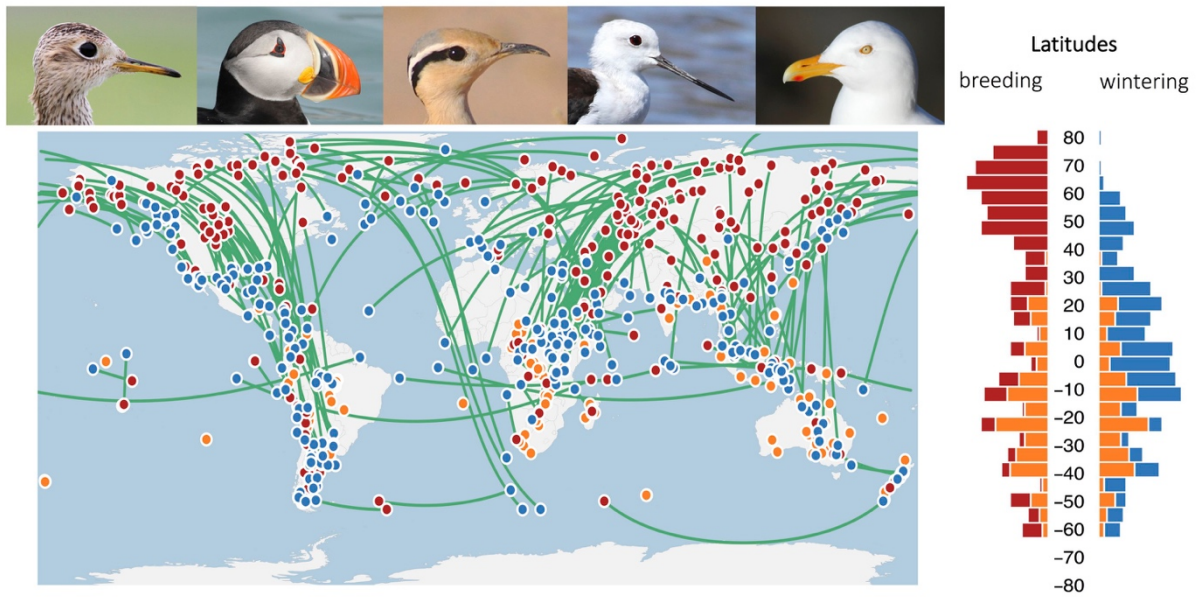


FIGURE 1. World map showing the median breeding and wintering positions for all Charadriiformes. Barplots showing the median of breeding and wintering latitudes of all Charadriiformes. Range positions of residents are colored in orange while the ones of migrants (partial and strict) are colored in red (breeding) and blue (wintering). Each position is calculated from BirdLife International (2020). Schematic migration roads (great circle path between median breeding and wintering positions) are drawn in green. Examples of Charadriiformes species are pictured on the top of the map, from left to right: *Bartramia longicauda* (Paul Doniol-Valcroze), *Fratercula arctica*, *Cursorius cursor*, *Himantopus himantopus*, *Larus hyperboreus* (Paul Dufour).

MATERIAL AND METHODS

Species, spatial and movement data

Our study follows the taxonomic reference of BirdLife International and the Handbook of the Birds of the World (HBW hereafter; del Hoyo and Collar 2014). We collected a total of 376 distribution maps of extant Charadriiformes species, collected from BirdLife International (2020) and gridded at a 10-minute resolution. These maps contain information on breeding distribution (either the breeding area for migratory species or the year-round residence area for non-migratory species) and wintering distribution (= non-breeding distribution; either wintering or resident area). We categorized the migration strategy of each species based on information provided by reference handbooks (del Hoyo et al. 2019). We considered three categories of strategies: *strict migrant* when all populations of a species overwinter in a different location from their breeding range, *partial migrant* for which the population of a

species consists of *strict migrant* and *resident* fractions, and *resident* when all populations of a given species remain in the same place all year round (Rappole 2013).

Phylogenetic reconstructions and fossil calibrations

Sequence data. – The most comprehensive phylogeny of Charadriiformes is the study of Baker et al (2007). Since then, several phylogenies of particular clades have been independently reconstructed (e.g. Gibson and Barker 2012; Dos Remedios et al. 2015) and the discovery of new fossils has led to a better understanding of the timing of lineages' origination (e.g. Bertelli et al. 2013; de Pietri et al. 2016). We made use of all genetic data and paleontological information available to date in order to reconstruct and calibrate a new phylogeny of Charadriiformes. To do so, we collected DNA sequences for six nuclear genes (LDHB, GAPDH, FIB7, MYO2, RAG1 and SWS1) and ten mitochondrial genes (COI, ND2, ND3, ND4, ND5, ATP6, ATP8, 16S, 12S and CYTB) covering 303 of the 376 species (81%) recognized by the BirdLife/IBW taxonomy. All sequences were retrieved from GenBank (see Table S1 for details of accession numbers), using the R package *seqinr* 3.6-1 (R Core team 2019; Charif and Lobry 2007).

Sequences were aligned using MAFFT 7.450 (Katoh 2005) with default parameters. Alignments were run through Gblocks 0.91b (Castresana 2000) to remove poorly aligned positions, then concatenated using FASconCAT 1.04 (Kück and Meusemann 2010). The common crane *Grus grus* (Aves: Gruiformes) was used as an outgroup in our phylogenetic reconstructions. The final concatenated supermatrix included a total of 12,838 sites and visually checked with SeaView 5.0.2 (Gouy et al. 2010). On average, each species had 5.8 genes and 4,865 sites in the alignment, and only 16 species (out of 303) were represented by a single gene.

Phylogenetic reconstructions, dating and fossils calibration. – We simultaneously inferred the tree topology and divergence times through a Bayesian analysis as implemented in BEAST 1.10.4 (Suchard et al. 2018). Due to the potential computational issues in performing a large unconstrained analysis, we reconstructed in parallel a maximum-likelihood tree using the edge-linked partition model in IQ-TREE 1.6.12 (Chernomor et al. 2016; Nguyen et al. 2015) with an ultrafast bootstrap approximation (UFBoot; Hoang et al. 2018). This allowed us comparing the tree topologies inferred with the two inference approaches. In BEAST, the molecular dating was done using an uncorrelated relaxed molecular clocks approach, which takes into account variation in the rate of molecular evolution among

lineages (Drummond et al. 2006). We performed two independent runs of 200 million generations for the Markov chain Monte Carlo (MCMC), sampling trees every 1,000 generations assuming a birth-death speciation process as a tree prior. We set a uniform prior from 0 to 10 with starting value of 0.1 for the birth rate, a uniform prior from 0 to 2 with starting value of 0.1 for the relative extinction rate and kept default values for the other priors. We checked the estimated parameters of the runs using Tracer 1.7.1 (Rambaut et al. 2018), determining convergence success based on the shapes of the MCMC traces (likelihood parameter), and their effective sample sizes (ESS > 200 representing an acceptable effective sample size). For each run, we discarded the first 15% generations as a burn-in and combined the two runs with LogCombiner 1.10.4. The trees were then summarized in TreeAnnotator (included in the BEAST package) to compute a maximum clade credibility (MCC) with posterior probabilities (PP) and median ages as well as their 95% credibility intervals (CI) of clades. We also randomly sampled 100 dated tree topologies from the post-burnin-in posterior distribution.

To calibrate the molecular clock, we used 10 fossil constraints covering several clades of Charadriiformes and following the latest paleontological discoveries (Table 1). We have mostly followed the recommendations proposed by Smith (2015) in his thorough review of the Charadriiformes fossil record, except for three fossil constraints. First, we chose to consider †*Scandiavis mikkelsenii* (Bertelli et al. 2013) to calibrate the node between the ancestral node of our ingroup (Charadriiformes) and the outgroup (Gruiformes). The minimum age of †*S. mikkelsenii* is estimated at 54 Ma ago (early Eocene), while Smith (2015) proposed to calibrate this node with an unclassified and still undescribed Charadriiform fossil (Mayr 2000) from the middle Eocene of Germany, with a minimum age of 46.5 Ma. On the basis of the information described in Bertelli et al (2013), it is reasonable to place †*S. mikkelsenii* at the stem of Charadriiformes. Second, Smith (2015) did not propose a fossil calibration for the divergence between Lari and Scolopaci. According to Mayr (2009) and De Pietri and Mayr (2012), †*Paractitis bardi* from the late Eocene of Canada lacks the foramen for the supracoracoideus nerve, a characteristic synapomorphy for Scolopaci. Since previous studies show little uncertainty for the placement of this fossil, we have therefore calibrated the Lari - Scolopaci node with †*Paractitis bardi* by considering a minimum age of 33.9 Ma. Third, we used †*Hakawai melvillei*, a stem representative of Pedionomidae, to calibrate the divergence between Thinocoridae and Pedionomidae within the suborder Scolopaci (De Pietri et al. 2015). We therefore considered a minimum age of 16 Ma as the divergence time between these two families. For all fossil calibrations, we employed a gamma prior using the

same alpha and beta parameter values (alpha= 2, beta= 4), and the minimum age of each fossil as the offset parameter (Table 1).

TABLE 1. Fossils used as calibration points and the prior distributions. Most of the fossils have been recommended by Smith (2015; see the Material and Methods section). For fossil calibrations, we employed a gamma prior using the same alpha and beta parameter values (alpha= 2, beta= 4) and the minimum age of each fossil as the offset parameter. The 5%, median and 95% quantiles of the prior distribution are indicated separated by “/”.

Node calibrated	Clade	Fossil name	Min Age	Location	Period	Prior distribution	References
1	Charadriiformes + Gruiformes	<i>Scandiavis mikkelsenii</i>	54	Denmark	early Eocene	55,4 / 60,7 / 73	Bertelli et al. 2013
2	Charadrii + other Charadriiformes	<i>Jiliniornis huadianensis</i>	41,3	China	middle Eocene	42,7 / 48 / 60,3	Hou and Ericson 2002
3	Burhinidae x Chionidae, Pluvianellidae	<i>Genucrassum bransatensis</i>	23,03	France	Oligocene-Miocene	24,5 / 29,7 / 42	De Pietri and Scofield 2014
4	Lari + Scolopaci	<i>Paractitis bardi</i>	33,9	Canada	late Eocene	35,3 / 40,6 / 52,9	De Pietri and Mayr 2012
5	Thinocoridae + Pedionomidae	<i>Hakawai melvillei</i>	16	New Zealand	early Miocene	17,4 / 22,7 / 35	De Pietri et al. 2016
6	Crown Jacanidae	<i>Nupharanassa bulotorum</i>	30	Egypt	early Oligocene	31,4 / 36,7 / 49	Rasmussen et al. 1987
7	Crown Calidridinae	<i>Mirolia brevirostrata</i>	11,62	Germany	middle Miocene	13 / 18,3 / 30,6	Ballmann 2004
8	Lari + Turnicidae	<i>Turnipax oechslerorum</i>	30	Germany	early Oligocene	31,4 / 36,7 / 49	Mayr and Knopf 2007
9	Crown Larimorphae	<i>Laricola elegans</i>	23,6	France	late Oligocene	25 / 30,3 / 42,6	De Pietri et al. 2011
10	Alcidae + Stercorariidae	Pan-Alcidae incertae sedis	34,2	USA	late Eocene	35,6 / 40,9 / 53,2	Chandler and Parmley 2002

Phylogenetic placement of species without DNA data. – To avoid the pitfall of phylogenetic bias related to missing species and missing data in our biogeographic reconstruction and diversification analyses, we added to the phylogeny species for which no DNA data were available. Nevertheless, analyses were repeated with and without the addition of these species. Species for which no DNA data were available (73 species) were added as polytomies to the phylogeny based on taxonomic affinities suggested in the reference handbooks (del Hoyo et al. 2019). This implies that missing species were placed as branches within a randomly selected node of the clade to which it is assumed to be a member following del Hoyo et al. (2019). In cases where taxonomic information allowed assignment to lower levels, like a sister species, the missing species were added half-way along the terminal edge

length to its supposed sister taxon. List of species with no DNA data and details on their positioning is available in Appendix S1. We then applied the function *bifurcatr* using the R package PDcalc 0.3.2.9000 (see Faith 2013) to resolve all tree polytomies. This function randomly resolves the polytomies using the procedure described by Rangel et al. (2015). We ran the analyses 1000 times to explore the range of potential solutions and then computed a MCC tree. We also applied the same procedure to the 100 randomly selected trees. The MCC tree was used in all downstream analyses unless otherwise stated.

Latitudinal ancestral areas reconstruction

To investigate the biogeographic history of Charadriiformes and its link to the evolution of migration strategies, we estimated ancestral areas based on the extant species' latitudinal distribution during both breeding and non-breeding periods. Our choice of not taking into account species' longitudinal distribution is motivated by the observations that the longitudinal distribution of shorebirds is relatively homogeneous with proportions of species relatively balanced between the major migratory systems and that a substantial proportion of Charadriiform species spend the winter period over large oceanic areas (see del Hoyo et al. 2019). Hence, we delineated the globe into four latitudinal sections according to the coarse distribution of the major terrestrial biomes, which also correspond to the different habitats occupied by the Charadriiformes during the breeding season. The different latitudinal bands considered are: the Boreo-Arctic zone ($>55^{\circ}\text{N}$; coniferous forests, tundra, ice caps), the northern temperate zone ($30^{\circ} - 55^{\circ}\text{N}$; chaparral, temperate grasslands and broadleaf forests), the tropical zone ($30^{\circ}\text{N} - 30^{\circ}\text{S}$; tropical forests, savannah and deserts), and the southern temperate zone ($-30^{\circ}\text{S} - -55^{\circ}\text{S}$). We assigned each species to one or more of these sections on the basis of its breeding distribution on one hand, and its non-breeding distribution on the other hand, in order to elaborate two distinct datasets depicting species latitudinal distribution during their breeding and on-breeding periods. We assigned a species to a latitudinal section if at least 20% of its distribution overlaps with it, otherwise the species is considered marginally distributed in the latitudinal section. Notably, two species partially occur under -55°S : *Chionis albus* and *Catharacta maccormicki*, which breed in Antarctica under -55°S but overwinter above this latitude. These two species were also categorized in the southern-temperate section and we did not consider latitudinal band below -55°S latitude. Even if this choice of latitudinal sections may seem simplistic given the complex distributions of Charadriiformes, we found to be a relevant solution to identify patterns of biogeographic movements in relation to the evolution of migratory behavior (see in particular Dufour et al. 2020).

We used the R package BioGeoBEARS 1.1 (Maztke 2014) to fit models of ancestral areas estimation separately for the breeding and non-breeding distributions. We fitted the Dispersal–Extinction–Cladogenesis (DEC; Ree and Smith 2008) and the DEC+ J (Maztke 2014) models of range evolution, both implemented in BioGeoBEARS. We chose to run and present these two models separately and did not compare them because of recently raised concerns about model choice and statistical validity of the J parameter in BioGeoBEARS (Ree and Sanmartín 2018). Both models imply underlying assumptions that may correspond to the expectations of geographic speciation in this clade. The J parameter allows for founder-event speciation (Maztke 2014), which seems relevant in the case of a bird group that has very high dispersal capacities (here potentially enhanced by migration behavior), and where we expect that geographical ranges can have evolved in a very punctual manner. Conversely, this model often infers null or extremely low extinction rates (Sanmartín and Meseguer 2016), which does not seem biologically reasonable given the age of the group.

Since it is technically difficult to reconstruct simultaneously the evolution of breeding distributions along with non-breeding ones, we chose to perform ancestral areas reconstructions separately for the two types of distributions. Because of the predominant distribution of Charadriiformes in tropical latitudes during the non-breeding period, we think our results were not biased by this choice. On the basis of these reconstructions, we estimated how many transitions through time occurred between latitudinal bands within each lineage by counting the number of shifts between latitudinal regions from the root of the phylogeny to each tip. Transitions are considered as a change of state between a node and a descending node. Namely, we considered: (1) transitions outside the tropics (from the tropical region towards temperate and Arctic regions), (2) transitions towards the tropics (from the Arctic and temperate regions towards the tropics), and (3) transitions between non-adjacent areas (from the Arctic and north-temperate regions to south-temperate regions and *vice versa*). Details about transitions considered to go out of or into the tropics can be found in Table S2.

Ancestral migratory reconstructions

Following the approach of Dufour et al. (2020), ancestral state reconstructions of migratory strategies (*resident*, *partial migrant*, *strict migrant*) were performed using constant-rate Bayesian models as implemented in the R package diversitree 0.9-13 (FitzJohn 2012). We tested three different transition rate models: equal rates for all state transitions, all rates different between states, and different rates with the transition rate between *resident* and *strict migrant* constrained to zero, i.e. a stepping-stone model. The hypothesis underlying the

stepping-stone model is that lineages necessarily need to go through a state of partial migration containing both the *strict migrant* and *resident* fractions to evolve from the *resident state* to the *strict migrant* one. The best-fit model was selected based on the sample-corrected Akaike information criterion (AICc) and used for ancestral state reconstructions. To test for potential bias of grafting species without molecular data, we repeated this analysis on the MCC tree containing only species with molecular data (303 instead of 376 species). Joint ancestral state reconstructions were used to assign the most likely migratory strategy to each internal node (FitzJohn 2012) and to calculate the gain and loss events of migratory behavior through the time. We computed how many events occurred in each lineage by counting the number of switches between migratory (partial and strict migrant) and resident states from the root of the phylogeny to each tip.

We also compared the temporal evolution of migratory behavior and the latitudinal shifts across regions by plotting cumulative lineages through time (LTT). The LTT plots can help to determine whether the pace of state-dependent lineages steadily accumulates, or alternatively tends to increase or decrease towards the present. We first compared the accumulation of lineages between migrant (strict and partial) and resident species through time. Then, we investigated the accumulation of lineages according to their latitudinal locations, and compared lineages that dispersed out of the tropics and colonized temperate and Arctic regions with lineages that left these regions, dispersed into the tropics and colonized the tropical latitudes. This served to examine whether the accumulation of migrant lineages was concordant with accumulation of lineages outside the tropics. We also tested whether the accumulation of migratory lineages was correlated with the accumulation of lineages that dispersed outside the tropics using the Pagel's test of correlated evolution (1994).

Analyses of diversification dynamics

To test the influence of transiting outside the tropics to higher latitudes on diversification processes, we studied the correlation between family richness and the average number of transitions outside the tropics (averaged over all species of the family). This analysis assumes a link between geographic transitions and the emergence of migration behavior. Nineteen families are recognized within the Charadriiformes (del Hoyo and Collar 2014), three of them (Charadriidae, Scolopacidae and Laridae) contain more than 50 species and five (Pluvianidae, Pluvianellidae, Dromadidae, Ibidorhynchidae and Pedionomidae) are monotypic.

Transitions are considered to be the passage to a descending node different from the ancestral node (see Table S2). To take into account the uncertainty of the ancestral

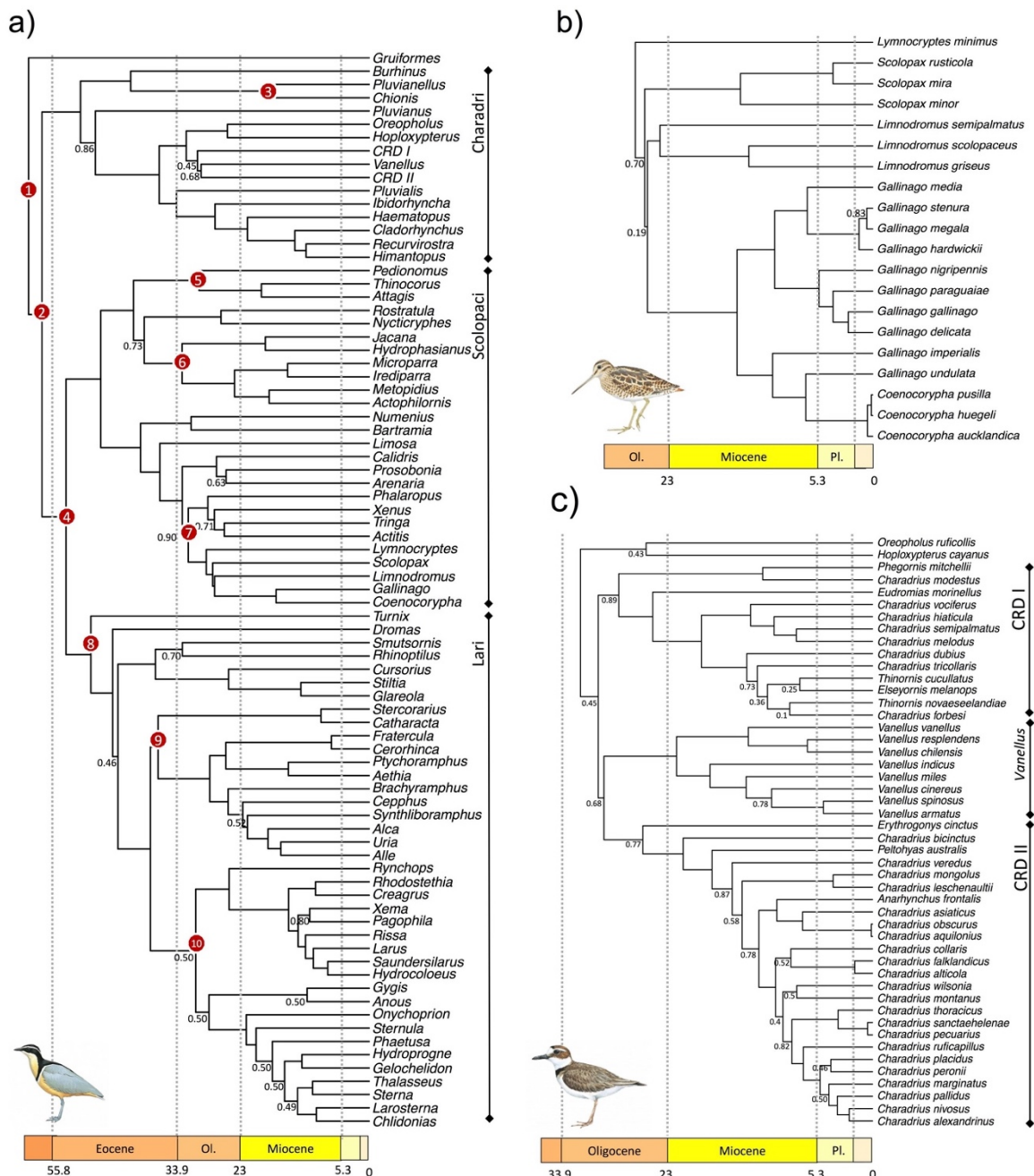
reconstructions, when several states were estimated for a given node, we randomly selected a state based on its probabilities, before calculating the number of transitions per family by repeating this procedure 1,000 times. Since families with more species are more likely to have transited between latitudinal regions, we tackled this issue by assessing the probability of transition within each family against the expected rate of transition based on the overall number of transitions within all Charadriiform families. As a null model, we hypothesized that the expected number of transitions in each family followed a binomial distribution with integers between 0 and the total number of species within a family and a probability of success (probability of a species to transit) equal to the expectation transition rate. We thus highlighted families that have transited less than expected (i.e. less than the number of species in the family would have allowed) or higher than expected. We tested this correlation by fitting a Phylogenetic Generalized Least Squares (PGLS) model using the R package *phylolm* 2.6 (Tung Ho and Ané 2014) controlling for phylogenetic relatedness with the Pagel's lambda (Pagel 1999). We used the MCC tree with tip labels pruned to contain a single representative for each family. We also investigated whether some families transited more than others to the tropics and between non-joining areas, using the same method of comparison with an expected transition rate calculated from all Charadriiform families.

To assess whether the diversification of Charadriiformes has been influenced by the colonization of Arctic and temperate regions during their evolutionary history, we also performed character-dependent diversification analyses using the R package *diversitree* 0.9-13 (Fitzjohn 2012). We specifically relied on the Cladogenetic State Speciation and Extinction (ClasSE) model (Goldberg and Igic 2012; Magnuson-Ford and Otto 2012) to investigate the speciation events ('symmetrical' and 'asymmetrical' speciation) and notably the influence of character change at speciation when for example a tropical species diversified into one temperate and one tropical species. Based on the latitudinal distribution of the species used in the biogeographic reconstruction analyses, we distinguished (1) non-tropical species, i.e. Arctic, temperate-north and temperate-south species together (denoted A hereafter), from (2) tropical species (denoted B). We have thus estimated the constant-change cladogenesis speciation rates (or symmetrical rates: λ_{AAA} and λ_{BBB} ; meaning that the two-daughter species resulting from the speciation event stay in the same latitudinal area inherit the ancestral character) and the state-change cladogenesis speciation rates (or asymmetrical rates: λ_{AAB} and λ_{BAB} ; meaning that there is a character change at speciation with for example a tropical species diversifying into one temperate and one tropical species in λ_{BAB}). We designed 8 ClasSE diversification scenarios of increasing complexity, and parameter number (see Table

2 for details). We disregarded the possibility of a species to diversify into two daughter species of different character ($\lambda_{ABB} = \lambda_{BAA} = 0$), as we assumed this kind of event has virtually never occurred. Since we expected potentially different results according to the clades considered, we repeated these analyses for all 376 species of Charadriiformes, and independently for the three largest families (Laridae, Scolopacidae and Charadriidae). Knowing the potential bias due to grafting species for the trait-dependent models (Rabosky 2015), we repeated these analyses for the MCC tree containing only species with molecular data (303 species). Following the procedure of Rolland et al. (2014a), we computed the likelihood, AICc and ΔAIC corresponding to each scenario. We checked support for the model with the lowest AIC against all models nested within it using a likelihood ratio test (LRT). If the model with lowest AIC was supported by LRT ($P < 0.05$), it was considered the best. If not, the model with less parameter was considered the best. Once the best model selected, we performed 10,000 steps of MCMC analyses on it and then applied a burn-in of 1,000 steps in order to obtain a better estimate of the parameters and their confidence intervals.

To cross-validate our ClaSSE analysis, we also applied the Hidden State Speciation and Extinction (HiSSE) model (Beaulieu and O'Meara 2016) to all Charadriiformes, Charadriiformes without the grafted species on the phylogeny (303 species), and the three largest families. This model represents an extension of the Binary State Speciation and Extinction (BiSSE) model (Maddison et al. 2007) and allows including a second hidden binary trait that can impact diversification in addition to (or instead of) the observed focal trait (Beaulieu and O'Meara 2016). Unlike the ClaSSE model, this model does not allow the estimation of asymmetrical speciation rates but remains comparable to a two-state ClaSSE model (itself equivalent to the BiSSE-ness model; Magnusson-Ford and Otto 2012). We tested four different models: a character-independent diversification model with two hidden states (CID-2), a character-independent diversification model with four hidden states (CID-4), a full BiSSE model, and a full HiSSE model. Marginal reconstructions of ancestral states and diversification rates under the four models were estimated and we incorporated uncertainty in model choice and reconstructions under the four models by averaging AIC weights. We thus obtained model-averaged rates for all tips and nodes of the phylogeny. In addition, to assess the robustness of the HiSSE analysis, we performed 500 HiSSE simulations with characters randomly distributed on tips of the entire Charadriiform phylogeny (376 species), and then compared the AIC values from these simulations with the AIC of the model with original data.

FIGURE 2. Bayesian genus-level chronogram of Charadriiformes summarized from two runs of 200 million iterations for 303 species (a). Details of the Bayesian species-level chronograms for snipes, woodcocks and dowitchers (b) and plovers (c). Numbers in red circles indicate the 10 calibration priors used in our fossil calibration (see Smith 2015 and Table 1). Posterior probabilities lower than 0.95 are indicated on nodes. The chronogram shows estimated molecular ages in million years ago (Ma) and a geological time-scale, at the bottom of each chronogram, indicates the epochs since 60 Ma (Ol., Oligocene; Pl., Pliocene; Paleocene and Pleistocene are not always indicated). The names of the three Charadriiformes suborders are indicated in (a), and the names indicated in (c) followed the taxonomic suggestion of Dos Remedios et al. (2015, namely CRD I and II).



RESULTS

Timetree of Charadriiformes

The independent Bayesian analyses of BEAST converged (ESS >> 200 for all parameters, excepting two calibration points) and we combined the runs to generate the MCC tree. Overall, the tree was well resolved (220 nodes out of 304, i.e. 72.3%, have PP>0.95) and all families were recovered as monophyletic with strong node supports (Fig. 2a). The maximum-likelihood tree inferred with IQ-TREE showed an identical topology and similar node supports (230 nodes out of 304, i.e. 75.6%, have UFBoot values >95).

While our phylogeny appears in line with current family-level systematics, several genera were not recovered as monophyletic. The first is the genus *Gallinago* (see also Gibson and Parker 2012): two South American *Gallinago* species (*G. undulata* and *G. imperialis*) form a well-supported clade with the New Zealand snipes of the genus *Coenocorypha* (PP=0.99; Fig. 2b), this clade being placed as sister to all remaining *Gallinago*. The genus *Charadrius* was also paraphyletic, with the genus *Vanellus* nested within it and separating two major clades of *Charadrius* (CRD I and II; see Barth et al. 2013, Dos Remedios et al. 2015; Fig. 2c). We found (though with low support) that the first species to diverge from clade CRD II are *Erythronyx cinctus*, *C. bicinctus* and *Peltohyas australis* while Dos Remedios et al. (2015) found that the first species to diverge from clade CRD II formed a clade composed of *C. asiaticus*, *C. veredus*, *C. mongolus* and *C. leschenaultii*. As already shown by Baker et al. (2007), we found that Charadriidae are paraphyletic (see position of the genus *Pluvialis* in Fig. 2a but see Baker et al. 2012). However, we found that *Hoploxypterus cayanus* and *Oreopholus ruficollis* form a basal clade to the subfamilies *Vanellinae* and *Charadriinae* (without considering *Pluvialis*) whereas *Hoploxypterus cayanus* has always been considered to belong to the *Vanellinae* (i.e. Pied Lapwing). We also found that *Ibidorhyncha struthersii* is placed as sister species of the genera *Haematopus*, *Himantopus*, *Cladorynchus* and *Recurvirostra* and not as sister species of the genus *Haematopus* only, as in Baker et al. (2007). Finally, we found many uncertainties (nodes with low support) in the phylogenetic relationships within *Larus* (see Pons et al. 2014; Sonsthagen et al. 2016).

FIGURE 3. Cumulative lineages through time plots of the migratory behavior strategies (a) and for events of latitudinal shifts towards and out of the tropics (b). Each plot is based on 1,000 simulations using node state probabilities, and depicts averaged values as white lines, with their confidence intervals as blue lines. The synchrony between accumulation of migrant species and transitions out of the tropics is illustrated in the panel (c). The global deep ocean temperature evolution (red line, data from Hansen et al. 2013) is also indicated in this panel.

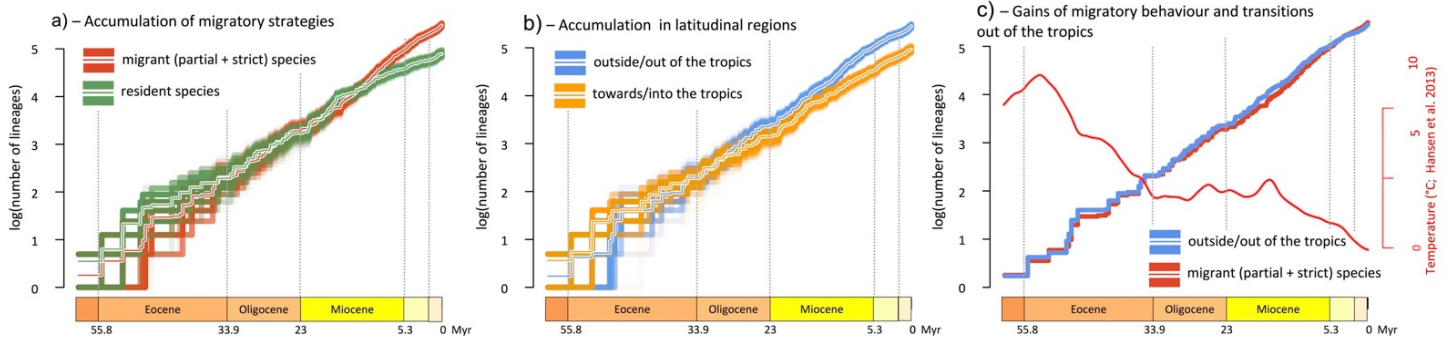


TABLE 2. Charadriiformes originated in the tropics. This table shows the results of DEC and DEC+*J* models for breeding and non-breeding distributions for the Charadriiformes phylogeny. For each model, the log-likelihood (lnL) value, the number of free parameters (Np), and the parameter estimates for *d* (dispersal), *e* (extinction) and *j* (founder-event speciation) are indicated. The inferred origin corresponds to the state estimated for the root, with its relative probabilities between brackets.

Model	Distributions	lnL	Np	<i>d</i>	<i>e</i>	<i>j</i>	Inferred origin
DEC	breeding	-740.594	2	0.02519	<0.0001	0	Tropical (0.45)
	non-breeding	-630.155	2	0.01977	<0.0001	0	Tropical (0.77)
DEC+J	breeding	-681.611	3	0.01835	<0.0001	0.10209	Tropical (0.53)
	non-breeding	-621.053	3	0.01745	<0.0001	0.02470	Tropical (0.80)

Ancestral latitudinal shifts and evolution of migratory behavior

As observed in the cumulative lineage-through-time (LTT) plots in Figure 3, the evolution of migration behavior and geographic ranges were tightly linked across the Charadriiformes, with the accumulation of migratory lineages closely lagging behind the colonization of temperate latitudes (Pagel's test of correlated correlation: $P < 0.001$). This colonization of high latitudes was not steady over time: a first burst of diversification of temperate/migratory species occurred around 50 Ma, with a second, more minor increase during late Eocene (35 Ma); the diversification of tropical species was gradual though and resident lineages remained dominant until the early Oligocene (Fig. 3c).

Biogeographic analyses showed that dispersal and extinction parameters were roughly similar in the DEC and DEC+J models and that biogeographic reconstructions were also similar for both the breeding and non-breeding ranges (Table 2, Fig. 4 and Fig. S2). For DEC+J models, the founder-event parameters were high, especially for breeding distributions, thereby confirming the well-known colonization abilities of Charadriiformes. The results of the ancestral areas reconstruction with the most likely ancestral ranges at each node are shown in Figure 4 (DEC+J model). We found that Charadriiformes likely diversified from a tropical ancestor and this result remained robust whether considering breeding distributions or non-breeding distributions (Table 2). However, the biogeographic history of Charadriiformes was much more complex when considering the breeding rather than the non-breeding ranges, suggesting greater evolutionary lability regarding the colonization of breeding areas (Fig. 4).

For breeding distributions, we indeed found several independent transitions out of the tropics into the temperate zones during different time periods in the evolutionary history of Charadriiformes (see capital letters and blue arrows in Fig. 4). For example, within the suborder Charadri, early-diverging families (Chionidae, Pluvianellidae) came out of the tropics towards the southern temperate latitudes (Fig. 4, node A) or towards both northern and southern latitudes (Haematopodidae and Recurvirostridae; node B; see also Fig. S4), whereas within the Charadriidae (node C), the genus *Vanellus* particularly diversified in the tropical latitudes and few clades in the Arctic latitudes (genus *Pluvialis*). For the suborders Scolopaci and Lari, we found similar and somewhat simpler colonization patterns from the tropics to higher latitudes. We also highlighted another reverse colonization patterns, from Arctic or temperate to tropical or southern latitudes, which occurred a few times in the history of the clade (see capital letters and red arrows in Figure 4). For example, within the Scolopacidae, some species of the genus *Gallinago*, *Scolopax* and in particular *Coenocorypha* seem to have colonized tropical and even temperate southern latitudes directly from the high latitudes of the

northern hemisphere (E; see also Fig. S4). Within the Lari, the shifts out of the tropics are difficult to count as a result of the poorly resolved phylogeny, but the most likely scenario involved only a few of such events: either one (node F) followed by a return to the tropics by early-diverging Laridae (noddies, part of the terns –node G), or two in (node F) and (node H) for the gulls (genus *Larus* and allies; see Fig. 4).

On the contrary, biogeographic reconstructions based on wintering ranges show considerably fewer dispersal events during the evolutionary history of Charadriiformes (Fig. 4), largely because most species, migrants included, reside in tropical latitudes during the non-breeding period. However, many Alcidae and some Stercorariidae (in the genus *Catharacta*) have expanded their breeding range into very high latitudes but do not migrate back to the tropics during non-breeding periods (K) and instead overwinter in temperate regions. The same is true for some of the Laridae lineages (inheriting from node J, Fig. 4). Thus, the evolution of migration strategies from tropical ancestors did not only involve northward shifts of breeding ranges with relatively greater stability of wintering ranges but also northward shifts of both breeding and non-breeding ranges.

The stepping-stone model with a root constrained to a *resident* state was retained as the best model depicting the evolution of migration strategies (see Table S3). We found a relative probability of 0.75 for a resident ancestor for the model with an unconstrained root (Fig. 4). We found very similar results by considering only the species with molecular data (Fig. S5b). Despite a likely resident ancestor, migratory behavior seems to have emerged early in the history of the Charadriiformes. The first nodes showing strict migratory behavior are the root of Alcidae and Stercorariidae within the suborder Lari ($P=0.74$) and the root of Scolopacidae for the Scolopaci ($P=0.69$), node that are dated to 36.3 Ma and 39.3 Ma in our dated tree, respectively. We also found several instances of loss of migratory behavior (from strict to partial migratory and from partial migratory to resident). For example, within the Scolopacidae, several species of the genus *Gallinago* and *Scolopax* have lost their ancestral migratory behavior and returned to a resident mode, notably in the south-temperate latitudinal section.

FIGURE 4. Bayesian chronogram of Charadriiformes showing estimates of ancestral migratory strategies (edge colors) and ancestral geographic origins (node colors). The left panel represents ancestral geographic origins based on breeding distributions, whereas the right panel represents non-breeding distributions. The chronogram gives estimated molecular ages in million years ago (Ma) for phylogenetic relationships between lineages (outgroups excluded). Nodes are colored according to the ancestral areas with the largest marginal probability (see legend). Colored rectangles at tips represent present-day distributions. Edges are colored according to the reconstructed ancestral migration strategies (see legend). Terminal edges are thus colored according to the strategies of current species. Red capital letters indicate the major events of shifts out and towards the tropics, as described in the results. Blue and red arrows show putative shifts and their direction (see legend). A geological time-scale is depicted at the bottom of the chronogram, spanning time since 58 Ma (Pl., Pliocene; Paleocene and Pleistocene are not indicated). The names of the three suborders and the 19 families are indicated. Illustrations © HBW Alive/Lynx Edicions.

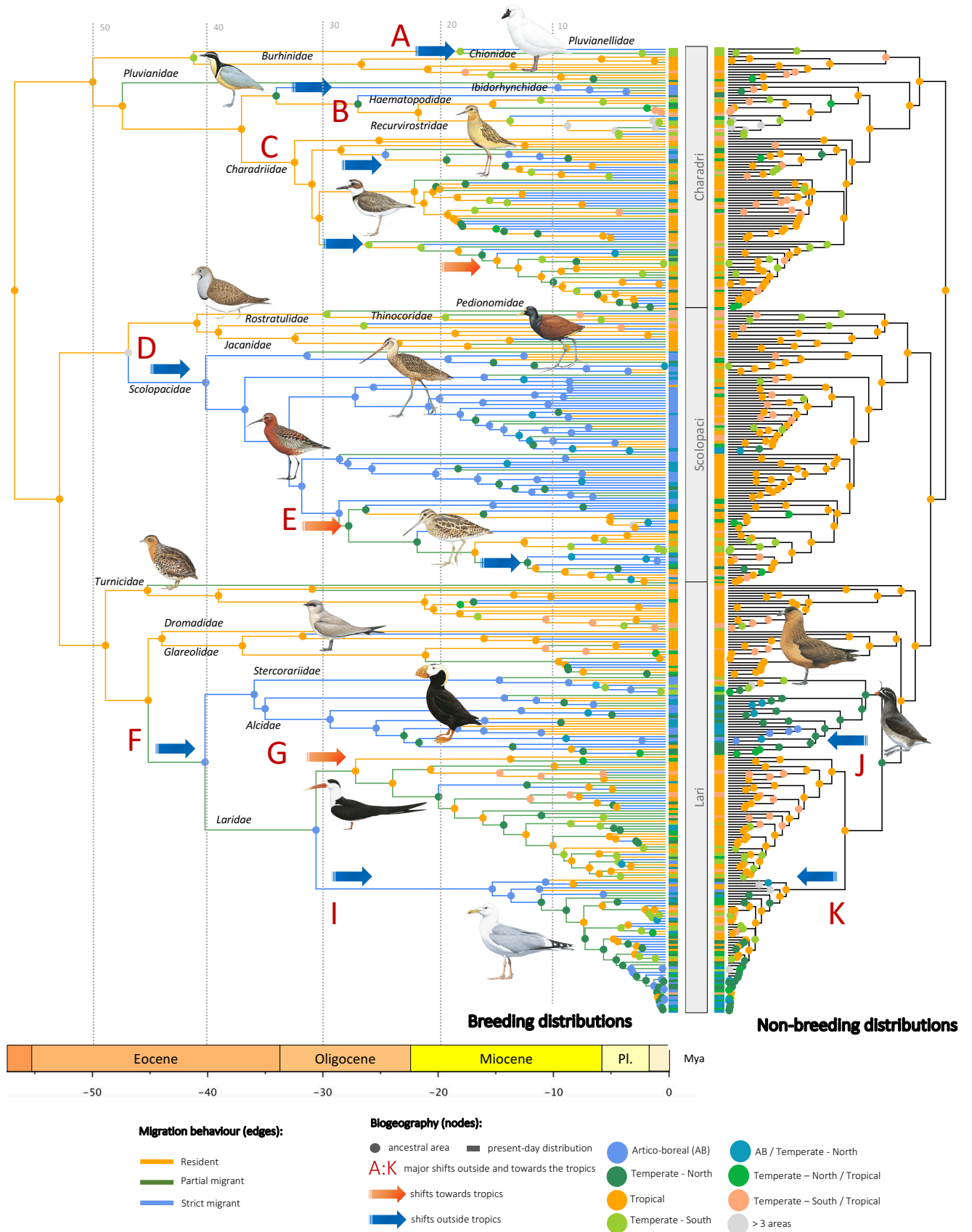


TABLE 3. Results of trait-dependent diversification models applied to different trees. For each model, the number of parameters (Np), the log-likelihood (LnL), the corrected Akaike information criterion (AIC), and the Δ AIC are indicated to show the best-fitting models. Parameters (λ = speciation, μ = extinction, and q = transition) were set to be equal or different between states (A for non-tropical species and B for tropical species in ClaSSE models). Models within 2 AIC units of the best model are shown in bold.

Charadriiformes					Charadriiformes (303 sp.)			Scolopacidae		
Model	Np	LnL	AIC	ΔAIC	LnL	AIC	ΔAIC	LnL	AIC	ΔAIC
Diversitree (ClaSSE)										
λAAA ≠ λBBB, μA ≠ μB, qAB = qBA	7	-1548.3	3110.6	3.2	-1220.5	2455.1	2.1	-366.5	747.0	29.5
λAAA ≠ λBBB, μA ≠ μB, qAB ≠ qBA	8	-1548.2	3112.3	4.9	-1220.5	2457.1	4.0	-352.6	721.3	3.7
λAAA ≠ λBBB, μA = μB, qAB = qBA	6	-1547.7	3107.3	0	-1220.5	2453.1	0	-372.0	756.1	38.6
λAAA ≠ λBBB, μA = μB, qAB ≠ qBA	7	-1550.2	3114.5	7.1	-1220.5	2455.1	2.0	-351.7	717.5	0
λAAA = λBBB, μA ≠ μB, qAB = qBA	6	-1562.0	3136.1	28.7	-1226.8	2465.7	12.5	-366.8	745.6	28.0
λAAA = λBBB, μA ≠ μB, qAB ≠ qBA	7	-1558.1	3130.2	22.8	-1226.8	2467.7	14.5	-356.3	726.7	9.1
λAAA = λBBB, μA = μB, qAB = qBA	5	-1560.2	3130.5	23.1	-1226.8	2463.7	10.5	-373.0	756.1	38.5
λAAA = λBBB, μA = μB, qAB ≠ qBA	6	-1549.6	3111.3	3.9	-1226.8	2465.7	12.5	-356.0	724.1	6.5
HiSSE										
CID-2	12	-1476.2	2976.4	13.3	-1214.8	2453.6	63.3	-334.7	701.4	0.8
CID-4	9	-1506.1	3030.2	67.1	-1220.7	2459.5	69.1	-342.0	708.1	7.6
Full BiSSE	12	-1518.6	3061.3	98.2	-1217.1	2458.3	68.0	-352.6	723.3	22.7
Full HiSSE	16	-1465.5	2963.0	0	-1179.1	2390.3	0	-338.2	700.5	0
Laridae					Charadriidae					
Model	Np	LnL	AIC	ΔAIC	LnL	AIC	ΔAIC			
Diversitree (ClaSSE)										
λAAA ≠ λBBB, μA ≠ μB, qAB = qBA	7	-332.5	679.0	1.0	-298.6	611.3	2.8			
λAAA ≠ λBBB, μA ≠ μB, qAB ≠ qBA	8	-331.5	679.0	1.0	-298.3	612.7	4.3			
λAAA ≠ λBBB, μA = μB, qAB = qBA	6	-333.0	678.0	0	-298.2	608.4	0			
λAAA ≠ λBBB, μA = μB, qAB ≠ qBA	7	-332.0	678.0	0.1	-298.9	611.8	3.4			
λAAA = λBBB, μA ≠ μB, qAB = qBA	6	-343.7	699.4	21.4	-299.9	611.9	3.4			
λAAA = λBBB, μA ≠ μB, qAB ≠ qBA	7	-343.7	701.4	23.4	-299.9	613.8	5.4			
λAAA = λBBB, μA = μB, qAB = qBA	5	-345.3	700.7	22.7	-300.1	610.3	1.8			
λAAA = λBBB, μA = μB, qAB ≠ qBA	6	-345.3	702.7	24.6	-298.9	609.9	1.5			
HiSSE										
CID-2	12	-325.6	683.3	7.5	-276.6	585.3	4.4			
CID-4	9	-325.8	675.7	0	-294.3	612.7	31.9			
Full BiSSE	12	-333.5	685.0	9.3	-282.1	582.3	1.5			
Full HiSSE	16	-331.3	686.6	10.8	-278.4	580.8	0			

Diversification dynamics in relation to latitudinal movements

For the Charadriiformes as a whole, we found that speciation rates were higher for non-tropical (temperate and Arctic species) than for tropical species (Fig. 5a and 6a), suggesting that the latitudinal transition from tropics to temperate areas favored speciation. We found consistent results with both ClaSSE and HiSSE analyses. For ClaSSE models, we found that the best-fitting model was a model including different speciation rate parameters between latitudinal ranges ($\lambda_{AAA} \neq \lambda_{BBB}$; see Table 3). This model also estimated slightly higher asymmetrical speciation rates for non-tropical than tropical species but with substantial standard deviation ($\lambda_{AAB} = 0.009 \pm 0.008$ and $\lambda_{BAB} = 0.006 \pm 0.006$; see Fig. 5a). Concerning HiSSE analyses, the full HiSSE model was a better fit than either models CID2 or full BiSSE (Table 3), suggesting that both the breeding distribution (non-tropical versus tropical) and the hidden character impacted diversification. Whereas we found mean speciation rates similar to those of the ClaSSE analysis for the A hidden state ($\lambda_{\text{NON-TROP A}} = 0.252$ and $\lambda_{\text{TROP A}} = 0.033$), we also found significant speciation rates for the second hidden state especially for tropical distributions ($\lambda_{\text{NON-TROP B}} = 0.067$ and $\lambda_{\text{TROP B}} = 0.105$). The 500 HiSSE-simulations with randomly distributed characters showed AIC values higher than the full-HiSSE model with original data (Fig. S8). The analyses performed without the species grafted on the phylogeny globally showed similar results (Table 3, Fig. S5 and S6).

In spite of this well supported pattern, the ranking between tropical and temperate rates of speciation varied substantially across families, with again similar patterns recovered by ClaSSE and HiSSE analyses. For Scolopacidae, despite a low number of tropical species (15 out of 91), we found a higher speciation rate in tropical areas (Fig. 5b and 6b). We also found in ClaSSE models a significantly higher asymmetrical speciation rate for tropical than non-tropical species ($\lambda_{BAB} = 0.037 \pm 0.012$ and $\lambda_{AAB} = 0.006 \pm 0.006$; see Fig. 5b), suggesting that the cladogenesis of tropical species into one non-tropical and one tropical species occurred at a greater rate than any other speciation scenario in Scolopacidae. For Laridae, we also found a much higher speciation rate in non-tropical areas (Fig. 5c and 6c), while speciation rates were somewhat similar in temperate and tropical areas for Charadriidae (Fig. 5d and 6d). Note that the HiSSE marginal reconstructions also revealed an ancestral tropical distribution followed by several shifts towards the temperate and Arctic latitudes (with subsequent transitions to the tropics in some cases; Fig. S7). Best-fitting ClaSSE models estimated low extinction rates for all clades ($\mu = 0.008 \pm 0.007$ for Charadriiformes; see Fig. S5), while HiSSE analyses showed more variable extinction rates with notably high extinction rates for Scolopacidae and Laridae (Fig. S7). Extinction rates are considered difficult to infer

from molecular phylogenies (Rabosky 2010, but see Beaulieu and O’Meara 2015). As can be seen from above, our results are not sensitive to, and not depend upon, variations in extinction rates between clades or biogeographic regions.

A positive correlation between the family richness (i.e. the number of species per families) and the number of inferred transitions outside the tropics was recovered (Fig. 7; PGLS: slope=17.1, $\lambda=0.99$; $P=0.012$). We found that three families diversified more (e.g. Scolopacidae; 91 species) than the average despite few transition events outside the tropics (number of transitions: $1.96 \pm \text{SD } 0.52$), while five families showed few speciation events compared to the number of inferred transitions (e.g. Haematopodidae, 9 species; number of transitions: $3.29 \pm \text{SD } 0.84$). Overall, three of the 14 families showed a lower rate of transitions outside the tropics (Fig. S4) than expected (i.e. the most diversified families: Scolopacidae, Charadriidae, and Laridae) and five of the families showed a higher rate than expected (Haematopodidae, Thinocoridae, Recuvirostridae, Chionidae and Rostratulidae).

FIGURE 5. Charadriiformes diversified faster in temperate and Arctic regions. The plots show the posterior density distribution of speciation rates as inferred by the best-fitting ClaSSE models for Charadriiformes (a) and the three largest families (b: Scolopacidae, c: Laridae, d: Charadriidae). Species breeding in non-tropical areas (i.e. Arctic, temperate-north and temperate-south species) are labelled as A in the model and tropical species labelled as B. The rates of ‘symmetrical’ (λ_{AAA} and λ_{BBB}) and ‘asymmetrical’ speciation (λ_{AAB} and λ_{BAB}) are indicated. The results suggest that temperate lineages of Charadriiformes diversified faster than tropical ones (λ_{AAA} is the highest rate), except for Scolopacidae and Charadriidae. Illustrations © HBW Alive/Lynx Edicions.

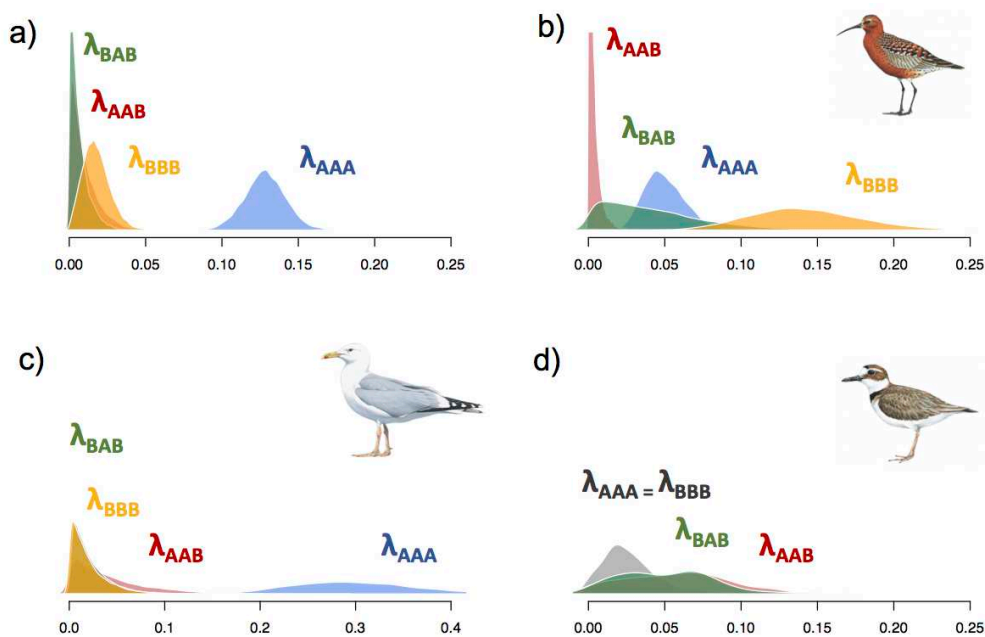


FIGURE 6. Speciation rates estimated from model-averaged HiSSE analyses for Charadriiformes (a) and the three largest families (b: Scolopacidae, c: Laridae, d: Charadriidae). We considered species breeding in non-tropical areas (i.e. Arctic, temperate-north and temperate-south species, denoted NON-TROP in the figure) and tropical species (denoted TROP). In agreement with ClaSSE results, speciation rates in temperate species tend to be higher than tropical species (except for Scolopacidae and Charadriidae). Illustrations © HBW Alive/Lynx Edicions.

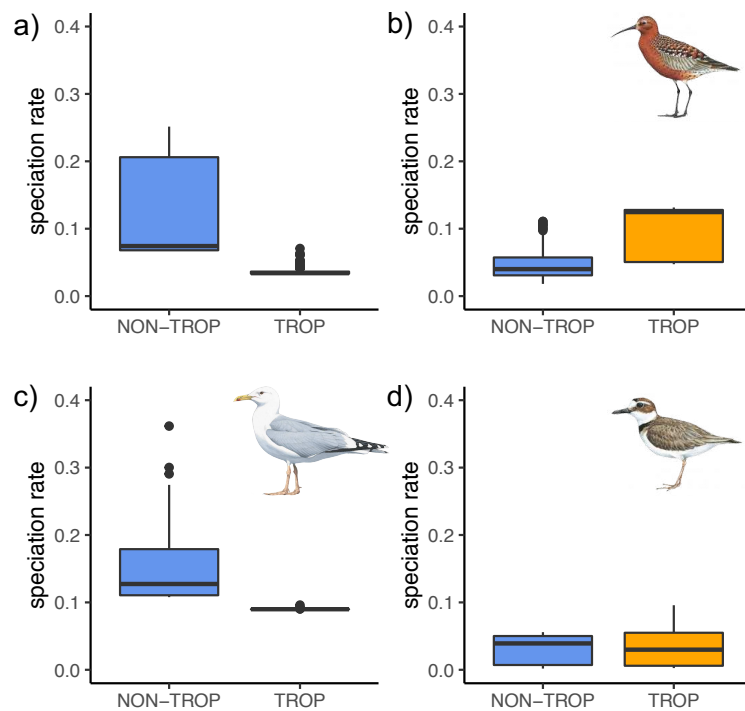
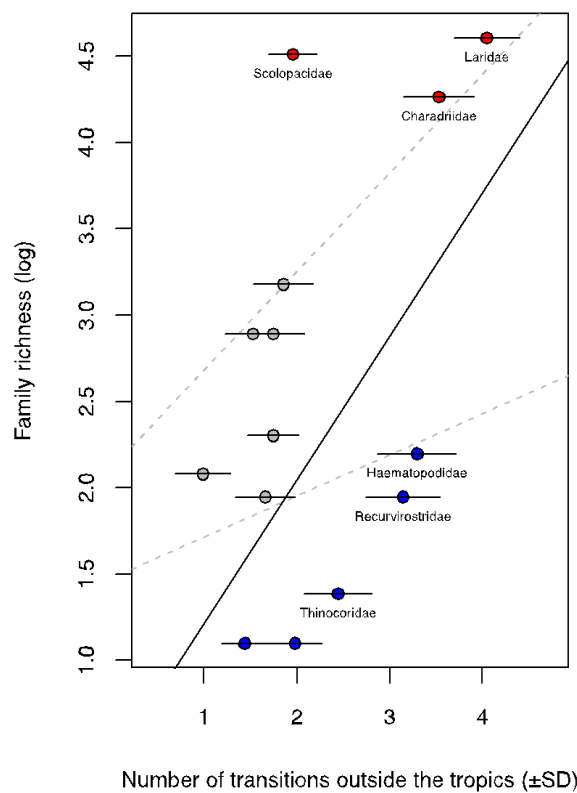


FIGURE 7. Relationship between Charadriiform species richness per family and the number of inferred transitions of breeding ranges outside the tropics. Transitions are calculated from ancestral areas reconstruction based on breeding distributions. The error bars represent the standard deviation of the average transition rates, calculated from 1,000 simulations of breeding range evolution. The solid line represents the regression line, and dashed lines represent the 95% confidence intervals for the expected number of transitions given a binomial distribution. Given the expectations, red points indicate families with significant lower rates of transition, whereas blue points indicate families with significant higher rates of transition. Monospecific families are not shown in the figure.



DISCUSSION

Charadriiformes is a large bird order remarkable for including the longest distance migratory species known on Earth and for exhibiting a rare example of an inverse latitudinal diversity gradient. In this study, we examined the concordance between the emergence of bird migration and shifts in range distribution towards seasonal regions, and also the potential influence of migratory behavior as a driver of speciation. So far, large-scale phylogenetic studies investigating the evolutionary origins of long-distance migration remain scarce (e.g. Winger et al. 2014, Dufour et al. 2020) and even fewer studies have tackled this question by jointly exploring biogeographic movements of migratory lineages and their diversification dynamics (but see Rolland et al. 2014a). More generally, our study provides an interesting exploration of the evolutionary mechanisms that generated a notable exception to one of the most conspicuous biogeographic patterns.

Biogeographic and temporal context of the emergence of long-distance migration

Previous studies focusing on particular clades showed that migration could evolve from temperate origins (NHT, e.g. Winger et al. 2014 in Emberizoidea, Winger et al. 2012 in Parulidae) or tropical origins (SHT, e.g. Licona-Vera and Ornelas in *Mellisugini*, Outlaw et al. 2003 in *Catharus*). Examining this question at the scale of large orders, Dufour et al. (2020) failed to uncover a clear pattern of preferential scenario at a global scale. The existing empirical evidence thus suggests that both tropical and temperate origins of the migratory lineages exist in avian history, in relation to the variety and lability of geographic distributions and migratory behaviors encountered in birds.

Our study clearly links the emergence of migratory behavior with transitions from tropical to temperate biomes, since most dispersal out of the tropics into the temperate and Arctic zones of both hemispheres coincide with the onset of (partial or strict) migratory behaviors. According to our results, migration has mainly evolved from tropical ancestors within Charadriiformes, following breeding ranges shift towards higher latitudes (through dispersal movements), while wintering areas remained in tropical latitudes. We also find a greater evolutionary lability of breeding grounds compared with wintering grounds (except for few specific families such as Alcidae or Laridae) suggesting that an important conservatism may exist on the evolution of wintering areas. Therefore, the emergence of migration in Charadriiformes fit well the SHT hypothesis proposing a tropical origin (see Cox 1968; Gauthreaux 1982; Levey and Stiles 1992; Rappole 1995). We do not know whether particular mechanisms put forward to explain the evolution of migration under the SHT, such

as avoiding competition by exploiting seasonally abundant resources outside the tropics (Cox 1968, Levey and Stiles 1992), can be applied to Charadriiformes but most Arctic-breeding species indeed depend on strongly seasonal resources such as insects or other invertebrates that are absent during winters, making long-distance migration an obligate strategy to cope with the very high seasonality of their breeding areas.

Our results also suggest that migratory behavior might have been an evolutionary key innovation that have enabled Charadriiformes to leave the tropics. Even though we have not formally tested it, our phylogenetic ancestral area reconstructions suggest that the accumulation of migratory lineages coincides with the global cooling initiated since the middle Eocene (Zachos et al. 2001) and linked to the appearance of markedly latitudinal seasonal climates (see Mosbrugger et al. 2005). The onset of the global cooling in the middle Eocene has been associated with a progressive retreat of tropical biomes and biota towards the latitudes they currently occupy (e.g. Pound et al. 2012; Pound and Salzmann 2017; Meseguer and Condamine 2020) and an expansion of tundra, taiga and steppe biomes during the Miocene (e.g. Edwards et al. 2010), which corresponds to the habitats used by most of the Holarctic Charadriiform species during the breeding period. Indeed, Louchart (2008) identified two main phases of contraction of tropical biomes (see Mosbrugger et al. 2005), at the end of the Eocene (33.9 Ma) and at the end of the Miocene (5.3 Ma), which may have had a positive influence on the emergence of migration (Figs. 3, 4). We thus hypothesize that the Neogene expansion of these environments created a major novel ecological opportunity that have favored the colonization of high latitudes by several Charadriiform clades, and that their breeding in these new environments has been almost exclusively possible through the emergence of migratory behavior (Winger et al. 2019). It would be interesting to explore this hypothesis through the use of the fossil record: even if few Charadriiform fossils dating from the Paleogene are known (Mayr 2009), several fossils from the late Oligocene - early Miocene have recently been discovered (e.g. de Pietri and Mayr 2012; de Pietri et al. 2013). Another approach would be to use paleoenvironment-dependent diversification models (Condamine et al. 2019) to correlate diversification and the temporal expansion of grasslands for instance (see Kergoat et al. 2018).

We also point out also that the "out of the tropics" transitions discussed here probably include two non-mutually exclusive scenarios: (1) northward shifts in the geographic location of breeding ranges from tropical to temperate biomes and (2) temporal persistence of high-latitude populations experiencing a change in climate from tropical to seasonal temperate, without geographic range shift. The first scenario is clearly illustrated by several clades that

colonized the current temperate regions after the retreat of the tropical biomes, such as the tropical-adapted genus *Vanellus* where some temperate species diverged from their tropical relatives after the retreat of the tropical habitats (e.g. *Vanellus vanellus*, which diverged approximately 13 Ma ago). The second scenario certainly cannot be “demonstrated” with confidence but is a plausible explanation when the ancestral area corresponds in high latitudes areas then occupied by tropical biomes, which was presented as the “adaptation for geographic persistence” hypothesis by Winger et al. (2019). For example, we estimate that the ancestor of the Scolopacidae already occupied the higher latitudes before the first phase of contraction of the tropical biomes (middle Eocene; see Louchart 2008), which suggest that this clade may have persisted under high latitudes by an adaptive niche shift from tropical (low seasonality) to temperate (high seasonality) environment (Winger et al 2019). To sum up, we believe our results bring support to the view of Winger et al. (2019) that the emergence of migration behavior was a key innovation to allow geographic persistence when confronted with increasing climatic seasonality. In Charadriiformes, we thus find that the emergence of migration mostly followed dispersal into new seasonal breeding areas (SHT) but we cannot totally exclude the scenario that the emergence of migration in some lineages may result the adaptation of high latitude breeding populations to increased seasonality, combined with a shift of breeding range toward the tropics (NHT) in high latitudes for some lineages. This study illustrates that these two scenarios can be difficult to disentangle from phylogenies of extant species and likely both contributed to the evolution of avian migration.

Increased diversification in temperate and Arctic areas

Our study unambiguously explains the inverse LDG of the Charadriiformes by higher diversification under temperate and Arctic or Austral latitudes than under tropical latitudes (Figs. 5, 6). This result is also supported by the fact that most species-rich families (>50 species: Scolopacidae, Laridae and Charadriidae) exhibited lower transitions outside the tropics than expected with the null model (Fig. 7). Such increased diversification rates in temperate and Arctic biomes contrasts with the general expectation of the LDG that diversification rates are higher in the tropics (Mittelbach et al. 2007; Hawkins et al. 2007a; Rodriguez-Castaneda et al. 2017; Meseguer and Condamine 2020). Hence, the evolutionary history of Charadriiformes is at odds with the metabolic theory of biodiversity, which stipulates that higher energy environments, mainly under tropical latitudes, promote diversification processes (Hawkins et al. 2007b; Condamine et al. 2019).

It is possible that climate change that occurred over the past tens of millions of years (Zachos et al. 2001) has allowed the colonization of highest latitudes by several Charadriiformes clades (see Weir and Schluter 2007) and promoted their diversification. The cooling occurring since the middle Eocene has potentially allowed the colonization of novel ecological niches. The lineages that colonized these latitudes were able to take advantage of these vacant habitats to diversify (Weir and Schluter 2007) with the possibility of evolutionary radiations, that is episodes of high speciation rates (see Schluter 1996). Indeed, large migratory families of Charadriiformes (e.g. Charadriidae, Scolopacidae) occupy a wide diversity of breeding habitats within the Boreo-Arctic biomes (i.e. various grassland and scrubland habitats, in taiga or tundra, at varying distance from water), harbor a large phenotypic diversity (plumage colors in Charadriidae, bill morphology in Scolopacidae) and display behaviors (see Jehl and Murray 1986), which altogether is consistent with the idea of adaptive radiation for these lineages. It is important to mention that the support for the full-HiSSE model (Table 3) suggesting that hidden character(s), other than the temperate/tropical distribution, impacted the Charadriiform diversification is consistent with this idea, and would deserve further phylogenetic studies using multi-trait approaches to depict how joint trait and niche evolution have spurred the diversification of these particular clades.

Seasonal geographic migration as a driver of diversification?

While our results support a tropical origin of Charadriiformes, they also show at least seven independent transitions from tropical to temperate biomes, which may have occurred through actual dispersal or temporal persistence under shifting climate (as discussed earlier). Importantly, we found a very strong concordance between these movements and the emergence of migratory behavior, in accordance with the hypothesis that the evolution of migration allowed the Charadriiformes to breed in highly seasonal habitats of temperate and Arctic latitudes. In this context, the increased diversification rates we found in temperate and Arctic latitudes fit well with the predictions of a so-called scenario of ecological opportunity (e.g. Glor 2010; Yoder et al. 2010). Seasonal migration has long been regarded as a barrier to speciation processes because it may enhance gene flows and thus reduce genetic divergence between populations (Helbig 2003; Claramunt et al. 2012). Few empirical studies suggested that seasonal migration could have a positive influence on speciation (e.g. Gómez-Bahamón et al. 2020). On the contrary, we found here that long-distance migration allowed multiple lineages to breed into new (and presumably underexploited) environmental conditions, which in turn spurred their diversification rate.

Moreover, our study supports another link between migration and speciation in birds in relation to events of extreme long-distance dispersal toward novel wintering grounds. It was shown earlier that individuals of migratory species may sometimes start breeding in their wintering range, thereby establishing new breeding populations very far away from their main breeding range (Winkler et al. 2017; see also Curtis and Koeslag 2007). This was recently documented in *Hirundo rustica erythrogaster*, where individuals historically migrating from North America to South America began breeding in their wintering range in Argentina (Winkler et al. 2017). Such long-distance dispersal events can result in speciation between the ancestral and derived breeding distributions, as suggested by G6mez-Baham6n et al. (2020) in Tyrannidae. Such a scenario was also suggested by the study of Rolland et al. (2014a), which proposed that the evolution of seasonal migration in birds has likely facilitated diversification through the divergence of migratory populations that became sedentary. In Charadriiformes, we identified several species that very probably originated from migrant ancestors, which remained on their wintering grounds and returned to a resident state (Fig. 3). For instance, snipes comprise many Holarctic migratory species (e.g. *Gallinago delicata*, *G. megala*, *G. hardwickii*), which spend winter in the southern hemisphere regions where other resident species also breed (e.g. genus *Coenocorypha* in Oceania, *G. undulata*, or *G. paraguayiae* in South America). Phylogenetic relationships and inferred loss of migratory behavior suggest that these latter two taxa may indeed result from speciation events that occurred after settlement on the wintering grounds of previously migratory taxa.

In other cases, such speciation by colonization of the wintering areas did not involve a loss of migration behavior: several migratory species of the genus *Sterna* breeding in the southern hemisphere (e.g. *Sterna hirundinacea*, *S. vittata*, *S. virgata*) are closely related to long-distance migratory species that breed in the northern hemisphere but winter in the southern hemisphere (*S. hirundo*, *S. paradisaea*; see Bridge et al. 2005). In a similar way, *Catharacta skua* breeds in the northern hemisphere but derive from a clade that mainly breeds mainly in the southern hemisphere and for which some species migrate to the northern hemisphere during the austral winter (see illustration of their distributions in Fig. S9). Last, vagrancy (i.e. the occurrence of “lost” individuals far from their normal breeding, migratory or wintering range) is expected to be more common in migratory species (Veit and Lewis 1996). While vagrancy rarely leads to long-distance colonization, because the number of individuals involved is typically too small for a successful establishment, examples of breeding populations following vagrant movements was reported in several species. One well-known example is the one of *Bulbulcus ibis* throughout South America (Massa et al. 2014)

and at least one species of Charadriiformes (*Thalasseus elegans*) is currently starting to breed in Europe even though its normal range is the Pacific coast of America (see Dufour et al. 2017). Whether such long-distance colonization can result in speciation remains to be tested though. In conclusion, we suggest that migration has boosted speciation in Charadriiformes not only by allowing them to breed in seasonal environments but seemingly also by promoting long-distance dispersal through the colonization of novel geographic areas visited during the non-breeding periods.

Insights into the evolutionary origin and systematics of Charadriiformes

This study assembled an amount of genomic data that had never been analyzed together. Our new phylogeny of Charadriiformes is thus based on a significant increase in both species sampling and gene coverage which allows to confirm the position of several lineages. Most importantly, the use of newly discovered fossils and entirely revised fossil ages provided new estimates for the origin and divergence times in this clade. Our phylogeny recovers the main relationships found in previous studies (Paton et al. 2003; Baker et al. 2007) but we estimated that the most recent common ancestor of the shorebirds originated in the Paleocene (57 Ma, 95% CI= 54–61 Ma), which is 20 million years earlier than the estimate of Paton et al. (2003) and 30 million years younger than the estimate of Baker et al. (2007). This is partly driven by the root calibration set at 54 Ma with †*Scandiavis mikkelsenii* (Bertelli et al. 2013) but the narrow posterior distribution for the divergence time at this node indicates that there was no conflict with the other calibration points.

Relying on fourteen fossil constraints, the study of Baker et al. (2007) provided the most comprehensive phylogenetic reconstruction of Charadriiformes so far and found that the emergence of the three suborders (and fourteen ancestors of extant lineages) pre-dated the K-Pg boundary. Taking into account the latest fossil discoveries (Smith 2015) and reassigning several fossils used by Baker et al. (2007), we found instead that the three suborders originated between 42 and 56 Ma during the early Eocene. Our estimates of the ages of deep divergences within Charadriiformes are indeed more consistent with the genomic study of Prum et al. (2015) who estimated their origins at around 50 Ma (depending on the inclusion of †*Vegavis*). This strongly supports fossil evidence that modern birds emerged through an explosive Cenozoic radiation following the K-Pg boundary (Feduccia 2003; Jarvis et al. 2014).

Compiling all available molecular data enabled us to identify species and clades that entirely lack molecular data or are represented by short DNA sequences, impeding a reliable

reconstruction of their evolutionary history (i.e. notably in the genera *Gallinago*, *Turnix* and *Vanellus*). The recovered paraphyly of the genus *Gallinago* questions the taxonomic position of the three other South American *Gallinago* species (*G. nobilis*, *G. stricklandii* and *G. jamesoni*) whose phenotypic resemblance suggest that they belong to the same clade but which have not been sequenced yet. Further research should be carried out to determine whether the genus *Coenocorypha* should be maintained and expanded to include the aforementioned South American *Gallinago* taxa or whether South American *Gallinago* constitute a genus in their own. Another major issue in Charadriiform taxonomy is the classification within the Charadriidae family. Firstly, as found by Baker et al. (2007), our phylogeny does not support the placement of *Pluvialis* within plovers (Charadriidae) but assigns it as a sister clade to the ibisbill, oystercatchers, stilts and avocets. However, support for the plover monophyly was found in Baker et al. (2012) by using eight nuclear genes, none of which are common with the six nuclear genes we considered in this study. Baker et al. (2012) argued that the plover paraphyly might have arisen through stochastic mutational variance in mitochondrial and nuclear (only RAG1) genes considered in Baker et al. (2007), we thus believe that more research should be conducted (using whole genome sequencing) on the placement of the genus *Pluvialis* before proposing taxonomic recommendations. Secondly, another issue is the monophyly of the genus *Charadrius* within the Charadriidae. Despite some minor differences in the placement of particular species, we concur with Barth et al. (2013) and Dos Remedios et al. (2015) that the genus *Charadrius* is paraphyletic, with the genus *Vanellus* nested within it and separating two major clades of *Charadrius*, called CRD I and CRD II by former authors. Although more research would be needed to improve the placement of the basal species of each of these two clades (CRD 1 and 2), our phylogeny confirms the proposition of Sangster et al. (2016) that the species of the CRD II clade should be renamed *Anarhynchus*.

CONCLUSION

We found that Charadriiformes likely originated in the tropics and that their biogeography has subsequently been shaped by several dispersal events out of the tropics. While the “out-of-the-tropics” hypothesis (Jablonski et al. 2006) was originally invoked to explain a greater diversity of tropical species (Rolland et al. 2014b), it is interesting to note that similar out-of-the-tropics movements may also result in a LDG inversed compared to most vertebrate clades. This was due to an increase of speciation rate of Charadriiformes toward higher latitudes, which makes a notable exception to the widespread evidence of increased rates of speciation

into the tropics. In addition, we found that the shifts towards higher latitudes were closely linked to the evolution of migration behavior, which appears as a necessary adaptation for persisting in very seasonal environments (Winger et al. 2019). These migratory lineages rapidly and widely diversified into the temperate and Boreo-Arctic regions, likely taking advantage of the opening up of vacant niches, in accordance with the hypothesis of ecological opportunity. Some Charadriiformes clades may have even undergone adaptive radiations in certain regions or environments (Glor 2010), but this clearly remains to be tested. Linking seasonal migration behavior and speciation is challenging, but we provide several lines of evidence for a direct positive influence of migration on speciation mostly through long-distance colonization events that allowed founding new breeding populations within wintering grounds (see Gómez-Bahamón et al. 2020). We have thus shown that the biogeographic history of Charadriiformes, in association with the evolution of migration, has likely shaped an inverse latitudinal diversity gradient, which contradicts biogeographic-based assumptions that the tropics served as an evolutionary cradle for most vertebrate lineages. Our study brings evidence that increased speciation rates, and perhaps adaptive radiations, have occurred in relation to the colonization of harsher and highly seasonal climatic niches, instead of stable, energy-rich environments.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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FIGURE S1. Details in addition of species with no DNA dataSpecies for which DNA data were unavailable:

<i>Actophilornis albinucha</i>	<i>Himantopus novaehollandiae</i>	<i>Turnix maculosus</i>
<i>Burhinus indicus</i>	<i>Ortyxelos meiffrenii</i>	<i>Turnix melanogaster</i>
<i>Charadrius bifrontatus</i>	<i>Procelsterna albivitta</i>	<i>Turnix nanus</i>
<i>Charadrius dealbatus</i>	<i>Recurvirostra novaehollandiae</i>	<i>Turnix nigricollis</i>
<i>Charadrius javanicus</i>	<i>Rhinoptilus bitorquatus</i>	<i>Turnix novaecaledoniae</i>
<i>Cursorius coromandelicus</i>	<i>Rhinoptilus cinctus</i>	<i>Turnix ocellatus</i>
<i>Cursorius cursor</i>	<i>Rynchops albicollis</i>	<i>Turnix olivii</i>
<i>Cursorius rufus</i>	<i>Rynchops flavirostris</i>	<i>Turnix worcesteri</i>
<i>Cursorius somalensis</i>	<i>Scolopax bukidnonensis</i>	<i>Vanellus albiceps</i>
<i>Esacus magnirostris</i>	<i>Scolopax celebensis</i>	<i>Vanellus coronatus</i>
<i>Esacus recurvirostris</i>	<i>Scolopax rochussenii</i>	<i>Vanellus crassirostris</i>
<i>Gallinago andina</i>	<i>Scolopax rosenbergii</i>	<i>Vanellus duvaucelii</i>
<i>Gallinago jamesoni</i>	<i>Scolopax saturata</i>	<i>Vanellus gregarius</i>
<i>Gallinago macrodactyla</i>	<i>Sterna acuticauda</i>	<i>Vanellus leucurus</i>
<i>Gallinago nemoricola</i>	<i>Sterna aurantia</i>	<i>Vanellus lugubris</i>
<i>Gallinago nobilis</i>	<i>Sterna repressa</i>	<i>Vanellus macropterus</i>
<i>Gallinago solitaria</i>	<i>Sterna virgata</i>	<i>Vanellus malabaricus</i>
<i>Gallinago stricklandii</i>	<i>Sternula balaenarum</i>	<i>Vanellus melanocephalus</i>
<i>Gelochelidon macrotarsa</i>	<i>Sternula lorata</i>	<i>Vanellus melanopterus</i>
<i>Glareola cinerea</i>	<i>Sternula saundersi</i>	<i>Vanellus novaehollandiae</i>
<i>Glareola lactea</i>	<i>Synthliboramphus scrippsi</i>	<i>Vanellus senegallus</i>
<i>Glareola ocularis</i>	<i>Thalasseus bernsteini</i>	<i>Vanellus superciliosus</i>
<i>Haematopus fuliginosus</i>	<i>Tringa guttifer</i>	<i>Vanellus tectus</i>
<i>Haematopus longirostris</i>	<i>Turnix castanotus</i>	<i>Vanellus tricolor</i>
<i>Haematopus moquini</i>	<i>Turnix everetti</i>	

Species for which no DNA data were available (73 species; see above) were added as polytomies to the phylogeny based on taxonomic affinities suggested in the reference handbooks (del Hoyo et al. 2019). This implies that a missing species was placed as a polytomy on a randomly selected node within the clade of which it was suggested to be a member. In cases where taxonomic information allowed assignment to lower levels (i.e. sister-species), species were added half-way along the terminal edge length to its sister taxon.

Details on assignment based on taxonomic information :

We detailed below the position assignments of specific species that do not follow the general rules of positioning explained above:

- The genus *Gallinago* is paraphyletic with *Coenocorypha* species nested within it. Our reconstruction placed *G. undulata* and *G. imperialis* as sister-species of *Coenocorypha* species (see also Gibson & Baker, 2012). We thus considered on the basis of their shared phenotypes to place *G. jamesoni*, *nobilis*, *stricklandii* within the clade containing *Coenocorypha* species, *G. undulata* and *G. imperialis*. *Gallinago andina*, *macroactyla*, *nemoricola* and *solitaria* were randomly placed in the crown-group of *Gallinago*.
- *Tringa guttifer* was randomly placed within the *Tringa* genus. Even if Liu and al. (2019) found a close relationship with *T. semipalmata*, the close morphological resemblance with *T. nebularia* (not present in the study) might suggest other relationships.
- Dos Remedios et al. (2015) confirmed that the *Charadrius* genus is paraphyletic (the paraphyly was already suggested in Barth et al. 2013) and proposed to consider two major clades (CRD I and CRD II) within the genus. Since *C. bifrontatus* has long been treated as conspecific with *C. tricoloris* we considered it as a sister species of this last within CRD I. *C. javanicus* has long been regarded as closely related to *C. marginatus*, *C. alexandrinus*, *C. dealbatus*, *C. nivosus* and *C. ruficapillus*, and all have on occasion been considered conspecific (Wiersma & Kirwan 2020), we thus placed *C. javanicus* randomly within CRD II. Based on Rheindt et al. 2011, we considered *C. dealbatus* as a sister-species of *C. alexandrinus* in CRD II.
- *Ortyxelos meiffrenii* was randomly placed within the genus *Turnix*.
- *Esacus magnirostris* and *recurvirostris* were placed in the crown-group of the genus *Burhinus*.

FIGURE S2. Comparison of the biogeographical histories of the Charadriiformes as inferred by DEC (a and b) and DEC+J (c and d) models, based on breeding distributions in (a and c) and on non-breeding distributions in (b and d). The Bayesian chronogram gives estimated molecular ages in million years (Mya) for phylogenetic relationships between lineages (outgroups removed). A geological time-scale, at the bottom of the chronogram, is spanning time since 58 Ma (Pli, Pliocene; Paleocene – left – and Pleistocene – right – are not indicated).

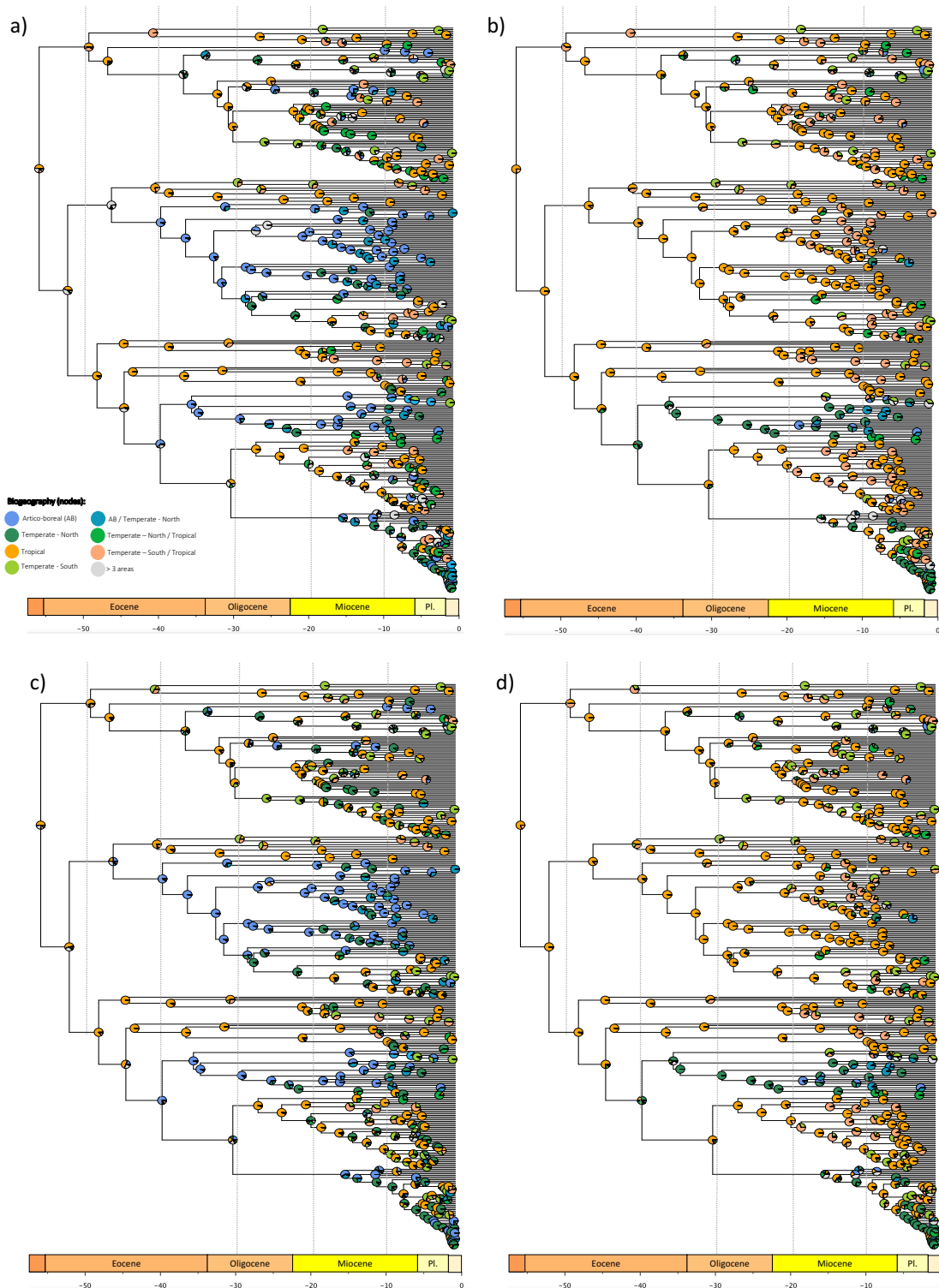


FIGURE S3. Reconstruction of ancestral migratory strategies (resident, partial migrant, strict migrant) across the Charadriiformes order performed with the MCC tree including grafting species (a) and the MCC tree only with species with molecular data available (b). Pie charts on nodes indicate the marginal likelihood for each state: orange for resident species, green for partial migrants and blue for strict migrants. Colored rectangle at tips represent present-day migratory strategies.

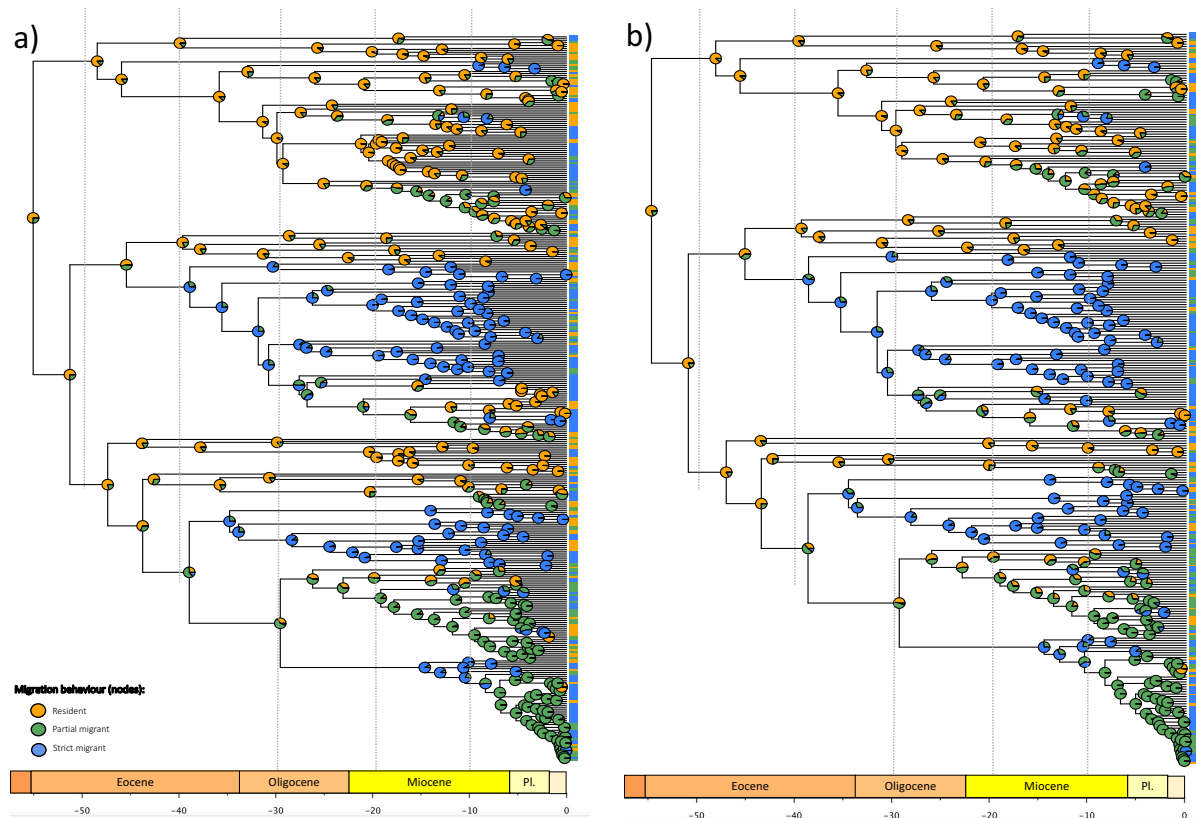


FIGURE S4. Number of transitions (a) towards tropics and (b) between non-joining areas in Charadriiformes families. For each family, the boxplot shows the distribution of the number of transitions calculated from 1000 runs of the regional states across all nodes. The red dot indicates the median of the expected number of transitions given the binomial distribution. Families marked with a '+' transited more than expected given their richness, while families marked with a '-' have significantly less. Only families with more than 5 species have been represented for visualization purposes.

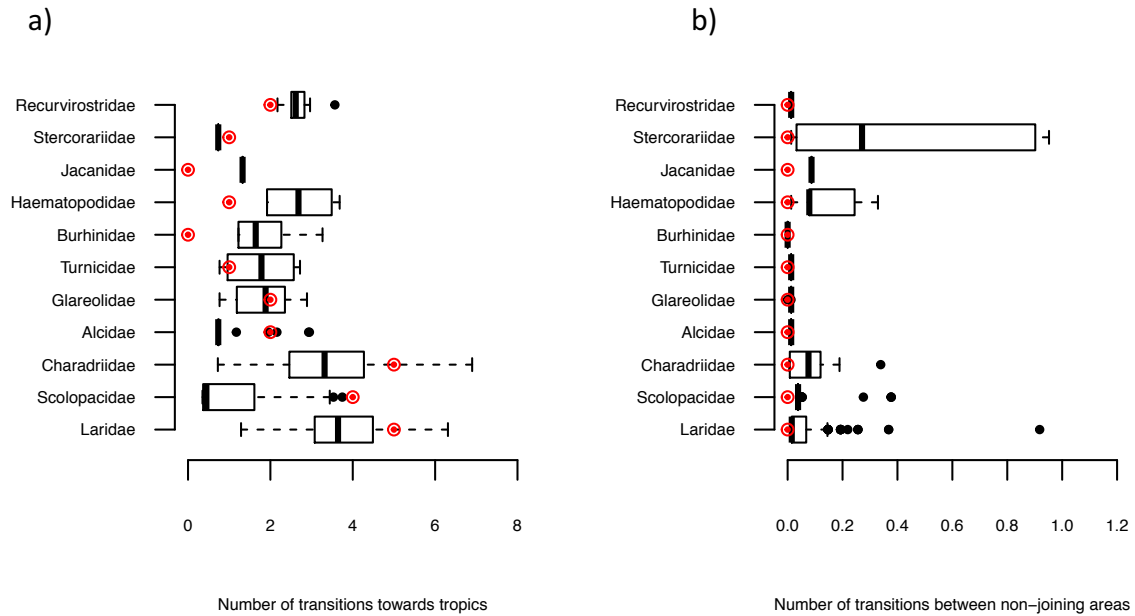


FIGURE S5. Posterior distribution estimates of speciation, extinction and net-diversification parameters as inferred by the best-fitting ClaSSE model for Charadriiformes (a), Charadriiformes without the grafting species on the phylogeny (b) and the three largest families (c: Scolopacidae, d: Laridae, d: Charadriidae). We considered species breeding in “temperate” areas (i.e. arctic, temperate-north and temperate-south species) and tropical species.

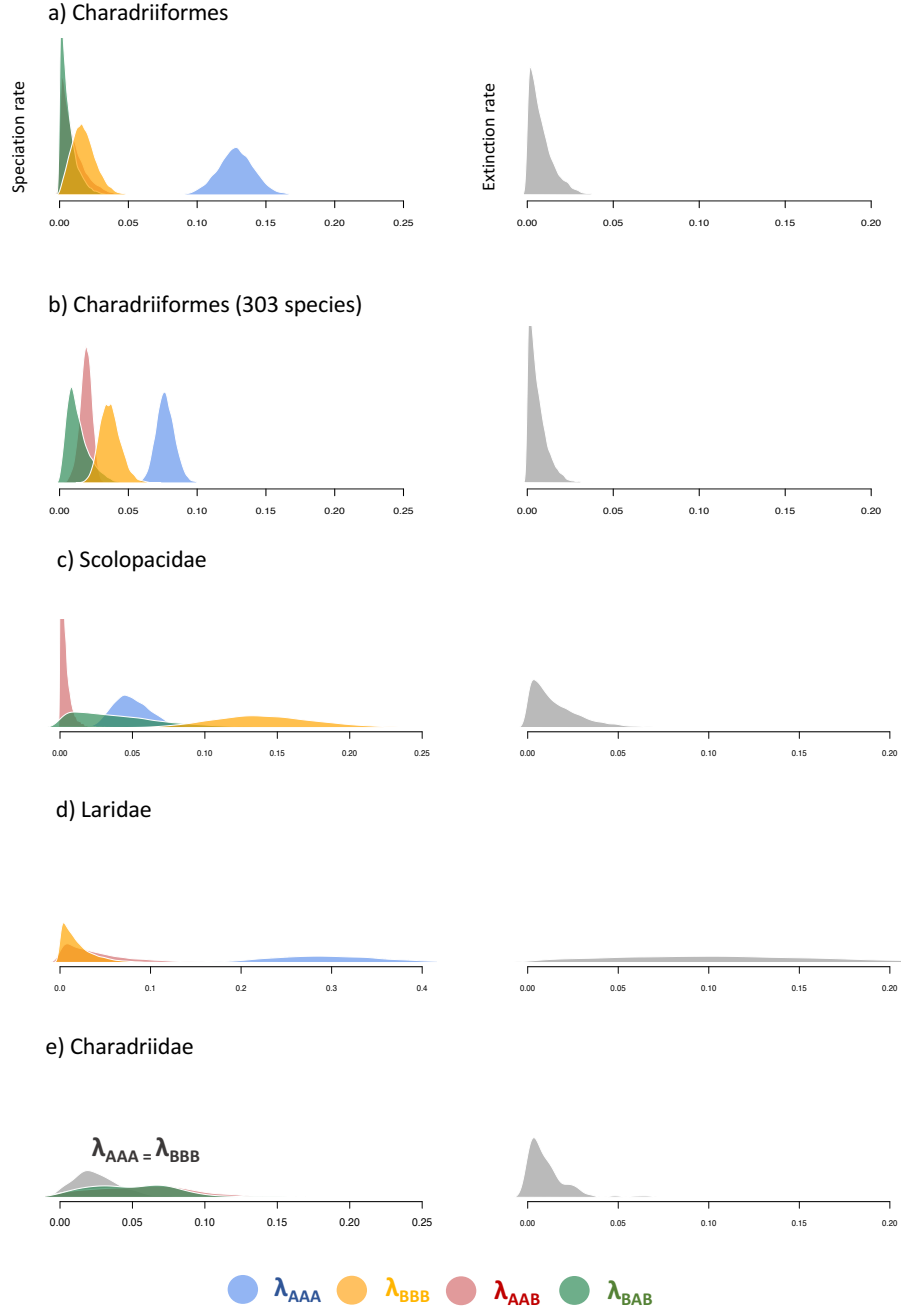


FIGURE S6. Boxplots representing speciation, extinction and net-diversification rates obtained from model-averaged HiSSE analyses for Charadriiformes (a), Charadriiformes without the grafting species on the phylogeny (b) and the three largest families (c: Scolopacidae, d: Laridae, e: Charadriidae).

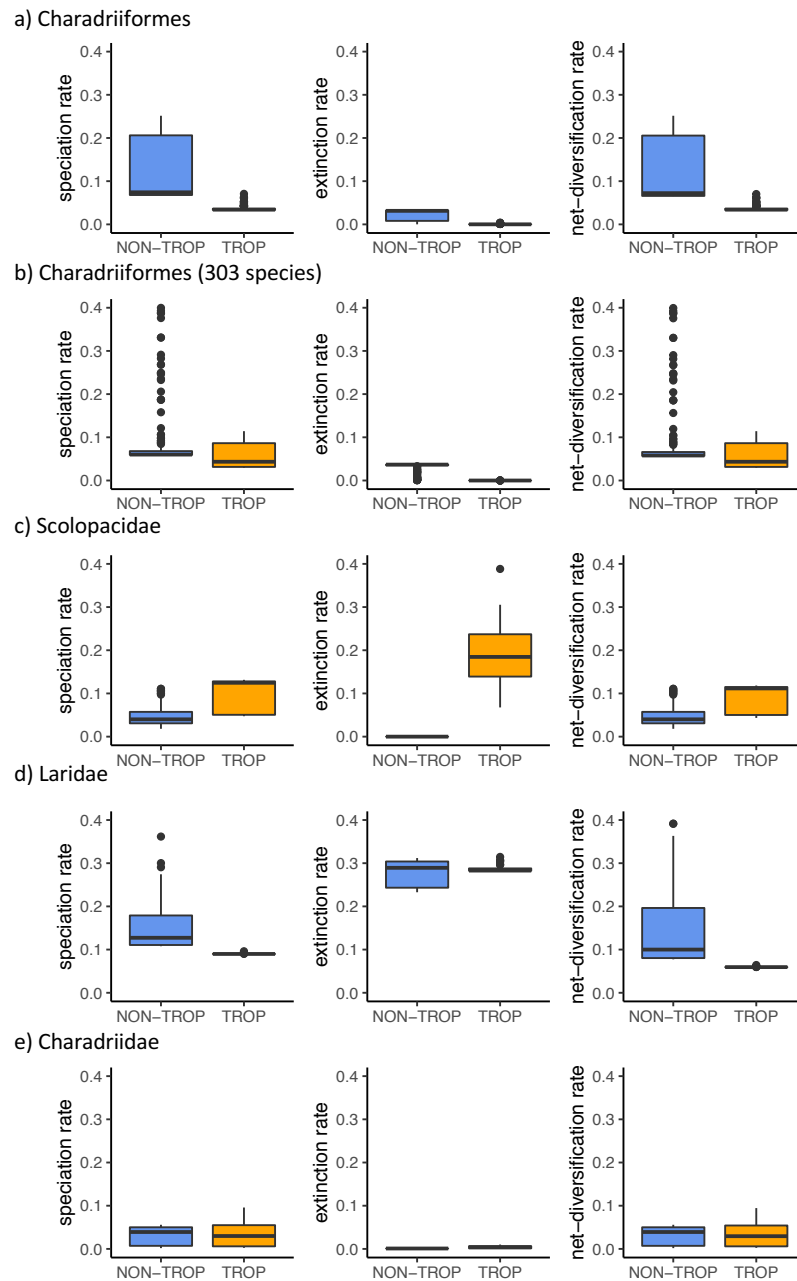


FIGURE S7. Model-averaged marginal reconstruction of net-diversification rates in relation to breeding distributions obtained from the HISSE analysis. Diversification rates are represented as color shading along branch edges (blue to red). Breeding distribution in “temperate” areas (i.e. arctic, temperate-north and temperate-south species) and “tropical” areas are represented as black/white shading inside branches. The inset represents the distribution of net diversification rates and character states across the tree.

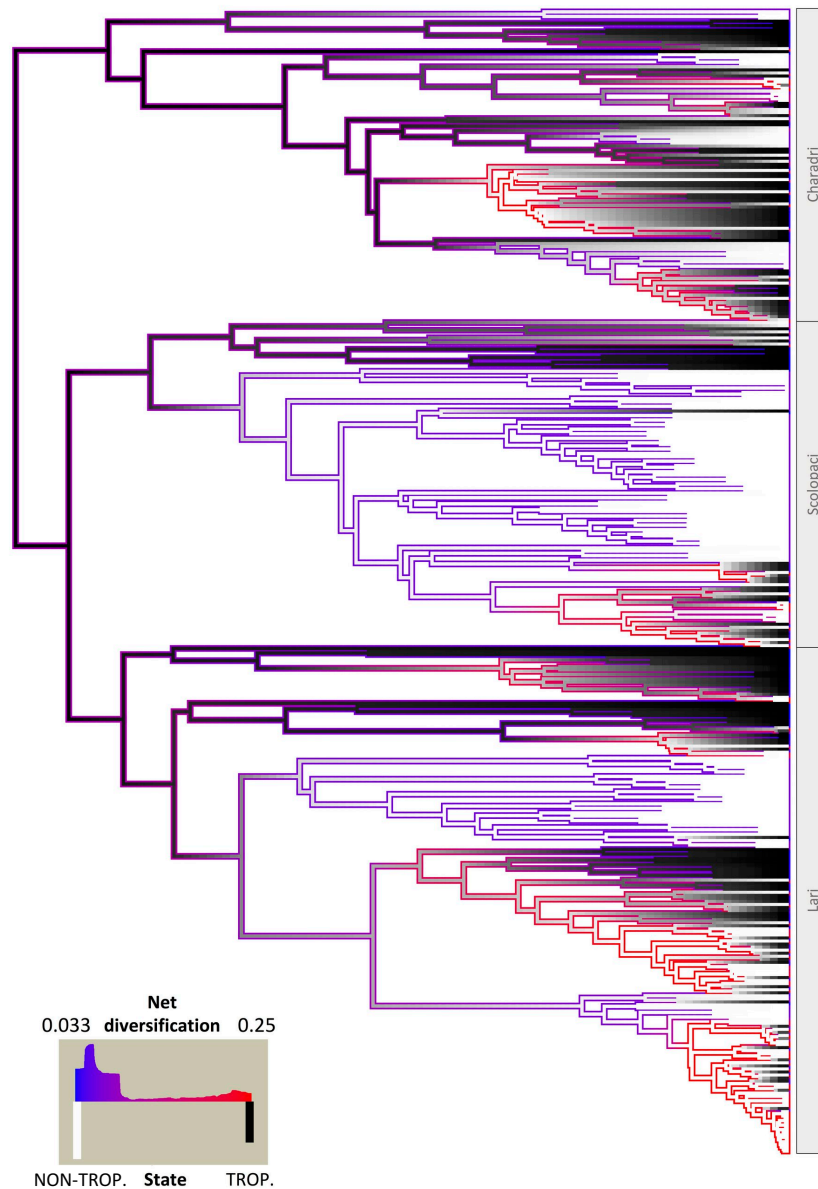


FIGURE S8. Comparison of corrected Akaike information criterion (AIC) between the full-Hisse model and 500 simulations with randomly distributed characters on tips of the Charadriiformes phylogeny.

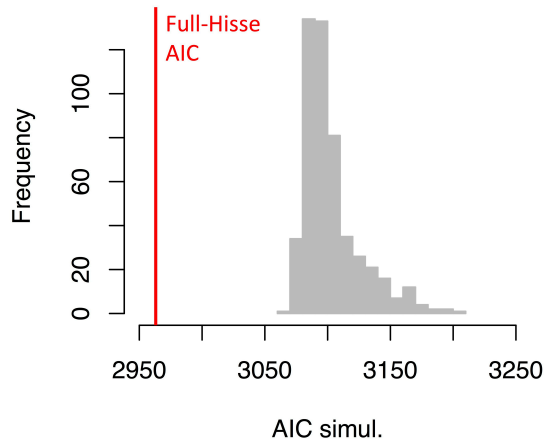


FIGURE S9. Illustration of the breeding and non-breeding distribution of species of the genus *Catharacta* (from BirdLife International 2020) with their phylogenetic relationships. Only *C. skua* nests in the northern hemisphere near the wintering grounds of *C. maccormicki*, while the other species nest below 70 degrees south latitude. Note that it has been proposed to assign *Stercorarius pomarinus* (breeding in the northern hemisphere) with the genus *Catharacta* (see Carlos 2017). The *Catharacta* phylogenetic tree has been pruned from the global phylogeny. Illustrations © HBW Alive/Lynx Edicions.

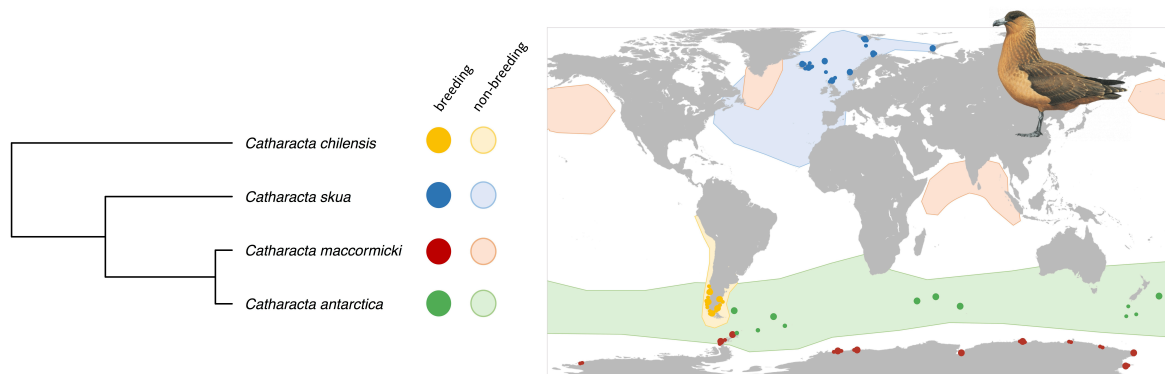


TABLE S2. Transitions considered to go out of or into the tropics. Transitions are considered as a change of state between a node and a descending node (even in the case of a state composed of the combination of several states). Namely, we considered: (A) transitions outside the tropics (from the tropical region towards temperate and Arctic regions), (B) transitions towards the tropics (from the Arctic and temperate regions towards the tropics). Transitions considered are indicated with a (+) and those not considered with ().

		State of the next descending node														
a)		Ab	Tn	Tr	Ts	AbTn	AbTr	AbTs	TnTr	TnTs	TrTs	AbTnTr	AbTnTs	AbTrTs	TnTrTs	AbTnTrTs
Current state of the node	Ab															
	Tn															
	Tr	+	+		+	+	+	+	+	+	+	+	+	+	+	+
	Ts															
	AbTn															
	AbTr	+	+		+	+		+		+			+			
	AbTs															
	TnTr	+	+		+	+		+		+			+			
	TnTs															
	TrTs	+	+		+	+		+		+			+			
	AbTnTr	+	+		+	+		+		+			+			
	AbTnTs															
	AbTrTs	+	+		+	+		+		+			+			
	TnTrTs	+	+		+	+		+		+			+			
	AbTnTrTs	+	+		+	+		+		+			+			

		State of the next descending node														
b)		Ab	Tn	Tr	Ts	AbTn	AbTr	AbTs	TnTr	TnTs	TrTs	AbTnTr	AbTnTs	AbTrTs	TnTrTs	AbTnTrTs
Current state of the node	Ab				+		+		+		+	+		+	+	+
	Tn				+		+		+		+	+		+	+	+
	Tr															
	Ts				+		+		+		+	+		+	+	+
	AbTn				+		+		+		+	+		+	+	+
	AbTr				+											
	AbTs				+		+		+		+	+		+	+	+
	TnTr				+				+		+	+		+	+	+
	TnTs				+		+		+		+	+		+	+	+
	TrTs				+											
	AbTnTr				+											
	AbTnTs				+		+		+		+	+		+	+	+
	AbTrTs				+											
	TnTrTs				+											
	AbTnTrTs				+											

TABLE S3. Model selection for ancestral state reconstructions of migration strategies (resident, partial migrant, strict migrant) for the Charadriiformes. Models were compared using Akaike information criterion (AICc) scores; model likelihood and delta AIC relative to the best model are also given. Three models were tested: equal transition rates between all states (ER), different transition rates between all states (ARD), and models without direct transition between resident and strict migrant states (stepping stone model; ST). For each model, four different root constraints were tested: no constraint, constrained to resident (root1), constrained to partial migrant (root2), or constrained to strict migrant (root3). The model in bold was considered the best model following corrected Akaike information criterion (AICc) selection.

Model	Nb. param.	Log-lik	AIC
ARD	7	-343.4	700.9
ARD.root1	6	-343.3	698.5
ARD.root2	6	-344.2	700.4
ARD.root3	6	-349.3	710.7
ER	2	-384.0	772.1
ER.root1	1	-383.8	769.5
ER.root2	1	-385.6	773.3
ER.root3	1	-384.8	771.6
NJ	5	-343.8	697.7
NJ.root1	4	-343.7	695.3
NJ.root2	4	-344.6	697.2
NJ.root3	4	-349.9	707.8

CHAPITRE 3

Etude des pressions de sélection rencontrées au cours du cycle annuel des oiseaux migrateurs : l'exemple de la coloration des Laridae

Résumé du chapitre : Les variations globales de coloration chez les animaux ont inspiré des règles éco-géographiques suggérant des mécanismes communs d'adaptations au climat. Cependant, peu d'études se sont intéressées à l'influence relative des différentes conditions climatiques rencontrées par les espèces migratrices au cours de leur cycle de vie annuel. Nous avons exploré cette question en testant quelles conditions du cycle annuel influencent le plus la coloration du plumage des Laridae (mouettes et goélands), un groupe cosmopolite d'oiseaux dont la coloration du plumage et les stratégies migratoires saisonnières varient considérablement.

Pour cela, nous avons utilisé des données bibliographiques et des images numériques pour évaluer deux caractéristiques de la coloration du plumage : la couleur du manteau et la proportion de noir sur le bout des ailes. Pour chaque espèce et sous-espèce, des données sur la distance de migration et les conditions environnementales rencontrées pendant et en dehors de la période de reproduction ont été collectées.

Nous montrons que ce sont les conditions climatiques rencontrées pendant la période d'hivernage qui expliquent le mieux les variations de coloration. Conformément à nos hypothèses sur le rôle de la coloration dans les processus de thermorégulation et de protection, nous trouvons que la coloration foncée du manteau est positivement corrélée à l'insolation et négativement à la température de l'air. La proportion de noir sur le bout des ailes est plus importante pour les migrateurs à longue distance, qui hivernent dans des conditions d'insolation importantes, que pour les migrateurs à courte distance (ou résidents) qui occupent des régions moins insolées.

Cette étude souligne l'importance de la prise en compte des différentes périodes du cycle annuel pour étudier les pressions de sélection subies par les animaux migrateurs et pour comprendre les variations globales de phénotype chez les oiseaux.

[Biogéographie, coloration, règle de Bogert, règle de Gloger, distance de migration, photo-protection, thermorégulation]

Note sur la participation : Ce travail est le résultat d'études préliminaires réalisées par Julia Guerra Carande que j'ai encadré pour son stage de Master 1 au LECA. Cette étude était pour mon travail de thèse une excellente opportunité de démontrer l'importance de considérer les pressions de sélection qui interviennent en dehors de la période de reproduction lorsqu'on étudie les oiseaux migrateurs, et de surcroît les migrateurs à longue distance. Le choix du modèle d'étude s'est fait au cours d'une discussion avec Pierre-André Crochet qui avait lui-même discuter de cette question de la coloration des goélands et des mouettes il y a plus de 20 ans sur Götland (Suède) avec l'ornithologue et artiste peintre Lars Jonsson.

Plumage colouration in gulls responds to their non-breeding climatic niche

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Abstract

Aim: Global variation in animal colouration has inspired ecogeographical rules that suggest common patterns of recurrent adaptations to climate. However, little attention has been paid to the relative influence of the different climatic conditions encountered by species during their annual life cycle. We explored this question by testing whether breeding or non-breeding climatic conditions most influence plumage colouration in gulls, a cosmopolitan group of birds with extensive variation in plumage darkness and seasonal migratory strategies.

Location: Global.

Time period: Contemporary.

Major taxa studied: All species and subspecies of gulls (Aves, Laridae).

Methods: We used literature data and digital images to assess two characteristics of plumage colouration in all 80 species and subspecies of gulls: the darkness of the mantle and the proportion of black on wingtips. For each species and subspecies, we collected data on migration distance and environmental variables across its breeding and non-breeding range for both breeding and non-breeding seasons. We performed a phylogenetic comparative analysis to quantify the relative influence of climatic conditions experienced during the breeding and non-breeding season on plumage colouration.

Results: The climatic conditions encountered during the non-breeding season explained interspecific variation in colouration better than the climate experienced during the breeding season. In accordance with hypotheses on the role of dark colouration in thermoregulation and feather protection, darker mantle colouration was positively correlated with insolation and negatively with air temperature. The proportion of black on wingtips was greater for long distance migrants wintering under insulated conditions than short distance migrants or residents occupying less insulated regions.

Main conclusions: In gulls, plumage colouration is predominantly shaped by selection experienced outside the breeding period, in accordance with the hypothesized photoprotective and thermoregulatory functions of avian plumage. This highlights the importance of taking into account seasonality and migration to understand global spatial patterns of avian colouration.

KEYWORDS

biogeography, bird colouration, Bogert's rule, Gloger's rule, migration distance, photoprotection, thermoregulation

1 | INTRODUCTION

Understanding the diversity and spatial distribution of animal colouration is a long-lasting puzzle in ecology and biogeography (Hill & McGraw, 2006; Lomolino, Riddle, & Brown, 2006). Large-scale variations in colouration have long been studied by evolutionary biologists and formalized as sometimes contradictory ecogeographical rules (Gaston, Chown, & Evans, 2008). For example, Gloger's rule, one of the most studied rule in colour research (Delhey, 2019; Gloger, 1833; Rensch, 1929), predicts that animals should be darker in warm and humid areas compared to colder and drier ones (Delhey, 2019; Rensch, 1929). Gloger's rule is supported by evidence from different groups of animals (e.g., Delhey, 2018; Lai, Shiroishi, Moriwaki, Motokawa, & Yu, 2008; Miller, Leighton, Freeman, Lees, & Ligon, 2019; but see Delhey, 2019) but is not fully understood yet. As recently reviewed by Delhey (2019), the proposed mechanisms explaining Gloger's rule are varied, 'including camouflage, protection against parasites, protection against solar radiation, or pleiotropic effects'. Moreover, several opposite results (i.e., darker animals found in colder regions) have recently emerged, mostly based on comparative analyses conducted on large bird families (Delhey, Dale, Valcu, & Kempaers, 2019; Friedman & Remeš, 2017). These results are consistent with another ecogeographical rule, known as the thermal melanism hypothesis (also called Bogert's rule; Bogert, 1949), which stipulates that darker animals should be more frequent in colder regions because dark colouration absorbs more solar radiation (i.e., thermoregulatory function; Clusella Trullas, van Wyk, & Spotila, 2007; Gaston et al., 2008). Although neither Gloger's nor Bogert's rule alone offers a comprehensive explanation for the global distribution of animal colouration, it is now well established that variations of colouration are partly determined by climatic conditions.

In birds, numerous studies support the effects of climate on the evolution of plumage colouration, both at the species level (e.g., Roulin, Wink, & Salamin, 2009) and above the species level (e.g., Delhey et al., 2019). However, a comprehensive understanding of how bird colouration responds to climate remains challenging because plumage has several functions and thus experiences multiple and sometimes conflicting selective forces (Cuthill et al., 2017). Plumage colouration can be selected for social signalling (e.g., intra-specific communication, sexual attractiveness; Cuthill et al., 2017; Hill & McGraw, 2006), camouflage against predators or prey (e.g., Roulin, 2004; Zink & Remsen, 1986) or protection against parasites (Burt & Ichida, 2004; Delhey, 2019). Body colouration can also influence thermoregulation, with dark species living in cold environments being able to heat up more easily compared to light species (see Delhey, 2018; Galván, Rodríguez-Martínez, & Carrascal, 2018). Likewise, since ultraviolet (UV) radiation breaks down the molecular

structure of feather keratin, dark pigments provide photoprotection against UV radiation, thereby increasing feather resistance for species living in geographical areas with high levels of insolation (e.g., Bonser, 1995). However, dark pigments may also prevent birds from colonizing hot environments (Delhey, 2018; Friedman & Remeš, 2017; Galván et al., 2018).

An additional complication to studying the link between bird colouration and climate is that the relative importance of these functions varies with species annual life cycles and, for species inhabiting seasonal environments, with the seasonal climatic conditions. Indeed, birds may encounter different environmental conditions (i.e., seasonality) between breeding and non-breeding periods (Delhey, 2018). Non-migratory birds living in a seasonal environment experience varied climatic conditions, while migratory species may winter under climatic conditions either similar (the so called 'niche tracking behaviour'), or different ('niche switching behaviour') from those of their breeding range (see Dufour et al., 2020). Understanding which function(s) and selective pressure(s) dominate during a given period is thus even more complex for those migratory birds that travel long distance and visit multiple regions during their seasonal cycle. In summary, the selective pressures influencing plumage colouration are complex and vary throughout the annual cycle. Some bird species respond to this variation by changing plumage colouration during their annual cycles while others retain largely identical colouration all year round. For the latter species, plumage colouration may thus result from the action of multiple selective pressures acting during different periods of their annual cycle.

Understanding how the multiple functions of bird colouration combine and vary with seasonal climatic conditions remains largely unexplored. To our knowledge, all previous studies of bird colouration have explained the distribution of different colours based on the environmental conditions encountered in breeding ranges, either all year round (e.g., Delhey et al., 2019) or during the breeding period only (Galván et al., 2018). The first option would be reasonable for sedentary species that do not change plumage over the year and the second one would be appropriate for species exhibiting a seasonal colour change (see McQueen et al., 2019). However, for species that do not exhibit seasonal colour change, considering the conditions encountered only during the breeding period (for sedentary species) or only in breeding areas (for migratory species) will likely lead to overlooking some selective pressures that can be exerted on plumage colour.

Gulls (members of the family Laridae) are a large clade of birds that includes approximately 52 extant species, distributed throughout the world from the Arctic to the Antarctic, and living in open habitats always close to water bodies, whether seaside or inland (Burger, Gochfeld, & Bonan, 2019). Gulls also show a large variation in migration strategies: while some species are long-distance migrants (e.g.,

Stenhouse, Egevang, & Phillips, 2012), others occupy either high latitudes or tropical latitudes all year round (e.g., Burger, Gochfeld, Kirwan, & Garcia, 2019; Gilg et al., 2010). Gulls generally have very different plumages between the first age class and adulthood. At adulthood, their plumage remains mostly similar all year round except for head colouration, with many species developing a dark hood in breeding plumage while others acquire a variable amount of head streaking in non-breeding plumage (Minias & Janiszewski, 2020, see also Howell & Dunn, 2007; Olsen, 2018 and the Discussion section). Most gulls have reasonably similar adult plumage that mostly differs by the grey shade of the upperparts (mantle colour hereafter, ranging from white to almost black) and the proportion of black on wingtips (from no black to a complete black outer wing; Olsen, 2018) while the underparts are white in most species. In the specialized gull literature (e.g., Olsen, 2018), 'mantle colour' refers to the colour of most upperparts such as the mantle, secondaries, tertials, scapulars and wing coverts, which all have the same colour in most gull species (with a few exceptions such as *Xema sabini*). Thus, the variation in mantle colour and the proportion of black on wingtips together capture most of the variation in upperpart colouration in gulls, while underparts are white in most species (see Figure 1).

The absence of sexual dichromatism and seasonal variation of these characteristics suggests that the mantle colour and proportion of black on wingtips are not under sexual selection (Skékely, Freckleton, & Reynolds, 2004). Their predominantly top-predator position in trophic networks suggests that the back colouration of adults does not experience selective pressures to escape predators as in many other bird species. Moreover, it is assumed that the mantle colour might have a thermoregulatory function as well as a protective role against solar radiation (see Bonser, 1995; Galván et al., 2018; Lustick, Battersby, & Kelty, 1978). While the study of Gay et al. (2009) suggested that the mantle colour of some gull taxa

(*Larus occidentalis* and *Larus cachinnans*) may follow Gloger's rule at the intraspecific level, another study by Bergman (1982) further suggested that a large proportion of black on the outer wing in *Larus fuscus fuscus* (compared to closely related species) is an adaptation to overwinter in sunny, tropical climates and to migrating over long-distance. Feathers with melanin have a thicker keratin layer compared to non-melanin feathers, which confers resistance to both UV radiation and mechanical abrasion (see Bonser, 1995; Borgudd, 2003; Voitkevitch, 1966). The marked variation of grey shades, in proportion of black on wingtips and in migration strategies, combined with the limited number of functions of plumage colouration in gulls thus provide a good opportunity to address the influence of climate on animal colouration in seasonal environments.

In this study, we use gulls to investigate how the different climatic conditions encountered in the breeding and non-breeding parts of the annual cycle influence the variation of avian plumage colouration. Intraspecific variation in gulls is sometimes strongly marked, so we aimed at taking into account all observed variability by collecting colour data in all species and subspecies, representing 80 taxa in total. We quantified the migratory behaviour of each taxon (subspecies or monotypic species), using maps of their breeding and non-breeding ranges, along with georeferenced environmental variables to describe climatic conditions experienced during their breeding and non-breeding periods. In order to reduce the number of models and explanatory variables, we tested biologically meaningful hypotheses on the basis of existing literature. If mantle colour has thermoregulation and/or photoprotective functions, we expected a link between mantle colouration and temperature and insolation. If black pigment on primaries increases their resistance, we expect a link between the amount of black on wingtips and migration distance and insolation encountered throughout the seasonal cycle. We used phylogenetic comparative analyses to test whether breeding or non-breeding climatic conditions best explain the variation of these two colour traits.



FIGURE 1 Lesser black-backed gull (*Larus fuscus graelsii*) in flight. Most of the upperparts (mantle, secondaries, tertials, scapulars and wing coverts) have the same grey colour, defined as *mantle colour* in this study. The yellow polygon delineates the outer wing area (the 10 primary feathers, greater and lesser primary coverts and alula) considered to measure the proportion of black on wingtip. Photo Daniele Occhiato

2 | MATERIALS AND METHODS

2.1 | Species data

We broadly adopted the taxonomy of BirdLife International and the Handbook of the Birds of the World (HBW; del Hoyo & Collar, 2014) where gulls are treated as the subfamily Larinae. We included all species and subspecies recognized by del Hoyo and Collar (2014) but made a few taxonomic modifications (see below). This represents 80 subspecies belonging to 52 species from the genera *Creagrus*, *Rhodostethia*, *Pagophila*, *Xema*, *Rissa*, *Hydrocoleus*, *Saundersilarus* and *Larus*. Distribution data were collected from BirdLife International and HBW (2018) and gridded at a 10-min resolution. Such a high spatial resolution was necessary to analyse the distribution of taxa with narrow and fragmented breeding ranges, such as many insular species. For species having two or more subspecies, we built distribution maps of each subspecies by cropping the original species map, following

the textual information on subspecies distribution provided by Olsen (2018) and del Hoyo, Elliott, Sargatal, Christie, and de Juana (2019). We thus produced a total of 80 different rasters (see Supporting Information Appendix S4) depicting for each taxon its breeding distribution (either the breeding area for migratory species or the residence area for non-migratory species) and its wintering distribution (either non-breeding or resident area). Each taxon was categorized according to its migration strategy as *strict migrant*, *partial migrant* or *resident* (Rappole, 2013) based on information provided by reference handbooks (del Hoyo et al., 2019). For each migratory taxon (*strict* and *partial migrant*), we estimated the median migration distance by randomly selecting 5,000 points within the breeding distribution and 5,000 points within the wintering range, calculating the distance between every possible pair of breeding and wintering points and retaining the median value of these 25×10^6 distances. We applied the same method to non-migratory taxa (*resident*) with the goal to quantify potential movements within their residence area. Indeed, even if they do not migrate from one location to another, gulls often exhibit large dispersal movements throughout their range during the non-breeding season (Burger et al., 2019), and we assumed that such movements could have consequences on the abrasion of flight feathers and therefore on the proportion of black on wingtips (see Bergman, 1982). Our method thus implies a positive relationship between range size and seasonal movements for these taxa, which remains to be tested. However, we think that this approach is more realistic than considering no movement at all for sedentary taxa.

Phylogenetic relationships of gulls have been the subject of much debate (e.g., Liebers, De Knijff, & Helbig, 2004). Today, there is still no consensus about relationships between 'large gull' species, mainly because of recurrent hybridizations between taxa of very recent origin (e.g., Pons, Sonsthagen, Dove, & Crochet, 2014; Sonsthagen et al., 2016). We downloaded from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) a sample of 500 phylogenetic trees with the Hackett backbone including 51 out of our 52 recognized species. Missing species and subspecies were added according to recent taxonomic studies (e.g., Liebers & Helbig, 2002; Pons, Hassanin, & Crochet, 2005; Sternkopf, 2010; Sonsthagen et al., 2016). For every topology, we added subspecies to species terminal branches as unresolved polytomies. To assign branch length for subspecies, we extracted for each topology the terminal edge lengths of all tips and the minimal value of the most recent divergence episode (mean across topologies: 55,000 years). We used half of this value as terminal branch length for adding genetically differentiated subspecies on each topology. For other subspecies, the divergence time between subspecies was set to 10,000 years (which roughly corresponds to the end of the Last Glacial Maximum episode; Clark et al., 2009). Topologies that did not support our infra-specific relationships (i.e., branch lengths too short) were discarded (6%). Hence, we eventually considered 470 different tree topologies in our analyses. A detailed description of methods can be found in Supporting Information Appendix S2. All steps were performed with the R packages *ape* (Paradis & Schliep, 2018; R Core Team, 2019) and *phytools* (Revell, 2012). A maximum clade credibility (MCC) tree

was also computed from all topologies with the *phangorn* package (Schliep, 2011; see Figure 2a).

2.2 | Plumage colour scoring

In this study, we focused on the colouration of adult birds. Immature plumage takes between 3 and 5 years to gradually transform into adult plumage, and is highly variable between individuals within species (Olsen, 2018). Moreover, for a given species immatures can have different dispersal and migratory strategies. For these reasons, we did not address the case of immature plumage in this study (but see the Discussion section dedicated to this issue). To characterize the shade of mantle colouration in adult gulls, the standard procedure compares the mantle with the Kodak grey scale Color Separation Guide (see Olsen, 2018). This scale contains 20 equal divisions, from 0 (pure white) to 19 (total black), made for adjusting grey tones in analogical photography. Kodak 3–5 is pale grey, 6–8 medium grey, 9–11 pale slaty-grey, 12–14 dark slaty grey and 15–17 slaty black. For each taxon, we collected the range of grey values from Howell and Dunn (2007) and Olsen (2018) and retained the mean value (called KGS hereafter; Figure 2b). When some subspecies did not exhibit variation in mantle colouration according to the literature, we kept the value of the nominal subspecies. We did not find published KGS values for *Larus novaehollandiae* and its two subspecies. For these taxa, we estimated the KGS values from HBW illustrations (del Hoyo et al., 2019). To do so, we first measured the modal luminance level in HBW illustrations, for the mantle of 20 taxa with known KGS value, using IMAGEJ software (Schneider, Rasband, & Eliceiri, 2012; using the mean luminance level yielded similar results). We then optimized a linear regression model between the known mean KGS values and the modal luminance levels ($R^2 = .87$), and used this model to predict KGS from the luminance level measured on illustrations of missing taxa (see details in Supporting Information Appendix S3).

The proportion of black on wingtips (PB hereafter) was measured from digital pictures of adult birds. For each taxon, we analysed between 2 and 5 photographs (mean = 4.6) of different individuals retrieved from the internet (all identifications were validated by ourselves; see the Table S1 in Supplementary Material with links to all retrieved photographs) and from our own picture collections. Photographs were selected to show birds in flight with one wing held flat and perpendicular to the camera (see Figure 1). Moreover, we included only pictures of birds without missing or moulting feathers. We used the GIMP software (gimp 2.10.12, The GIMP Development Team, 2019) to calculate the area (in pixels) of the outer wing (i.e., the hand, including the 10 primary feathers, greater and lesser primary coverts and the alula), and then the area of black pixels within the outer wing after thresholding the image to 25% luminance. PB was eventually calculated as the average, over all photographs of a given taxon, of the ratios of these two areas (i.e., black area/wing area); PB thus varies between 0 and 1 (Figure 2b). The only two taxa with grey wingtips were omitted from the analysis. Indeed, the grey colour is also produced by melanins and it is thus possible that the

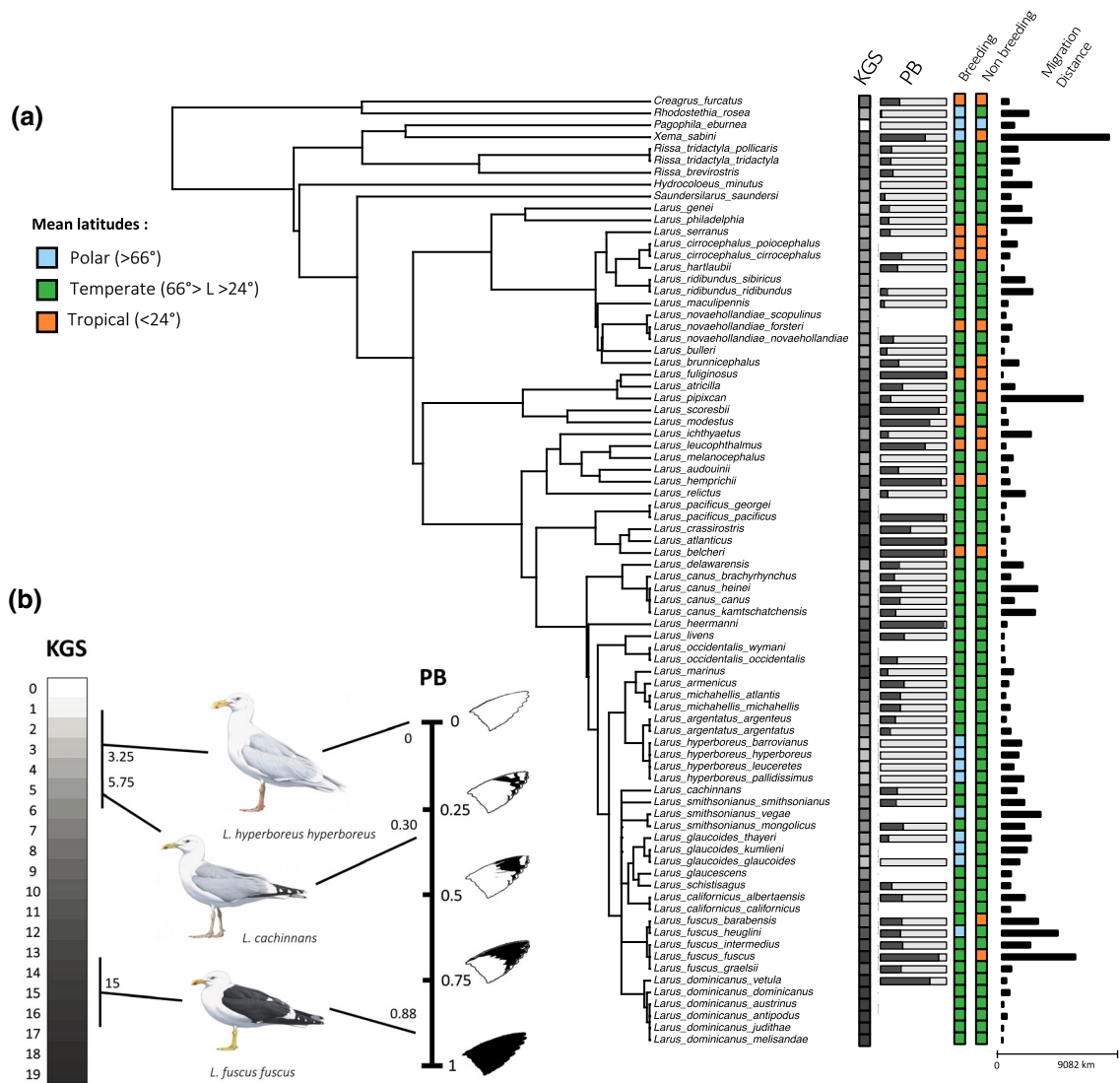


FIGURE 2 (a) The maximum clade credibility tree of gull taxa and their plumage colour (KGS = mantle colour; PB = proportion of black on wingtips). Rectangles with relative black proportion represent the PB value for each taxon; no rectangle means that the species was omitted for data availability reasons. The mean latitude of breeding and non-breeding regions is represented by a three-class (polar, temperate, tropical) variable. The migration distances between breeding and non-breeding regions are indicated with horizontal bars. (b) Examples of KGS and PB values for three taxa. Illustrations © HBW Alive/Lynx Edicions

keratin feathers of these two taxa (*Larus glaucescens* and *Larus glaucoideus kumlieni*) are more effective at resisting abrasive wear than white keratin feathers (see Bonser, 1995; but also Voitkevitch, 1966). Because of this uncertainty we preferred not to consider them rather than considering they had an entirely white wing tip. Finally, as we could not find appropriate photographs for several of the subspecies, PB was calculated for 65 taxa (82%) out of the 80 species and subspecies (see Figure 2b).

2.3 | Environmental data

Many gull species spend part of their non-reproductive season at sea. For this reason, we analysed climatic variables available for both land and water surfaces. In relation to the possible photo-protective

and UV-resistance function of gull plumage, we extracted an insolation variable defining the solar irradiance energy received on the Earth's surface in W/m^2 (Clouds and the Earth's Radiant Energy system, Nasa Earth Observations; <https://neo.sci.gsfc.nasa.gov/>). Monthly averaged measurements were downloaded for the entire period of available data (from 2006 to 2018). As we hypothesized a thermoregulation function of mantle colouration, we also considered a temperature variable by combining air and sea temperatures into a single variable describing the ocean and terrestrial monthly average temperature. Monthly averages of mean air temperature (from 1960 to 1990) were extracted from the WorldClim database (Hijmans et al., 2005) and monthly averages of mean sea surface temperature (from 1971 to 2000) were provided by the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Division (<http://www.esrl.noaa.gov/psd/>). We checked the correlation

TABLE 1 Average values of generalized least square phylogenetic models applied to all topologies of phylogenetic trees. For each plumage variable [a: colour of the mantle (KGS); b: proportion of black on wingtips (PB)], models were performed with climatic conditions encountered either during the breeding or non-breeding period. Lambda values (Pagel, 1999) indicate the phylogenetic correlation parameter.

	Model	AIC	Variable	Estimate	SE	t-value	p-value	Lambda
(a)	KGS	383.2	Intercept	6.90	4.83	1.43	.157	.98
	Breeding		Insolation	-3.08	1.23	-2.50	.015	
			Temperature	-1.83	1.50	-1.22	.225	
	Non-breeding		Insolation	9.54	1.56	6.11	< .001	
			Temperature	-5.61	1.64	-3.42	< .001	
(b)	PB	-9.93	Intercept	0.07	0.19	0.37	.710	.85
	Non-breeding		Migration	0.05	0.52	0.10	.920	
			Insolation	0.47	0.17	2.72	.009	
			Migr. × Insol.	1.05	0.58	1.83	.072	
	Breeding		Insolation	0.37	0.16	2.32	.024	
			Migr. × Insol.	-4.39	1.08	-4.05	< .001	

AIC = Akaike's information criterion.

between air temperature and sea surface temperature in grid cells of coastal areas, where both variables were available (see Supporting Information Appendix S1, Figure S1). These climatic variables were also gridded at 10-min resolution to match distribution data.

We considered December, January and February as the winter period and June, July and August as the summer period, and assumed that these are the main breeding and non-breeding seasons for the focal species in the Northern Hemisphere (reversed for species breeding in the Southern Hemisphere). The remaining months were considered migration periods; environmental data for these months were not used in our analyses. Environmental variables were calculated for both boreal and austral locations, and for winter and summer periods. We made the assumption to assign northern summer to all breeding ranges above the equator (and vice versa for the Southern Hemisphere). Overall, we analysed five environmental variables: mean insolation during breeding (INSOL breeding) and non-breeding (INSOL non.breeding) periods, mean temperature during breeding (TMEAN breeding) and non-breeding (TMEAN non.breeding) periods, and mean migration distance (DIST migration).

In order to test all possible climatic effects of Gloger's rule as defined by Rensch (1929) (i.e., precipitation and temperature), we conducted a separate analysis to test the influence on KGS and PB of precipitation conditions encountered during either the breeding or non-breeding period on all species. Because these data are available only for the terrestrial and coastal regions (Karger et al., 2017; <http://chelsa-climate.org/>), not for marine regions, we considered only the terrestrial and coastal occurrence of the species.

2.4 | Statistical analysis

With the R package *phylolm* (Tung Ho & Ane, 2014) we fitted phylogenetic generalized least squares (PGLS) models to test how our

environmental explanatory variables correlate with the two colour variables (KGS and PB), while controlling for phylogenetic relatedness with the Pagel's lambda (Pagel, 1999). All variables were centred and scaled prior to analyses to facilitate interpretation (effect sizes were obtained from regression coefficients of the model; Schielzeth, 2010) and correlations between climate variables were examined to highlight potential collinearity effects (Supporting Information Appendix S1, Figure S2). We tested the importance of interaction effects between variables and removed them when not significant. All analyses were carried out on the MCC tree and on the 470 tree topologies in order to account for phylogenetic uncertainty.

To understand whether the geographical distribution of colouration in gulls is influenced by the seasonality of environmental conditions, for each colour metric we performed models that considered climatic conditions encountered during the breeding period and the non-breeding period for each colour index. For models with mantle colouration (KGS) as the response variable, we included temperature and insolation of breeding and non-breeding periods as explanatory variables: we expected that a thermoregulatory function of KGS would lead to a negative correlation between KGS and temperature while a photoprotective function of KGS would generate a positive correlation between KGS and insolation. For models with the amount of black on wingtips (BP) as the response variable, we included the migration distance and the insolation in both periods as explanatory variables. This allowed us to test the hypothesis that the proportion of black on wingtips increases feather resistance in taxa experiencing high solar radiation in winter regions and/or travelling over long distances.

Finally, in order to test the importance of considering intraspecific variation of subspecies, we replicated all analyses at the species level (52 species) by averaging subspecies values for the plumage and climatic variables. We conducted these analyses on the MCC tree pruned to match the species list using the *ape* package (Paradis & Schliep, 2018).

3 | RESULTS

The mantle colour of gulls (KGS) ranged from 0 (white, *Pagophila eburnea*) to 19 (black, *Larus atlanticus*, *Larus pacificus pacificus*) with a mean of 7.35 and standard deviation (SD) of 3.54. The proportion of black on wingtips (PB) ranged from 0 (8 taxa, see Supporting Information Figure S3) to 1 (*Larus fuliginosus*) with a mean of .32 and SD of .29. The within-taxon SD of PB ranged from 0 to .25 with a mean of .03 (for KGS the literature we used only reported range and not variance so we cannot compute a within-taxon SD for KGS).

We found that variations of mantle colour and wingtip pattern across taxa responded to climatic conditions of both breeding and non-breeding seasons but that conditions experienced during the non-breeding season had a stronger effect than the conditions of the breeding season (Table 1). For mantle colour (KGS), climatic variables of the non-breeding period had lower *p*-values and bigger effect sizes than for the breeding period (Table 1). For black proportion on wingtips (PB), the differences between breeding and non-breeding climatic conditions were weaker, but again with a lower *p*-value consistently observed for climatic variables encountered during the non-breeding period (alone or in interaction with migration distance; Table 1).

Comparative models indicate a strong phylogenetic signal for both KGS and PB (Table 1), indicating that at the scale of our analysis gull colouration is strongly determined by shared ancestry. Nevertheless, we found consistent results between the different tree topologies investigated (Supporting Information Table S2), which suggests that phylogenetic uncertainty does not impact our results. Last, replicating our analyses at the species level yielded qualitatively similar results (see Table S1 in Supporting Information Appendix S1), yet with lower phylogenetic signal. This result indicates that the high phylogenetic signal most likely results from closely related subspecies having similar plumage characteristics.

We found a positive effect of insolation during the non-breeding period on KGS, meaning that darker-mantle taxa (KGS > 10) predominantly winter in more highly insolated areas compared to

lighter-mantle taxa (KGS 4–7, Figures 3 and 4a). By contrast, we found a negative effect of non-breeding range temperature on mantle colour, with darker-mantle taxa wintering in colder areas than lighter-mantle taxa (those varying between KGS 4–7), even when controlling for insolation.

The interaction between insolation and migration distance was the most influential factor explaining interspecific variation in PB (Table 1), yet with opposite effects between breeding and non-breeding seasons. A positive effect for non-breeding conditions indicates that the higher the insolation, the greater the effect of migration distance on PB (Figure 4b). This suggests that PB increases for taxa that travel long distances and experience more highly insolated conditions during the non-breeding period. For climatic conditions of the breeding season, the opposite effect suggests that non (or moderate) migratory taxa that occupy areas with low insolation have less black on wingtips (Figure 4b). We also found that insolation conditions during the non-breeding season are positively correlated with PB but we found no effect of migration distance and insolation conditions during the breeding season alone.

We found no influence of precipitation conditions on mantle colouration (Supporting Information Table S3). However, we found that precipitation conditions encountered outside the breeding season, and in particular the interaction between these conditions and the migration distance, had a positive influence on the distribution of the proportion of black on wingtips (PB; Supporting Information Table S3). This suggests that PB increases for taxa that travel long distances and experience more rainy conditions during the non-breeding period.

4 | DISCUSSION

The study of animal colouration has played a major role in understanding the basic process of natural selection (Kettlewell, 1961) and how multiple and variable selective forces interact to shape

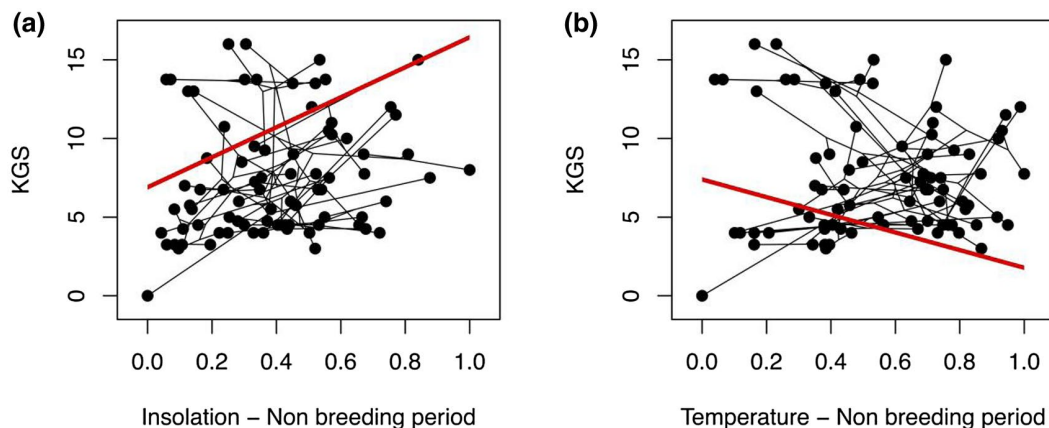


FIGURE 3 Relationship between mantle colour (KGS) and climatic variables (a: insolation; b: temperature) estimated from non-breeding ranges. Thin black lines represent the phylogenetic relatedness between taxa. Thick red lines represent the regression line of phylogenetic generalized least squares (PGLS) models (drawn with the R package *phytools*; Revell, 2012)

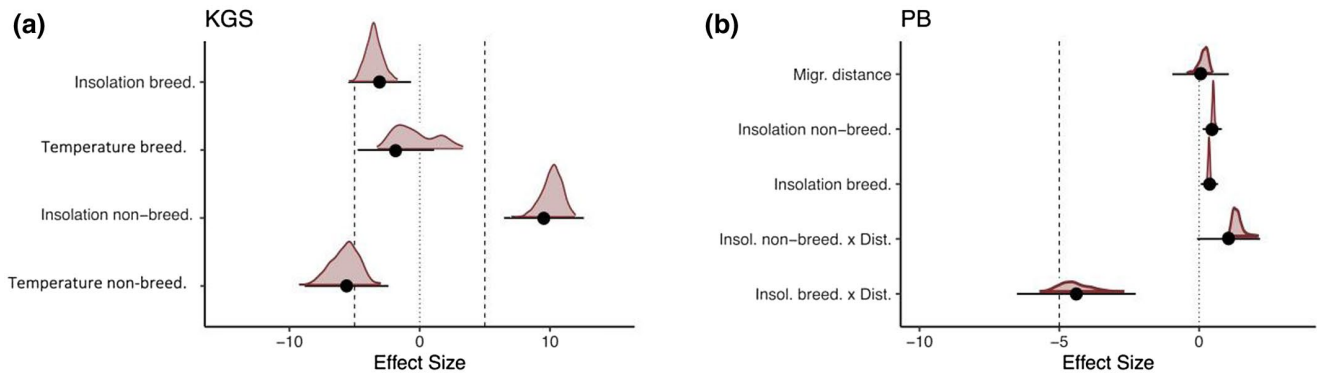


FIGURE 4 Forest plot of effect sizes and their 95% confidence intervals for mantle colour (a: KGS) and black proportion on wingtips (b: BP). Black dots and segments indicate effect sizes and confidence intervals for correlations with climatic variables accounting for the maximum clade credibility (MCC) tree. Red density curves show the distribution of effect sizes over 500 alternative tree topologies

phenotypes (Cuthill et al., 2017). Recently, an extensive research agenda has highlighted the influence of climatic conditions on animal colouration. However, because climatic conditions are determined by several environmental variables (e.g., humidity, temperature, solar radiation) that can interact and vary throughout the life cycle of an animal, the precise role of climate in explaining the evolution and geographical distribution of animal colouration remains unclear. Here, we investigated the effect of seasonality in climatic conditions experienced by populations on the geographical distribution of plumage colouration in gulls. We found that colouration in gulls is more influenced by the environmental conditions encountered during the non-breeding period more than by conditions experienced during the breeding period. This result highlights that accounting for seasonality, whether it is due to moving between different environments or to remaining in a single seasonal environment, is crucial for understanding the biogeographical rules of animal colouration.

4.1 | Darker mantle provides feather protection and thermoregulation

We found that darker mantle colouration is positively correlated with insolation, and negatively with air temperature. The fact that lighter birds tend to inhabit the warmer areas matches the predictions of Bogert's rule (Clusella-Trullas et al., 2007). In contrast, we did not find support for Gloger's rule since we revealed that mantle colour does not seem to be influenced by precipitation conditions. Thus, gulls seem to differ from passerines (Delhey et al., 2019), in which lighter birds also inhabit warm areas (thus following Bogert's rule), but darker species tend to inhabit more humid habitats (thus following Gloger's rule).

Our results also suggest that the grey shade of the mantle plays a role in both thermoregulation and protection against solar radiation. In support of the thermoregulatory function, several dark-mantled taxa occupy high latitudes (polar and north-temperate regions) all year round where temperatures are cold especially outside the breeding period. Although heat transfer through bird plumage is complex,

Walsberg and Wolf (2000) suggested that darker coats (hence those with greater absorptivity) acquire greater heat loads from solar radiation than do lighter plumages. This assumption is mostly based on a study by Lustick et al. (1978), who found that skin temperatures is higher under dark plumage than under white plumage in *Larus argentatus*, which suggests that dark plumage has a higher radiative heat load. In the same study, the authors also showed that gulls orient themselves towards the sun when the solar irradiation becomes too intense, such that only the white surfaces of their bodies are exposed to the sun in order to decrease the absorption of solar radiation. These two results strongly suggest that a large surface of dark plumage facilitates body warming in very cold climates, where day length is generally reduced (see also Clusella Trullas et al., 2007). In support of the photoprotective function of mantle colouration, several dark-mantled taxa occupy strongly insolated environments, especially during the winter period. For example, within the *Larus fuscus* complex the darkest subspecies winter in the most insolated areas even though all subspecies nest at roughly similar latitudes (see Bergmann, 1982). Dark plumages presumably confer protection against solar radiation because melanin pigments increase the resistance of feathers against UV abrasion (Bergman, 1982; Bonser, 1995). Yet several species seem to deviate from the general pattern we described among gull taxa: for example, the all-white *Pagophila eburnea* and taxa of the *Larus glaucoideus* and *Larus hyperboreus* complexes experience cold temperature during the non-breeding period while displaying very light body colouration (see Olsen, 2018). For these species occupying open polar regions, it has been proposed that white feathers would confer a thermal advantage by acting like optical fibres conducting solar energy to the skin (Grojean, Sousa, & Henry, 1980; Reynolds & Lavigne, 1981; but see Zimova et al., 2018).

4.2 | Black on wingtips may provide feather resistance to wear

The proportion of black on wingtips was mostly influenced by the positive interaction between insolation and migration distance, and

by the interaction between the amount of precipitation encountered during the non-breeding season and migration distance. The influence of precipitation should be interpreted with caution, though, because only a fraction of the geographical distribution of species was included in this analysis. Our results however bring much more support to the prediction that birds travelling long distances and overwintering in highly insolated areas have more black on wingtips. In contrast, sedentary species inhabiting areas of low insolation have less black on wingtips. This result is explained by the observation that melanin pigments reduce damage to keratin induced both by UV (Bergmann 1982; Borgudd, 2003) and abrading particles (Bonser, 1995). Species with a high proportion of black are thus more likely to tolerate long migration distances, which may cause mechanical damage, and more likely to spend the winter in highly insolated conditions where UV radiation can also damage their plumage. In addition to their role in photoprotection, thermoregulation, and resistance to abrasion by particles, melanin pigments may also increase the resistance of feathers to bacteria (e.g., Burt & Ichida, 2004; Goldstein et al., 2004), particularly in humid environments where bacteria can have higher keratinolytic capacities than those from arid regions (Burt & Ichida, 2004). It is thus possible that the melanin in the mantle and wingtips also plays this function in gulls, although this prediction requires further analyses.

4.3 | Perspectives on the study of gull colouration

In this study, we have only considered adult plumages because they vary little within taxa and are relatively easy to describe. However, as explained in the Introduction, they are shaped by the interplay of natural and sexual selection. Immature plumages (at least in the first age-classes) are very different from adult plumages and are presumably not influenced by sexual selection, so they could provide an even more direct test of the effects of climate on plumage evolution. Unfortunately, the immature plumages of gulls show complex variations, as all species go through several successive plumages between their juvenile (sporting usually for a very short time) and full adult plumage. Adult plumage is obtained between 2 full years (e.g., *Larus ridibundus*) and 4 years (all large white-headed gulls), making interspecific comparisons even more complicated to design. In addition, the first age-classes (especially juvenile and first-winter plumage) of large white-headed gulls are tricky to characterize as plumage patterns are complex (many feathers have an intricate pattern of dark and pale elements). Furthermore, even within a given age-class immature plumages can change rapidly due to variable timing and extent of moult and to feather wear; as a result the amount of inter-individual variation within taxa is often perplexing. Last, the distribution and migration patterns of immature birds can differ from those of adult birds (e.g., Marques et al., 2009). For all these reasons, investigating the links between abiotic environmental conditions and immature colouration would require a dedicated study, probably requiring more sophisticated methods to quantify plumage darkness.

Since the main aim of our study was to test whether breeding or non-breeding climate contributes most to plumage evolution, we did not include head colouration, which is seasonally variable in most species: dark hoods sported in breeding plumage usually disappear in winter while many species that are white-headed in breeding plumage develop dark streaks in winter. Furthermore, dark hoods are presumably under intense sexual selection as they are lost outside the breeding season and the size influences mate choice (Indykiewicz et al., 2017; Minias & Janiszewski, 2020). In addition, studying head colouration would require a more sophisticated measurement of melanism in order to accommodate the variable patterns of head colouration, from the grey to brown head streaking developed by many large white-headed gulls in winter to the uniform dark hood exhibited by other species in breeding plumage. Indeed, hood presence/absence in breeding plumage only loosely captures the quantitative variation of head colouration among hooded species, which ranges from light grey in *Larus cirrocephalus* to jet black in, for example, *Larus leucophthalmus* (Olsen, 2018). In spite of these limitations, Minias and Janiszewski (2020) found that hood occurrence in gulls was less frequent at higher latitudes. This result is at odds with our findings that melanism tends to decrease at higher latitudes (lighter mantle colour at higher latitude). However, the effect of latitude on melanism in our study was mainly apparent when considering non-breeding climate, whereas hood occurrence is limited to the breeding season. Taken together, these findings reinforce our hypothesis that hood occurrence may be subject to other selection pressures than the colouration of the rest of the plumage. A study of head plumage evolution incorporating age- and season-related variations should thus allow us to better understand the interplay between sexual and natural selection in gull plumage evolution.

4.4 | Conclusion: how ubiquitous is the influence of seasonality on the evolution of avian colouration?

Gulls have several biological traits that are not ubiquitous in birds. Firstly, many species of gulls are migratory but a large majority of bird species are sedentary (Eyres, Böhning-Gaese, & Fritz, 2017). Indeed, several previous studies on avian colouration focused on clades made up mostly of non-migratory species (for example Australian birds that mostly undertake nomadic movements in Dalrymple et al., 2018; Delhey, 2018; Friedman & Remeš, 2017). In addition, gulls exhibit limited seasonal change in colouration while many other birds undergo marked seasonal changes (see Dale, Dey, Delhey, Kempnaers, & Valcu, 2015; McQueen et al., 2019). Finally, gulls occupy open environments and the selective pressures on their plumage are potentially different from those of birds that occupy other environments. For example, we would expect a limited effect of vegetation cover on the colouration of adult gulls whereas vegetation has a major effect on colouration in passerine birds (Delhey et al., 2019). Likewise, it has also been shown in Procellariiformes that the distribution of colouration appears to be related to feeding

ecology and species behaviour at sea (Bretagnolle, 1993) with solitary feeding and 'squid eaters' being large white species, whereas flock-feeding or diving 'fish eaters' tend to have cryptic and darker plumage to escape predation or to benefit from counter shading as an adaptation to fish behaviour.

However, our finding that colouration in gulls is influenced by the climatic conditions experienced during the non-breeding season is likely to extend to many other bird species, even though selection pressures may vary among taxonomic groups (e.g., Friedman & Remeš, 2017). A large proportion of birds perform seasonal movements (see the different types of movements in Eyres et al., 2017; Rappole, 2013) and many migratory birds spend more time on migration and in the non-breeding grounds than on the breeding grounds (see e.g., Jacobsen et al., 2017). For those species that migrate and that do not change plumage between the breeding and non-breeding season, colouration should be influenced by non-breeding as much as, or even more than, breeding climatic conditions. Our results thus highlight the importance of taking into account seasonality and migratory movements to understand global spatial patterns of animal colouration and suggest that the effects of seasonality we uncovered in gulls could also apply to many other animals that perform seasonal movements or experience seasonal changes in their climatic niches.

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DATA AVAILABILITY STATEMENT

Some data are publicly available; bird range maps at www.birdlife.org, environmental data at www.worldclim.org, <http://www.esrl.noaa.gov/psd> and <https://neo.sci.gsfc.nasa.gov/>, and bird phylogenetic data at www.birdtree.org. A table (Table S2) reporting plumage colouration and migration data for each species and subspecies is available in the Supporting Information, as well as a table (Table S1) containing the internet links to access all the photos used in this study.

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BIOSKETCH

Paul Dufour is an experienced field ornithologist with a broad interest in the ecology of birds who currently focuses on the evolution of long-distance avian migration for his PhD. He worked on this project with a MSc student, Julia Guerra Carande, who is interested in the biology of animal colouration. The other co-authors are all interested in evolution and ecology with focuses on the evolution of phenotypes and signals (JPR and PAC) or macro-evolution and global biodiversity patterns (SL and JR).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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Appendix 1 : Supplementary figures and tables

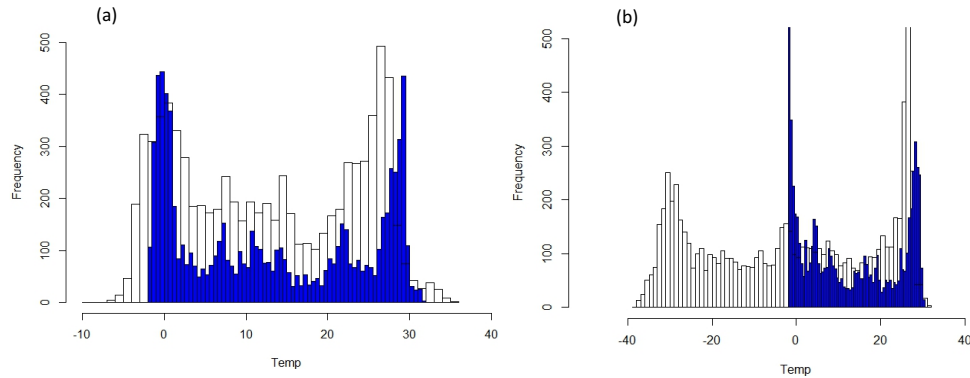


Figure S1. Histograms comparing the mean sea surface temperature and the mean air temperature in coastal grid cells at the global scale between May and August (a) and between November and February (b). (a) Temporal variations in average sea surface temperature (blue) match those of mean air temperatures (white) in coastal cells between May and August. (b) Comparison of the average sea surface temperatures (blue) and mean air temperatures (white) in coastal cells from November to February. The minimum sea surface temperature is -1.8°C , the freezing temperature of oceanic waters. The air temperature gets much colder.

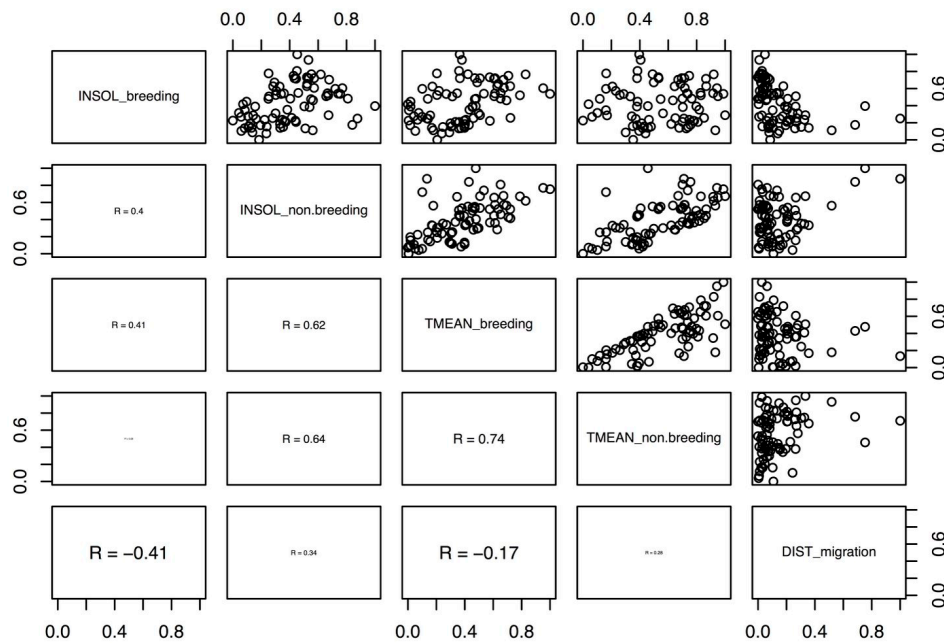


Figure S2. Scatterplot matrix of the environmental variables within the phylogenetic generalized least square models (upper right panel) with Pearson correlation coefficient between the variables (lower left panel). The size of the characters are proportional to the value of correlation coefficients.

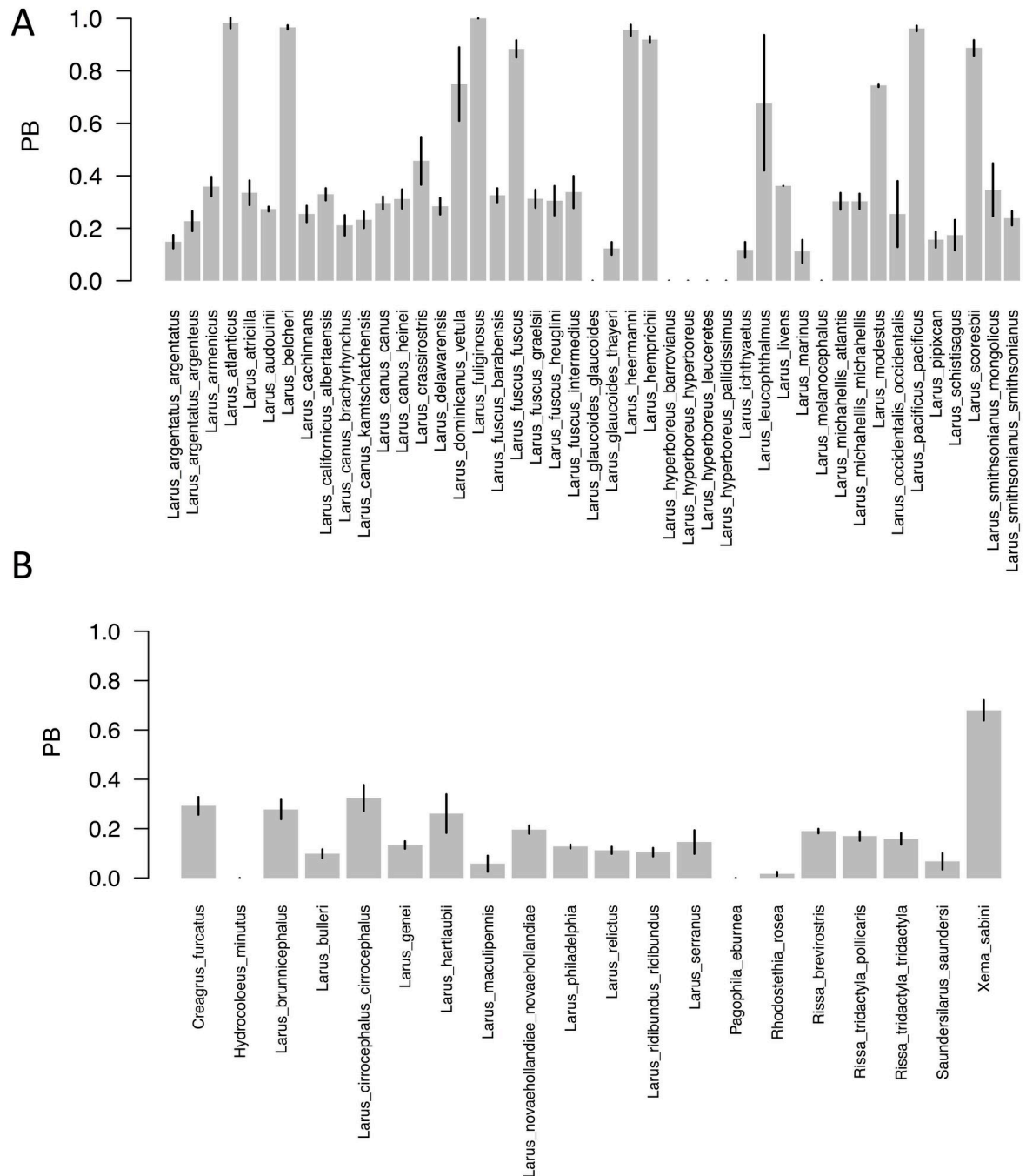


Figure S3.

Proportion of black on wingtips (PB) for each taxon (A: Larines, B: Sternines; see Chu 1998). Values are averaged over different photographs; vertical black lines represent the standard deviation.

	Model	AIC	Variable	Estimate	SE	t-value	p-value	Pagel's λ
a)	KGS	275,3	Intercept	5,90	2,12	2,79	0,008	0,607
			Breeding	Insolation	-0,71	2,39	-0,30	
			Temperature	5,91	3,55	1,67	0,103	
	Non-breeding		Insolation	5,71	3,00	1,90	0,063	
			Temperature	-7,81	3,26	-2,39	0,021	
b)	PB	7,612	Intercept	0,08	0,21	0,41	0,682	0,736
				Migration	0,29	0,86	0,34	
	Non-breeding		Insolation	0,48	0,22	2,23	0,161	
			Migr. x Insol.	1,20	0,84	1,43	0,031	
	Breeding		Insolation	0,38	0,21	1,86	0,069	
			Migr. x Insol.	-5,85	1,70	-3,43	0,001	

Table S1. Results of the phylogenetic generalized least square models applied to the maximum clade credibility tree pruned to the 52 recognized species. For each plumage variable (a: colour of the mantle/KGS; b: proportion of black to wing-tips/PB), models were performed with climatic conditions encountered during the breeding and non-breeding periods. Lambda values (Pagel, 1999) indicate the phylogenetic correlation parameter.

	Model	AIC	Variable	Estimate	SE	p-value	Pagel's λ
a)	KGS	389.4/388.4	Intercept	7.16/7.11	3.98/3.90	0.079/0.074	0.987/0.985
			Insolation	-3.61/-3.73	1.34/1.32	0.017/0.013	
			Temperature	0.42/0.15	1.63/1.59	0.505/0.481	
			Insolation	9.38/9.25	1.78/1.75	< 0.001	
			Temperature	-6.82/-6.99	1.73/1.71	< 0.001	
b)	PB	-11.50/-11.94	Intercept	0.07/0.07	0.19/0.18	0.729/0.720	0.879/0.869
			Migration	0.03/0.01	0.49/0.48	0.858/0.836	
			Insolation	0.43/0.42	0.17/0.16	0.018/0.016	
			Migr. x Insol.	1.14/1.11	0.55/0.54	0.050/0.041	
			Insolation	0.41/0.40	0.16/0.15	0.014/0.013	
			Migr. x Insol.	-4.26/-4.31	1.04/1.03	0.001/0.001	

Table S2. The 95% confidence interval of parameters estimated by phylogenetic generalized least square models applied to all alternative topologies of the gull phylogeny. For each plumage variable (a: colour of the mantle/KGS; b: proportion of black to wing-tips/PB), models were performed with climatic conditions encountered during the breeding and non-breeding period. Lambda values (Pagel, 1999) indicate the phylogenetic correlation parameter.

Table S3. Average values of generalized least square phylogenetic models applied to all topologies of phylogenetic trees. For each plumage variable (a: colour of the mantle/KGS; b: proportion of black to wing-tips/PB), models were performed with precipitations conditions encountered either during the breeding or non-breeding period. Lambda values (Pagel, 1999) indicate the phylogenetic correlation parameter.

	Model	AIC	Variable	Estimate	SE	t-value	p-value	lambda
a)	KGS	385.6	Intercept	5,91	4,31	1,37	0,175	0.97
	<i>Breeding</i>		Precipitation	0,20	1,20	0,17	0,867	
	<i>Non-breeding</i>		Precipitation	-0,51	1,02	-0,50	0,617	
b)	PB	16.57	Intercept	0,35	0,40	0,89	0,379	0.98
			Migration	-1,15	0,42	-2,76	0,008	
	<i>Non-breeding</i>		Precipitation	-0,53	0,15	-3,68	0,001	
			Migr. x Precip.	3,43	0,72	4,77	<0,001	
	<i>Breeding</i>		Precipitation	-0,09	0,16	-0,55	0,588	
			Migr. x Precip.	1,30	1,16	1,11	0,270	

Appendix 2: Phylogenetic framework

A sample of 500 phylogenetic trees with Hackett backbone, containing 51 species out of the 52 species we recognize (*Larus smithsonianus* is not recognized by HBW/Birdlife), was downloaded from birdtree.org (Jetz *et al.*, 2012). The names of tip labels that did not correspond to our reference taxonomy were firstly corrected (e. g. *Larus minutus* becomes *Hydrocoleus minutus*). Then, for each tree of this distribution, we have added the missing species and subspecies based on recent taxonomic studies and following the same scheme as explained below. All steps were performed with functions of the R packages *ape* (version 5.3; Paradis & Schliep, 2018) and *phytools* (Version 0.6-99; Revell, 2012).

For every topologies, we added subspecies to species terminal branches as unresolved polytomies. To provide a branch length for subspecies, we extracted for each topology the terminal edge lengths of all tips and the minimal value of the most recent divergence episode (mean across topologies: 55,000 years). We used half of this value as terminal branch length for adding genetically differentiated subspecies on each topology. For other subspecies, the divergence time between subspecies was set at 10,000 years ago (which roughly corresponds to the last glacial maximum episode; Clark *et al.*, 2009; “DT” hereafter).

1) Simple cases

For species with no information on the divergence time between subspecies, or for which subspecies are known to be genetically close, we linked non-nominal subspecies to the nominal subspecies with a short divergence time. This divergence time was set to 10 000 years, which corresponds to the last episode of gladiation period (Clark *et al.* 2009). This concerned:

Larus argentatus argenteus & *Larus argentatus argentatus*
Larus californicus albertaensis & *Larus californicus californicus*
Larus pacificus georgei & *Larus pacificus pacificus*
Larus occidentalis wymani & *Larus occidentalis occidentalis*
Larus glaucoides kumlieni & *Larus glaucoides glaucoides*
Larus michahellis michahellis & *Larus michahellis atlantis*
Larus ridibundus sibiricus & *Larus ridibundus ridibundus*
Larus cirrocephalus poiocephalus & *Larus cirrocephalus cirrocephalus*
Rissa tridactyla pollicaris & *Rissa tridactyla tridactyla*

2) Complex cases

a- *Larus hyperboreus ssp.*

No study has so far been able to unambiguously decipher relationships between the four recognized subspecies of *Larus hyperboreus* (*hyperboreus*, *pallidissimus*, *leucerestes*, *barrovianus*). Sonsthagen and her colleagues (2016) suggested recurrent episodes of hybridization at least with *L. argentatus* in Europe, and with *L. smithsonianus* and *glaucoides* in North America. We thus decided to add these subspecies as polytomies crafted around the nominate subspecies, and considered the same time of divergence as in case 1).

b- *Larus canus ssp.*

Sternkopf (2011) suggested that the subspecies *brachyrhynchus* (North-America) is genetically distinct from the three other Eurasian subspecies of *L. canus* (*canus*, *heinei*, *kamtschatchensis*). We thus considered a DT value between *brachyrhynchus* and other subspecies, whereas other

subspecies have been added as in case 1.

c- *Larus novaehollandiae* ssp.

Subspecies *novaehollandiae* and *forsteri* have been treated as in case 1 whereas the subspecies *scopulinus* (sometimes treated as a separate species; see Given et al., 2005) was considered to have diverged from this group DT year ago.

d- *Larus fuscus* ssp.

Our reference taxonomy (BirdLife & HBW taxonomy; del Hoyo & Collar, 2014) considers five subspecies in the *L. fuscus* complex : *fuscus*, *graellsii*, *intermedius*, *heuglini* and *barabensis*. Liebers & Helbig (2002; but also Sternkopf 2011) identified two groups in this complex : a western group containing *graellsii*, *intermedius* and *fuscus* and an eastern group with *heuglini* (and *taimyrensis*). *Barabensis* was also closely related to *heuglini*, explaining why both taxa are sometimes considered conspecifics. With that perspective, we grouped *graellsii*, *fuscus* and *intermedius* together as in case 1), and *heuglini* and *barabensis* were considered conspecifics, and diverging from other subspecies by a DT value.

e- *Larus dominicanus* ssp.

Six subspecies of *Larus dominicanus* are recognized and relationships between five of them (*austrinus*, *antipodus*, *dominicanus*, *vetula*, *judithae*) have been investigated by Sternkopf (2011). Results showed a complex biogeographical story for this species with several episodes of dispersal from the African continent. We therefore chose to treat *austrinus*, *antipodus*, *judithae* and *melissandae* as in 1) (polytomy, 10.000 years of divergence time) with this 4-taxa clade and *vetula* forming a polytomy with *dominicanus* and having diverged from *dominicanus* DT years ago.

Species consideration

Larus (glaucoides) thayeri has long been regarded a full species and was considered as such by Jetz et al. (2012) in their phylogeny. This taxon is now lumped under the *L. glaucoides* complex in our reference taxonomy (BirdLife & HBW; del Hoyo & Collar 2014), nevertheless we decided to keep its position (close to *L. glaucoides* and *L. glaucescens*) in the phylogeny.

Larus smithsonianus was still considered a subspecies of *L. argentatus* in the taxonomy followed by Jetz et al. (2012). It is now treated as a distinct species including three subspecies: *smithsonianus*, *vegae* and *mongolicus*. As for several species in the ‘white-headed’ gull complex, the relationships remain unclear and, in accordance with the latest studies (Pons et al., 2005; Sternkopf 2011; Sonsthagen et al., 2016), we have decided to branch *L. smithsonianus* to the node grouping *L. californicus* and *L. glaucescens*. Numerous studies have also shown that subspecies *vegae* and *mongolicus* should be treated as specifically distinct from *smithsonianus* (Liebers & Helbig, 2002; Sternkopf 2011; Olsen 2018). We thus have decided to add a clade containing *vegae* and *mongolicus* as a sister species of *L. smithsonianus* with 10 000 years of divergence between *vegae* and *mongolicus* (subspecies as in case 1)).

The position of *Larus delawarensis* as a sister group of the *L. canus* complex is now unanimous (e.g. Pons et al. 2005; Sternkopf 2011). We have therefore modified the position of this species in each topology. On the contrary, since the position of *Larus cachinnans* is very controversial

(see Sonsthagen et al. 2016; Sternkopf 2011), we have decided to branch this taxon to the same node supporting, among other taxa, *Larus smithsonianus*, *L. fuscus*, and *L. dominicanus*.

del Hoyo, J. and Collar, N. J. (2014) HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 1: Non-passerines. Lynx Edicions and BirdLife International, Barcelona, Spain and Cambridge, UK.

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W. & McCabe, A.M. (2009) The Last Glacial Maximum. *Science* 325, 710–714.

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Paradis E. & Schliep K. (2018). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35: 526-528.

Pons, J.-M., Hassanin, A. & Crochet, P.-A. (2005) Phylogenetic relationships within the Laridae (Charadriiformes: Aves) inferred from mitochondrial markers. *Molecular Phylogenetics and Evolution*, **37**, 686–699.

Revell, L.J. (2012) phytools: a R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.

Sonsthagen, S.A., Wilson, R.E., Chessier, R.T., Pons, J.-M., Crochet, P.-A., Driskell, A. & Dove, C. (2016) Recurrent hybridization and recent origin obscure phylogenetic relationships within the ‘white-headed’ gull (*Larus* sp.) complex. *Molecular Phylogenetics and Evolution*, **103**, 41–54.

Sternkopf, V. (2011) Molekulargenetische Untersuchung in der Gruppe der Möwen (Laridae) zur Erforschung der Verwandtschaftsbeziehungen und phylogeographischer Differenzierung.

Appendix 3: Estimation of missing KGS values

We did not find published KGS values for *Larus novaehollandiae* and its three subspecies (*L. n. novaehollandiae*, *L. n. forsteri* and *L. n. scopulinus*). To estimate these KGS values, we measured the mean and the modal grey values from HBW illustrations (del Hoyo et al., 2019) with the ImageJ software (Schneider, Rasband & Eliceiri, 2012) by considering the feathers of the mantle, the scapulars as well as the coverts (we did not consider the tertiaries; see the Figure 1 below). The modal value represents the grey value that appears most often in a set of data (from 0 - totally black to 255 - white). We used paintings rather than photographs because it is difficult to find neutral and similar lighting conditions for many taxa.

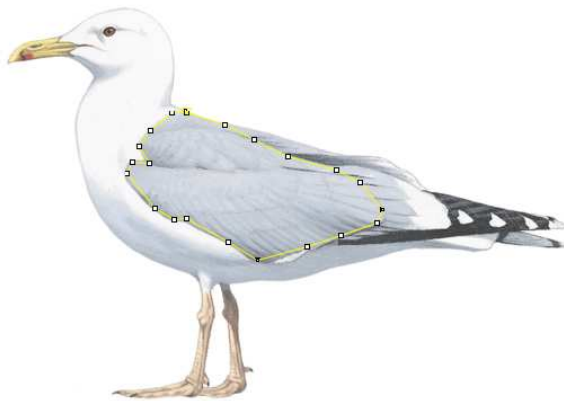


Figure. Surface considered (mantle, scapular and covert feathers) in each taxon (here *L. cachinnans*) to calculate the mean and the modal grey values. Illustrations © HBW Alive/Lynx Edicions.

To validate this procedure and extract KGS values comparable to the ones we used for the other species, we measured KGS values on HBW paintings for 20 randomly chosen taxa with published KGS values included in our dataset. We then performed linear regressions between mean published KGS values and mean and modal values extracted from the paintings separately.

We found a higher coefficient of determination for modal values (Adjusted R-squared: 0.87 against 0.84 for mean values; see Figure below) and used it to predict the KGS values of missing taxa with confidence interval.

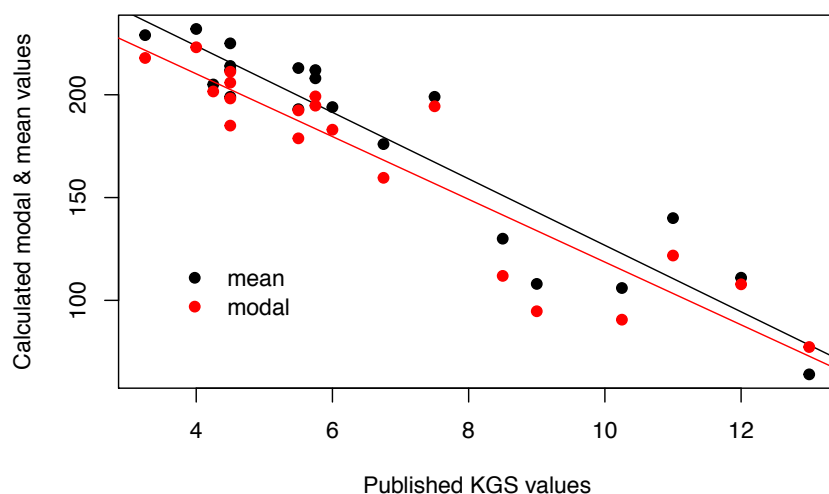


Figure. Correlation plot between published KGS values and calculated modal and mean values from ImageJ. The red and black lines represents the regression lines for both linear regressions.

We thus predicted a KGS value of 4.27 (CI: 3.60 – 4.94) for *L. n. novaehollandiae* and 4.87 (CI: 4.27 – 5.47) for *L. n. scopulinus*. *L. n. forsteri* is said to have the same upperparts coloration as the nominal subspecies (Olsen 2018). Rounding up, we included in our analyses the following KGS values for these missing taxa:

L. n. novaehollandiae = 4.25

L. n. forsteri = 4.25

L. n. scopulinus = 5

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (2019) *Handbook of the Birds of the World Alive*, Lynx Edicions. Barcelona.

Olsen, K.M. (2018) *Gulls of the world, A photographic Guide*, Helm Editions, London.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.

CHAPITRE 4

Analyse de l'impact des stratégies de migration sur la reproduction d'un migrateur à longue distance aux coûts de vol élevés

Résumé du chapitre : Peu d'étude ont évalué si la variation de la distance de migration au sein d'une population peut avoir des conséquences sur les paramètres de reproduction. Grâce au suivi à l'aide de géolocalisateurs, nous avons étudié les variations de distance de migration au sein d'une colonie de mergule nain (*Alle alle*) de Svalbard et les conséquences de ces variations sur la reproduction de l'année suivante. Cette espèce, très abondante dans le Haut-Arctique, présente comme la plupart des alcidés un coût de vol élevé.

Nous avons mis en évidence deux zones d'hivernage distinctes, au nord de l'Islande et au sud-ouest du Groenland, impliquant une différence de distance de migration très importante, plus de deux fois supérieure (1500 contre 3100 km en moyenne depuis la colonie). Alors que cette distance de migration entre la colonie de Hornsund (Svalbard) et le sud-ouest du Groenland figure comme l'une des plus longues enregistrées chez un alcidé, nous avons montré que les oiseaux qui parcourent cette distance sont plus souvent des femelles et des oiseaux de petites tailles. De façon importante, nous avons également montré que cette stratégie de migration n'a pas d'effet apparent sur la reproduction (ni sur la phénologie, ni sur le succès reproducteur).

Ces résultats semblent contredire les études prédictives suggérant que l'établissement des routes de migration vers différentes destinations hivernages pourrait être limité par les contraintes énergétiques liées au vol. Ils invitent à s'intéresser à l'origine évolutive de ces stratégies (peut-être en lien avec les voies de colonisation postglaciaire) mais à analyser les conséquences de ces choix de destination d'hivernage sur la survie et les performances de reproduction à long terme.

[Mergule nain, migration saisonnière, coût de vol, succès de reproduction, océan Atlantique, géolocalisateurs]

Note sur la participation : La réalisation de cette étude a été murie au cours d'une saison de terrain dans l'Isfjorden (Svalbard, Norvège) lors de l'été 2018, avec Sébastien Lavergne et Sébastien Descamps de l'Institut Polaire Norvégien. Nous souhaitons trouver un modèle

d'étude avec des destinations d'hivernages très variables pour étudier les potentiels *carry-over effects* de ces différentes destinations ainsi que leur évolution. En étudiant une espèce d'alcidé, nous avons aussi l'opportunité d'appliquer ces questions à une espèce présentant un coût de vol élevé, en raison de son double mode de locomotion (vol et nage). Notre choix s'était donc porté sur le guillemot de Brünnich (*Uria lomvia*). L'espèce montre en effet des stratégies d'hivernages très différentes suivant la localisation des colonies de part et d'autre de l'archipel de Spitzberg et nous disposions d'échantillons pour réaliser une analyse phylo-géographique dans le but de comprendre l'évolution de ces stratégies en lien avec la colonisation de l'archipel. Mais la forte baisse des effectifs dans l'Ouest de l'archipel de Spitzberg, notamment sur la colonie de Diabasodden (Isfjorden), ainsi que des difficultés rencontrées pour extraire l'ADN à partir des échantillons disponibles, nous ont contraint à trouver un autre modèle d'étude. Par chance, Katarzyna Wojczulanis-Jakubas et Dariusz Jakubas, chercheurs à l'université de Gdansk (Pologne) et travaillant depuis plusieurs années sur la colonie de mergules nains d'Hornsund (sud de Svalbard), ont accepté de me fournir une partie de leurs données pour aborder cette question.

A two-fold increase in migration distance does not have breeding consequences in a long-distance migratory seabird with high flight costs

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ABSTRACT: Whether variation of winter migration distance among individuals within a population has consequences on their reproductive performance has rarely been assessed. Using individual global location sensor-tracking, we determined variation in migration distance, and its breeding consequences, in a Svalbard colony of the little auk *Alle alle*, a high-Arctic seabird with high flight costs. We found 2 distinct wintering quarters (north of Iceland and SW Greenland) implying a 2-fold difference in migration distance (1500 vs. 3100 km on average from the colony). This migration route from Svalbard to Greenland is among the longest recorded distances for an alcid species. Birds travelling a longer distance were more likely to be females and smaller, but more importantly, migration strategy had no apparent effect on reproductive performance (either timing or success). Our results contradict predictive studies which suggested that the establishment of migration routes to different winter destinations may be limited by the energetic **constraints of flight**.

KEY WORDS: Alcid · Little auk · *Alle alle* · Bird migration · Flight cost · Breeding success · North Atlantic · Logger

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1. INTRODUCTION

The evolution of the migration strategies of birds is predicted to be shaped by, among other factors, the energetic constraints of flight (Alerstam & Lindström 1990). Since migratory flights require time and energy (Weber & Houston 1997), this expenditure will increase with the distance covered but will also depend on the type of flight and wind conditions experienced (soaring vs. flapping species; Watanabe 2016). It has been shown in several migratory bird species that variability in wintering sites, habitats and/or migration phenology can be shaped by intra-specific competition (Croxall et al. 2005, Phillips et

al. 2011) and may have important consequences for annual survival (Alerstam & Hedenstrom 1998, Reneerkens et al. 2020) and/or subsequent breeding performance (Alves et al. 2013) through carry-over effects (Gunnarsson et al. 2005, Norris 2005, Norris & Marra 2007, Harrison et al. 2011, Bogdanova et al. 2017). The great energetic costs during migratory flights experienced by individuals migrating over longer distances may entail fitness consequences (e.g. Hotker 2002, Bearhop et al. 2004, Bregnballe et al. 2006). However, under certain conditions, migrating farther may have no effect on reproduction (e.g. Kentie et al. 2017, Reneerkens et al. 2020) or may even be positively associated with reproduction and

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survival (e.g. Alves et al. 2013). Individuals performing long-distance migration may indeed compensate for these extra flight costs by taking advantage of optimal wintering conditions (i.e. high resource availability, low competition or predation; e.g. Alves et al. 2012, 2013, Conklin et al. 2017). The high energetic expenditure associated with a long migration distance may thus not always lead to higher fitness costs, and this relationship between energetic and fitness costs is likely to vary both at inter- and intra-species levels (Fayet et al. 2016).

In some seabird lineages like the alcids, the ability to fly has evolved under strong selective pressure toward a trade-off between flying and diving abilities. It has resulted in high flight costs (Thaxter et al. 2010, Elliott et al. 2013). In species using flapping flight, migration distance is therefore expected to be limited by the maximum physiological capabilities of a species and may also serve as a driver of individual fitness (Watanabe 2016, Fayet et al. 2017). Consequently, little variation in migration distance is expected within a given population for such species, as an increase in migration distance would lead to significant fitness costs and migrating farther would not be an adaptive strategy. While the co-existence of distant wintering grounds within the same population has been observed for this bird family (Fort et al. 2013a), the link between fitness and migration distance has rarely been assessed for alcids (but see Fayet et al. 2017). Likewise, it has never been shown in species with high flight costs, such as alcids, that wintering conditions and resource abundance may compensate for the additional flight costs that some individuals would endure (see Fort et al. 2013b).

The little auk (or dovekie) *Alle alle* is a small, colonially breeding, diving seabird. Like other alcids, it is characterised by flapping flight and high wing-loading values (Sakshaug et al. 2009) imposing high flight costs (higher than in other non-alcid seabirds using flapping or soaring flight). The species is restricted to the high Arctic in summer but spends the winter in various locations in the North Atlantic Ocean (e.g. Mosbech et al. 2012, Fort et al. 2013a). Preliminary results have suggested 2 wintering areas of the Svalbard breeding populations located near Iceland and in the Labrador Sea (Isaksen 1995, Fort et al. 2013a). Little auks that breed in Svalbard are thus good candidates to study the mechanisms leading to such different wintering destinations and their ecological and demographic consequences (Gabrielsen et al. 1991, Harding et al. 2009, Fayet et al. 2017). Using individual global location sensor (GLS) tracking data from little auks breeding at

Hornsund, one of the largest colonies in Svalbard (Isaksen & Bakken 1996, Keslinka et al. 2019), we assessed individual variation in migration distance and its potential costs for subsequent reproduction. More specifically, we tested whether individuals travelling longer distances exhibit delayed breeding phenology (later breeding) and lower reproductive performance. Late breeding is usually associated with poor breeding success and/or offspring quality in birds, especially at high latitudes (Hipfner et al. 2010, Ramírez et al. 2016), including in the little auk (Jakubas & Wojczulanis-Jakubas 2013). We tested for different environmental conditions (e.g. sea surface temperature, SST) encountered on wintering grounds that could motivate and compensate for longer travels (see Alves et al. 2013). Finally, we also investigated the role of bird body mass, body size and sex as potential drivers of the inter-individual variation in wintering destination (Croxall et al. 2005, Phillips et al. 2011, Zhao et al. 2018).

2. MATERIALS AND METHODS

2.1. Geolocator deployment

Between 2015 and 2017 (3 consecutive breeding seasons), 113 GLS loggers were deployed on 92 different adult little auks breeding in the Hornsund colony, southwest Spitsbergen (77°00' N, 15°22' E; 21 birds were equipped over 2 non-consecutive years). Respectively, 30, 26 and 17 birds were tagged in 2015, 2016 and 2017. Birds were captured in the nest burrow during late incubation or early chick-rearing, and all birds were ringed using a metal ring on one leg, and a geolocator (MigrateTech models C65 and F100) attached to a plastic ring was fitted on the other leg. Body feathers were collected for molecular sexing (following the protocol of Jakubas & Wojczulanis 2007).

The GLS with accompanied elements (plastic ring, wire and glue) weighed 1.8 g, which constituted ~1% of body mass. All individuals were measured (wing and head-bill length, ± 1 and ± 0.1 mm, respectively), and weighed (± 2 g) both at deployment and at GLS retrieval. We did not find a negative logger effect on bird body mass, and mass at retrieval was similar to mass at deployment. We also found no difference in body mass between logger-equipped individuals at retrieval and control individuals (i.e. individuals not burdened with any logger, captured for the purpose of another project, at a similar breeding phase as GLS-equipped birds;

see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/dxxxpxxx_supp.pdf).

In total, 73 % of loggers ($n = 82$) were retrieved (2 loggers were retrieved 2 yr after their deployment). Of these loggers, 11 % ($n = 9$) experienced technical failure and gave no (or incomplete) information on the non-breeding movement of the individual; these were excluded from the analyses. The percentage of GLS recovered varied between years: 91 % in 2015/2016, 88 % in 2016/2017 and 44 % in 2017/2018. A total of 73 loggers (65 % of all deployed) carried by 61 different individuals were included in this study (11 birds were tracked over 2 different non-breeding seasons).

2.2. Migration route and activity analysis

Light data from both types of loggers (MigrateTech C65 and F100) were decompressed and processed using the method detailed by Merkel et al. (2016), implemented in the 'prob_algorithm' function ('prob-GLS' package) with the **R software** (R Core Team 2019). Due to the high latitudinal position of the colony, and logger deployment and retrieval occurring during periods of continuous daylight, location data were only available from early September to early April (when birds are expected to arrive at Svalbard, Stempniewicz 1981). In addition, due to the equivalent day length everywhere on Earth at the autumnal and spring equinox, latitudinal positions within 15 d on each side of the 2 equinox dates could not be estimated accurately (see Phillips et al. 2004), just as the error of GLS locations is known to vary up to 200 km (Phillips et al. 2004). After computing, each computed track was visually inspected and erroneous locations, particularly around polar night and midnight sun periods, were removed.

The maximum distance from the colony was then calculated as the great-circle distance between the colony and the farthest recorded position of the bird (Hijmans et al. 2015). We estimated the total distance covered during migration by summing the great-circle distances from averaged positions per 10 d period between 15 September and 9 April (outside the period of continuous daylight), thus excluding the distance between the colony and the moulting area.

We illustrated the different wintering and post-breeding locations of Hornsund birds using GLS positions of birds and the kernel density function of the ArcGIS software (ArcGIS Desktop 10.6, ESRI). Density values were then obtained for each location point and ranked (only in the case of wintering) into 3 classes of densities (25, 50 and 75 %).

2.3. Environmental conditions on wintering grounds

To test whether environmental conditions, being a proxy for resource availability (see Fort et al. 2012) on the wintering grounds, differ between migration strategies, we extracted SST ($^{\circ}\text{C}$) values (mean, minimum and maximum) from polygons defined by individual locations (convex hull) in December and January. We extracted the average SST from 2002–2017 from the NASA OceanColor data (<https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MYD28M>). Gaps occurring in the raster files were filled using the kriging method in ArcGIS software. These monthly averaged SST values were then averaged into 1 wintering SST value for each individual. We chose SST, rather than a proxy for food availability such as primary productivity (i.e. chlorophyll *a* concentration), because it was the most complete at these latitudes during the winter months. Moreover, it has been shown that the distribution of prey (e.g. copepods) of little auks is temperature dependent, with more energetic prey (richer in lipids) frequenting colder waters and preferentially fed upon by little auks (Karnovsky et al. 2010, Jakubas et al. 2011, Gré-millet et al. 2012), and that SST is a good proxy explaining copepod distribution (Fort et al. 2012). We therefore used SST as an indicator of food availability and/or productivity in the different wintering areas.

2.4. Breeding parameters

Due to the difficulty of direct observation in focal nests, breeding parameters (of the post-winter breeding season) could not be collected for all individuals. Hatching success (little auks lay only 1 egg) was recorded for 68 tracked individuals (93 % of all tracked). To test the putative effect of wintering destination on hatching date, we calculated the relative number of days between the individual hatching date and the median hatching date for the colony ('relative hatching date' hereafter). Hatching date, corresponding to the first date on which a chick was recorded (nests were checked every 2–3 d), was recorded for the nests of 59 tracked individuals (81 % of all tracked). For each breeding season, the median hatching date was calculated for a group of control nests ($N = 104$ in 2016, 50 in 2017 and 65 in 2018), varying between 7 and 13 July. Hatching dates are used as

a proxy of the breeding phenology and are expected to reflect the laying dates, since the incubation duration is virtually constant among individuals (mean $\pm$ SD = of 29 ± 0.8 d, based on 332 nests monitored in another project and for which both laying and hatching dates were available; K. Wojczulanis-Jakubas unpubl.). Finally, chick survival (present/absent, i.e. alive/dead), expected to be a good proxy for parental performance (see Stempniewicz 2001), was recorded during the last nest control performed when chicks were up to 15 d old. Since it is unlikely not to find living chicks, chicks that were not found during this last check were considered dead.

2.5. Statistical analyses

To assess the variation in migration distance, we used a hierarchical cluster analysis (using the functions 'hclust' in R) on the winter location farthest from the breeding colony of each tracked individual (R Core Team 2019). Based on the higher relative loss of inertia criteria, we found that no more than 2 areas were used by migrating little auks (Iceland and Greenland wintering grounds, Fig. 1).

To assess little auk structural body size, we used the first principal component (PC1) of a principal component analysis (PCA), reducing the 2 body measurements (wing length and head-bill length) to a body size index (BSI; Freeman & Jackson 1990, Wojczulanis-Jakubas et al. 2011). PC1 extracted from the 2 variables accounted for 71.2% of the variability, with high BSI values indicating larger birds with a larger head and longer wings.

We used generalised linear and linear models ('lme4' package, Bates et al. 2014) to test the effect of the wintering grounds (Greenland vs. Iceland) on relative hatching date (using a Gaussian distribution), as well as on hatching success and chick survival in the following breeding season (using binomial distributions). Visual inspection of model residuals indicated a normal and homoscedastic distribution. To test whether the effect of the

wintering grounds differs among sexes, we included the interaction between sex and wintering grounds in our models. We also included year as a fixed effect in the models with hatching success and chick survival as variables to be explained, to take into account the inter-annual variation in breeding performance. Statistical significance was assessed with likelihood ratio tests comparing full and null models.

To test the effects of sex, body condition and body size as drivers of winter distributions, we fit a generalised linear model (GLM) with wintering destination as the dependent binary variable (coded as 0: Greenland, 1: Iceland) and BSI, body mass and sex as fixed effects. To deal with the collinearity detected between the explanatory variables (see Fig. S2) and to

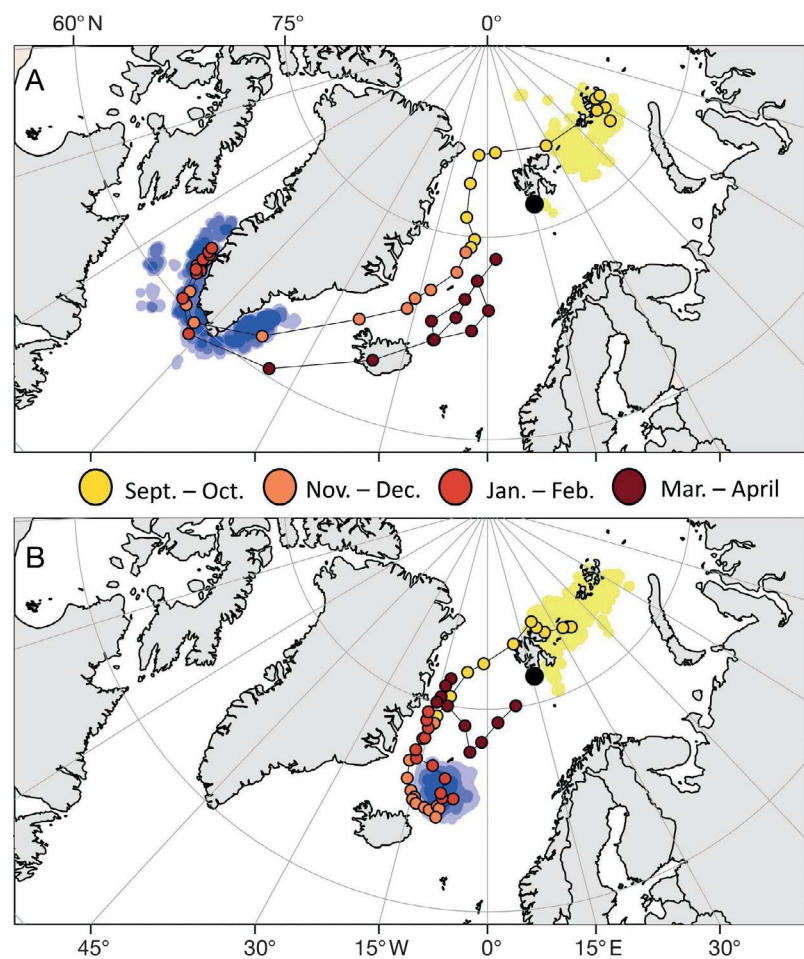


Fig. 1. Winter tracks of 2 global location sensor-equipped little auks breeding at the Hornsund colony (marked with a black dot) migrating to (A) Greenlandic waters (GRE) or (B) Icelandic waters (ICE). Each coloured point is a 5 d average position, and each colour represents a different period. Kernel density estimation of wintering areas for all birds of each wintering ground (N = 22 in GRE for 19 individuals and N = 51 in ICE for 45 individuals) are indicated in blue (see Section 2.2); yellow areas indicate putative moulting areas of staging positions during September and October

disentangle the effect of each variable, we considered in our model the residuals of the BSI adjusted for sex and body mass, and the residuals of the body mass adjusted for sex and BSI. Even if some individuals had been tracked for several years, using mixed models (generalised linear mixed models) with bird identity as a random effect or GLM (without this random effect) led to the exact same results and we have thus decided to only present results from the GLM. The amount of deviance explained by the model was calculated with the function 'Dsquared' (Barbosa et al. 2014).

3. RESULTS

Little auks breeding at Hornsund spent the non-breeding season either in marine areas located between Iceland and Spitsbergen, south of Jan Mayen (hereafter 'ICE') or in the Labrador Sea, southwest of Greenland, which they reach through the Denmark Strait (hereafter 'GRE'; Fig. 1). These 2 wintering areas were used by 70 and 30% of study birds, respectively, and this proportion remained relatively similar over years (varying respectively between 65 and 72% and between 28 and 35% in the period 2015–2018). We found that birds usually adopted the same migration strategy in consecutive years (8 out of 11 birds tracked over 2 yr followed the same routes; see Fig. S4). The categorisation into 2 wintering groups is well illustrated by the non-overlapping distances from the breeding colony when birds reached the farthest positions in December and January (Fig. 2A): GRE and ICE wintering birds reached on average 3145 ± 245 km (SD) and 1516 ± 273 km from the colony, respectively.

The total distance travelled over winter differed between the individuals wintering in the 2 distinct grounds (t -test: $t = -8.66$, $df = 71$, $p < 0.001$), with ICE birds covering considerably less distance ($6347 \pm$

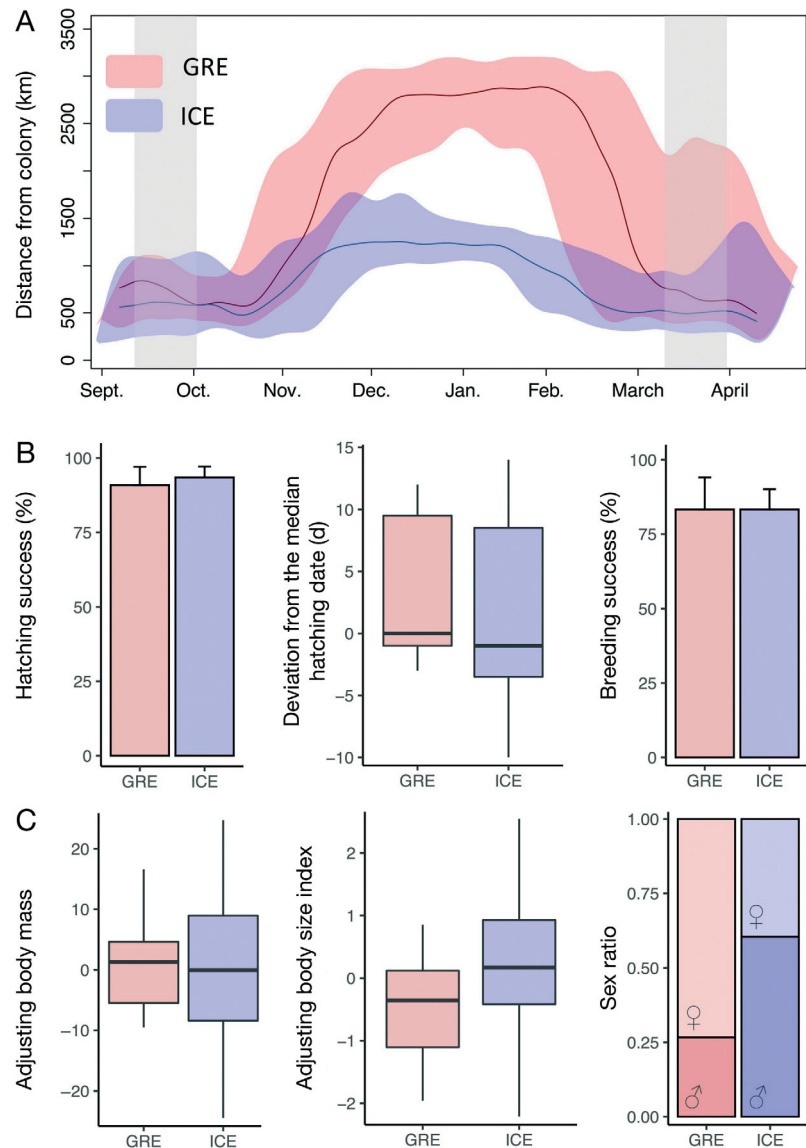


Fig. 2. (A) Estimated distance from the breeding colony in Hornsund for global location sensor-equipped little auks spending winter around Greenland (GRE, $N = 22$) and Iceland (ICE, $N = 51$). The solid line represents the median of each category. Upper and lower limits indicate 5 and 95% percentiles. Grey shaded areas in September and March indicate equinox periods. (B) Breeding parameters (hatching success, hatching date and breeding success) as a function of winter destination. None of these comparisons was significant. (C) Morphometric measurements and sex ratio as a function of winter destination. Adjusted body size index (BSI) and body mass represent the residuals of these variables (see Section 2.5). Boxplots show the median (band inside the box), the first (25%) and third (75%) quartile (box) and the lowest and the highest values within $1.5 \times$ the interquartile range (whiskers)

1265 km) than GRE birds (9569 ± 1930 km; see also Fig. S3). Despite this, birds spending the winter in both areas showed a similar general migration pattern in that they left the expected moulting areas (between Spitsbergen and Franz Josef Land) at the end of September to reach their wintering area in

November. In addition, for each wintering group, we found no difference in phenology and migration routes between the sexes after the breeding period and during the winter season (Fig. S3); we only found a significant sex difference for individuals spending winter in Greenland quarters during the first days of April (between 1 and 9 April), with females located farther from the colony compared to males (Student's t -test: $t = 2.66$, $df = 25$, $p = 0.01$; Fig. S3).

Winter SST differed significantly between the 2 wintering areas, with GRE birds spending winter in colder waters (mean $\pm$ SE = $3.73 \pm 0.26^\circ\text{C}$) than ICE birds ($4.50 \pm 0.11^\circ\text{C}$) (Fig. 3). The difference was greatest for **minimal temperatures** (difference of 1.07°C ; t -test: $t = 4.90$, $df = 67$, $p < 0.001$; Fig. 3), followed by **maximal values** (1.07°C ; t -test: $t = 3.91$, $df = 67$, $p < 0.001$) and by mean values (0.76°C on average for GRE birds; t -test: $t = 3.55$, $df = 67$, $p < 0.001$).

Birds migrating to ICE and GRE exhibited similar breeding phenology (likelihood ratio test, LRT, $p = 0.63$), hatching success (LRT, $p = 0.53$) and chick survival (LRT, $p = 0.89$; see Fig. 2B) in the subsequent season.

Migration routes were independent of body mass but dependent on BSI (Table 1; see Fig. 2C), with large birds (high BSI) spending the winter more

Table 1. Results of the generalised linear model (with a binomial distribution where 0: Greenland, 1: Iceland) testing the effect of sex, body condition and morphometry as drivers of winter distribution. Adjusted body size index (BSI) and body mass represent the residuals of these variables (see Section 2.5). Significant variables are indicated in **bold**

Variables (fixed)	Estimate	SE	z	p
Intercept	0.48	0.41	1.17	0.242
Adjusted BSI	0.69	0.34	2.01	0.045
Adjusted body mass	0.00	0.03	0.11	0.911
Sex (male)	1.57	0.70	2.24	0.025

frequently in ICE. Similarly, the sex ratio differed among the 2 wintering destinations, being female-biased in GRE and male-biased in ICE (Table 1; GRE: 70.5 % females, ICE: 40.9 % females). We found that 14.7 % of deviance was explained by the model.

4. DISCUSSION

Our study shows that little auks breeding in Hornsund, Svalbard, have 2 distinct winter destinations, and these locations are consistent with previous findings from another colony in Svalbard (Kongsfjorden, Fort et al. 2013a). The co-existence of distinct wintering destinations within the same population has also been observed in other alcids (e.g. Brünnich's guillemots *Uria lomvia*, Frederiksen et al. 2016; Atlantic puffins *Fratercula arctica*, Fayet et al. 2017) and in other seabirds in general (e.g. Kopp et al. 2011, Rayner et al. 2011). However, the dichotomy of migration routes observed in little auk breeding in Hornsund is remarkable. In fact, the estimated distance travelled from Hornsund to southwest Greenland (ca. 10 000 km) is among the longest recorded distances to date for an alcid species (McFarlane Tranquilla et al. 2013, Frederiksen et al. 2016, Fayet et al. 2017), and is comparable to soaring species (e.g. northern fulmar *Fulmarus glacialis*, Hatch et al. 2010; great skua *Catharacta skua*, Magnúsdóttir et al. 2012).

In several bird species, travelling longer distances during the non-breeding period entails costs in the following breeding season through carry-over effects (see Bearhop et al. 2004, Bregnballe et al. 2006). However, our results show that even in seabirds with high flight costs, such as alcids (Elliott et al. 2013), migration distance may not have any apparent carry-over effect on subsequent reproductive performance. Little auks that overwintered in Greenland travelled twice as far as those wintering in Iceland; neverthe-

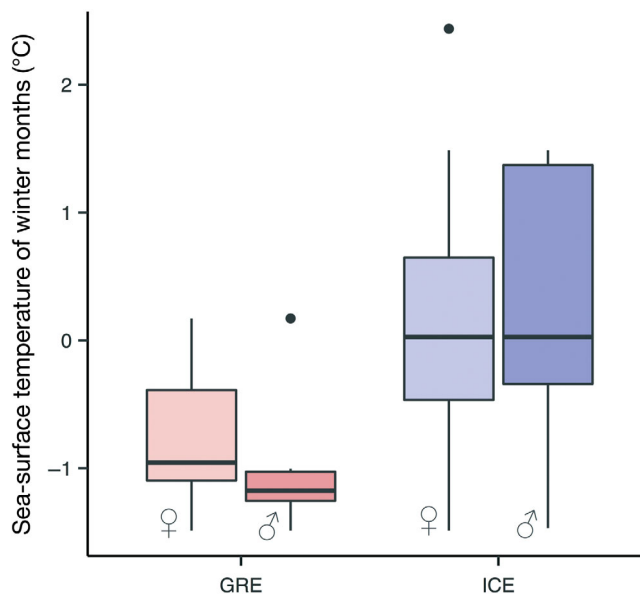


Fig. 3. Winter conditions encountered by little auks according to adopted wintering strategy (GRE: Greenland wintering area, ICE: Iceland wintering area) and sexes (♀: female, ♂: male). Sea surface temperatures (here minimal values) are for December and January. Boxplots show the median (band inside the box), the first (25%) and third (75%) quartile (box), the lowest and the highest values within 1.5× the interquartile range (whiskers) and outliers (dots)

less, we did not detect any apparent differences in breeding parameters in the following season between these 2 groups. Our results are consistent with those found in several species of shorebirds (Conklin et al. 2017, Kentie et al. 2017, Reneerkens et al. 2020), which show no effect of long migration distance on reproduction. Although these 2 wintering distances may in theory be associated with different survival rates (see Reneerkens et al. 2020), our study does not support the hypothesis that migrating farther leads to reduced breeding performance in little auks. However, this does not mean that migrating farther has no fitness cost. This study focusses on the potential costs on subsequent reproduction, but migrating farther may also entail costs to long-term survival and lifetime reproductive performance of individuals (Frederiksen et al. 2016). This lack of effect likely indicates that increased travel costs are compensated for by potentially higher energetic benefits at the wintering grounds (Lundberg 1988, Grémillet et al. 2012, Fort et al. 2013b), such that these higher energetic costs do not translate into breeding costs. In support of this, we found that winter SST differed significantly between the 2 wintering areas, with Greenland birds spending winter in colder waters than Iceland birds. Even if colder waters increase the energetic expenditure of the birds (Fort et al. 2009), the differences in SST observed between wintering areas could indicate that birds in these areas access a different composition or abundance of prey (Fort et al. 2012), since more energetic prey (richer in lipids) may occupy colder waters (Karnovsky et al. 2010, Grémillet et al. 2012). While we currently lack empirical support confirming this mechanism, such a trade-off between prey availability/profitability and distance to the wintering grounds could explain why Hornsund birds have the same reproductive output regardless of different wintering grounds. Further research on the winter diet and energy intake of little auks would be needed, but this result still suggests that even for a species with high flight costs, a migratory journey of several thousand kilometers could be compensated for by finding more energetic resources at the wintering sites.

Our results also indicate that more females winter around Greenland than males while the opposite is true for Iceland. This suggests a partial spatial sex segregation during winter. Sex segregation has been observed in several migratory seabirds, and in migratory birds in general (Marra & Holmes 2001, Croxall et al. 2005, Ruckstuhl 2007). However, previous studies demonstrating sex segregation in seabirds have found that males and females segregate

for the entire non-breeding season and occupy different ecological niches (Phillips et al. 2011). In little auks, a possible explanation for sex differences could come from the fact that females end their breeding season before chick fledging (Konarzewski et al. 1993), may leave the colony before males and have more time to reach a more distant destination. However, here we found sex segregation only in the wintering areas, whereas there were no apparent sex differences in bird locations prior to reaching their wintering destinations, when they are migrating and potentially moulting between Spitsbergen and Franz Josef Land (see Mosbech et al. 2012).

Another hypothesis for this sexual segregation could come from sex-specific requirements (see Phillips et al. 2011), since females may need to replenish after the breeding season. Indeed, they spend a lot of energy to produce their egg. While the production cost is unknown (see Williams 2005), it is assumed to be high given the size of the egg (~20% of the female body mass; Stempniewicz 2001). We also found that individuals wintering in Greenlandic waters have a smaller body size (independent of sex), suggesting that intra-specific competition may cause smaller and potentially less competitive individuals to migrate farther (Marra & Holmes 2001). On the other hand, it has also been shown that smaller birds are more likely to travel long distances (Zhao et al. 2018) and with relatively low flight costs (Alerstam 2003, Watanabe 2016), which is consistent with this result. Collectively, these results indicate that differential migration may exist in little auks (see Cristol et al. 1999), but the reasons behind such winter spatial segregation remain unclear. Competition for food mediated by sex or body size (Ruckstuhl 2007) could drive such a segregation. Even if there is no indication for sex partitioning in the winter diet of little auk (Rosing-Asvid et al. 2013), food intake may still be different between sexes, but information on little auk winter diet is thus far very limited.

An alternative potential explanation is based on the observation of a body size gradient in little auks between the west and east of their distribution range (Wojczulanis-Jakubas et al. 2011), with birds getting larger from west to east. This suggests that smaller individuals from Svalbard may be more closely related to Greenland birds and may have retained their overwintering habits in Greenlandic waters, assuming imprinted migration and wintering choices. Since major glacial events have probably shaped the little auk distribution many times, it is possible that the locations of the wintering areas observed today are the result of a post-glacial re-colonisation pathway of

the species. This hypothesis remains speculative for now and should be tested with a tailored phylogeographic approach. In addition, since we observed a few individuals that changed their wintering destination among the birds followed over 2 wintering seasons, we may assume that wintering quarters and migration routes are not completely imprinted and that individuals are flexible in their migration strategies. It would be interesting to track both parents of a pair. This would allow testing if the choices of one parent, and/or the change in wintering destination, have consequences on the following breeding season (see Fayet et al. 2017), as well as testing if reproductive success has an effect on the wintering destination of the parents (see Bogdanova et al. 2011). It would also be interesting to track the wintering destinations of the juvenile birds (Péron & Grémillet 2013) to test whether the orientation of a juvenile depends on that of the male, which accompanies the juvenile when it leaves the colony (Bradstreet 1982). If the juvenile accompanies the male during its first winter, it can be assumed that the male leads the juvenile to overwintering areas near the colony (to avoid a long and difficult trip). Such a constraint would then be invalid in the case of failed breeding.

To conclude, this study, based on one of the longest journeys to the wintering area recorded among alcid species, suggests that migration distance may not be tightly related to individual fitness, and travel cost may be compensated for by resource benefits, even in species with high flight costs. This study also invites an examination of the consequences that these migratory choices have on survival and breeding performance in the long term. Such results may have important implications for understanding how little auks will be able to adapt their migration strategies in response to the rapid environmental changes they are facing at their wintering grounds (see Amélineau et al. 2019, Clairbaux et al. 2019).

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Supplementary information: Additional data and results on individual parameters (Figure S1-S2), on phenology between sex for each winter destinations (Figure S3), on birds tracked during two different non-breeding seasons (Figure S4).

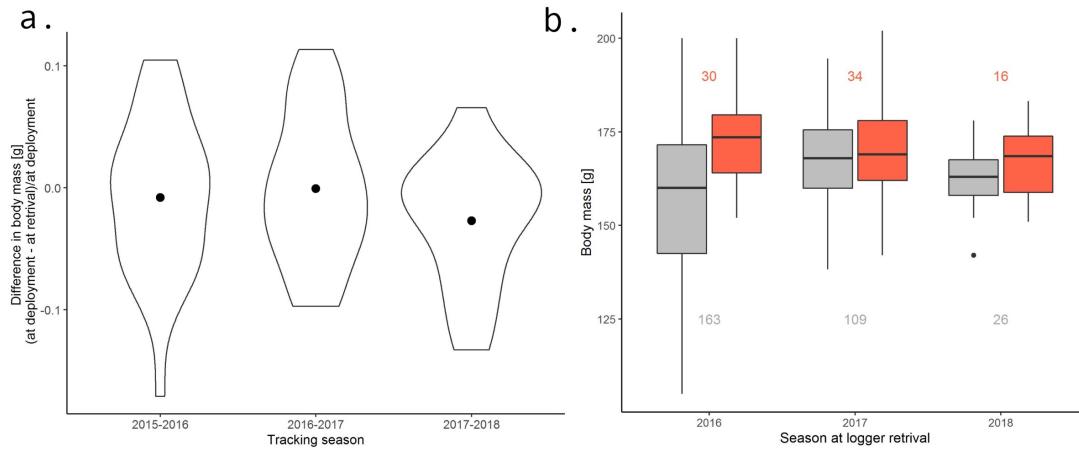


Figure S1. Body mass comparisons for the different breeding seasons between (a) individuals at logger deployment and retrieval, (b) tracked individuals at logger retrieval and control individuals. Number of weighted birds are indicated in orange for GLS-equipped birds and in grey for control individuals. Boxplots show the median (band inside the box), the first (25%) and third (75%) quartile (box), the lowest and the highest values within 1.5 interquartile range (whiskers) and outliers (dots).

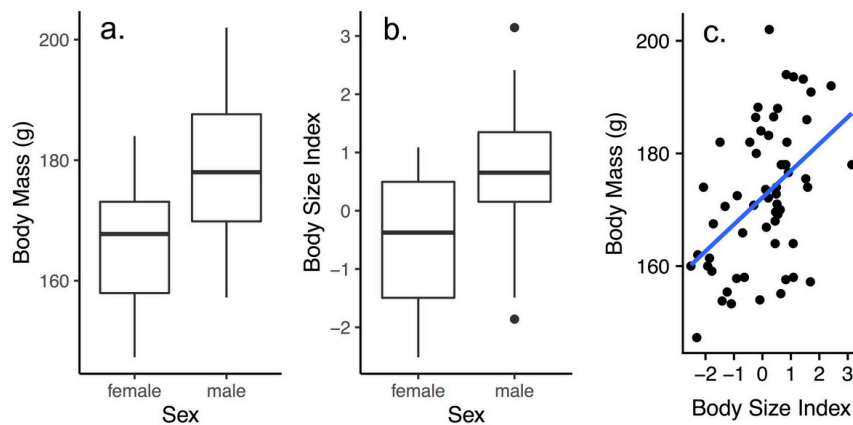


Figure S2. Boxplot and plots of correlations between body size index, body mass and sex variables. The blue line in (c) represents the regression line for a significant relationship ($R^2 = 0.65$). Boxplots show the median (band inside the box), the first (25%) and third (75%) quartile (box), the lowest and the highest values within 1.5 interquartile range (whiskers) and outliers (dots).

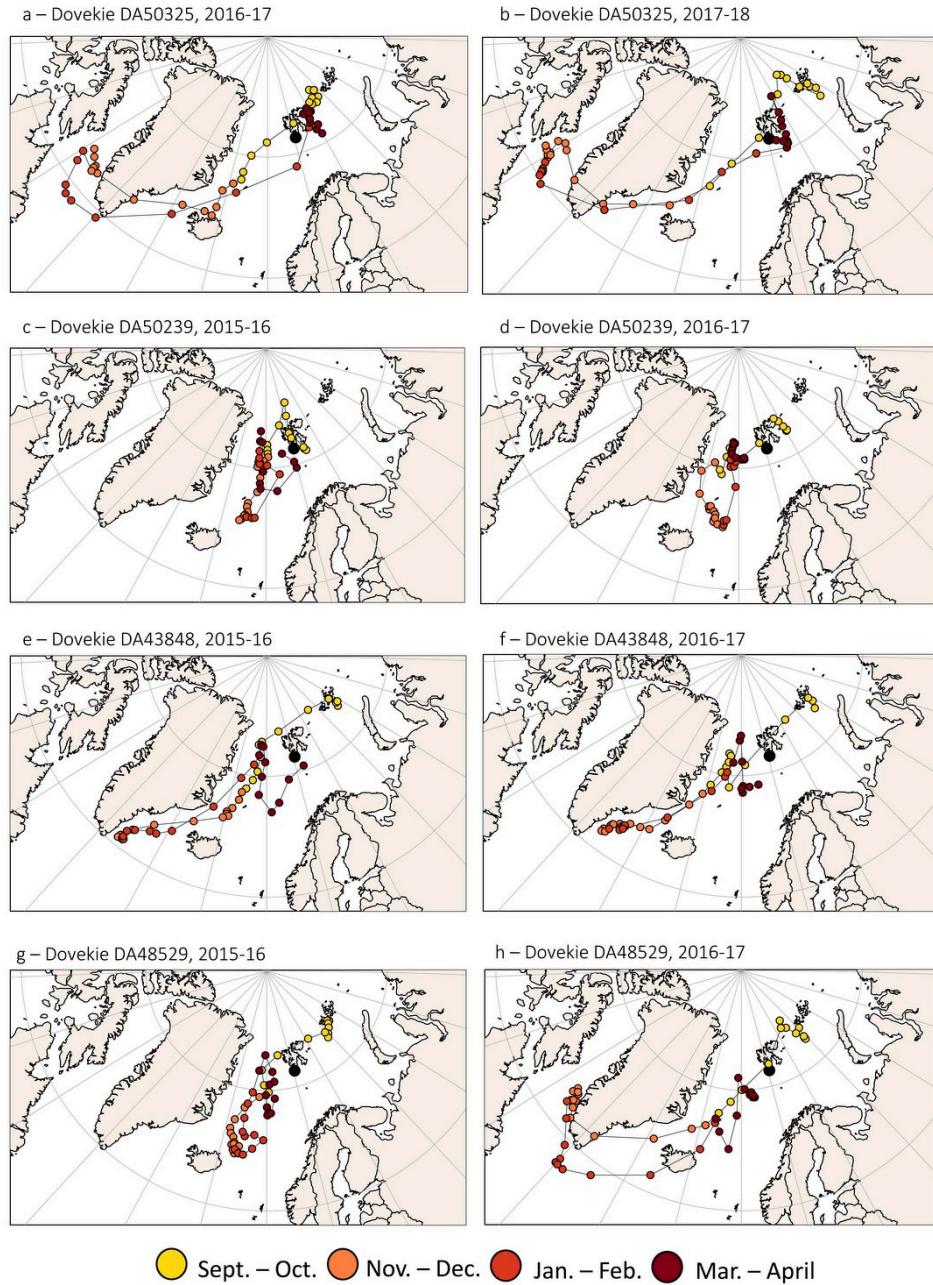


Figure S3. Three examples of spatial and temporal route fidelity (a-b, c-d, e-f) and one switch (g-h) of GLS-logger equipped little auks during migration during two different non-breeding seasons. The Hornsund colony is marked with a black dot. Each coloured point is a 5-days average position and each colour represents a different period. We found that out of 11 birds tracked over two years, three birds switched between routes (two birds switched from ICE to GRE and one from GRE to ICE). Increasing this number of individuals tracked over several years not would be needed to better understand how these two strategies are maintained over time. It should be noted that it is very unlikely that the birds will fly over southern Greenland (i.e. above land; in a, b and g). Therefore, since the distance travelled was calculated from averaged positions per 10-day period, it is thus likely that we underestimated it for some individuals.

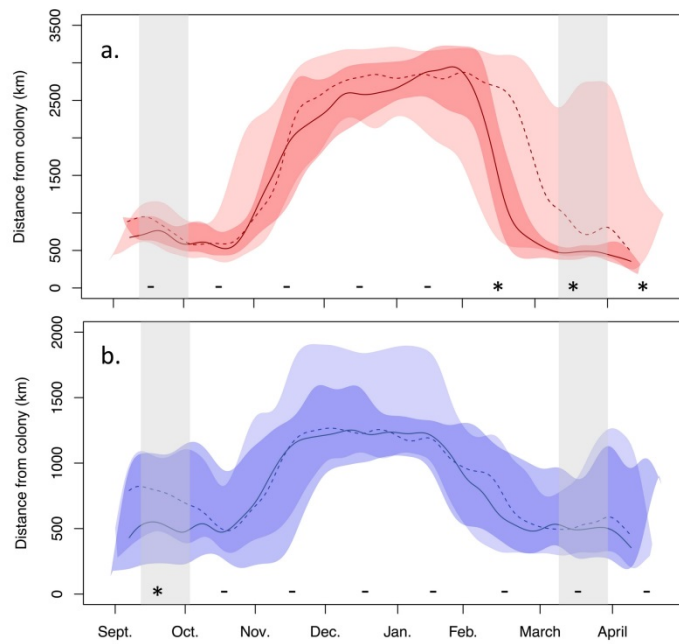


Figure S4. Distance from the breeding colony in Hornsund for GLS-logger equipped little auks spending winter close to Greenland (GRE) (a) and Iceland (ICE) (b) during the non-breeding period. Plain (male) and dashed (female) lines represent the median of each category. In each case, the darker color represent male distributions. Upper and lower limits indicate 5 and 95% percentiles. Grey shaded areas indicate equinox periods. Significant differences between sexes are noted with asterix for each month, the significance for equinox months need to be regarded with caution. In spring (February – April), the distance from the colony differed significantly between the two groups (*t-test*: $t = -2.88$, $df = 67$, $p < 0.001$; on average 958 km versus 568 km for GRE and ICE birds, respectively) and also within strategy between sexes, with GRE females located farther from the colony during the first days of April compared to males (*t-test*: $t = 2.66$, $df = 25$, $p = 0.01$).

CHAPITRE 5

Etude de l'évolution de nouvelles voies de migration chez deux espèces de passereaux sibériens

Résumé du chapitre : L'évolution de nouvelles voies de migration chez les oiseaux est un processus mal compris, car il est rarement détectable sur de courtes périodes et peut être, au moins dans ses premiers stades, facilement confondue avec des mouvements de *vagrancy*.

Le pipit de Richard (*Anthus richardi*) et le pouillot à grands sourcils (*Phylloscopus inornatus*) sont deux passereaux entièrement migrateurs qui se reproduisent en Sibérie et en Asie centrale et hivernent notamment en Asie du Sud Est.

Ces deux espèces sont observées de façon occasionnelle depuis longtemps en Europe, mais leur présence y a rapidement augmenté au cours des dernières décennies, notamment pendant la période hivernale et dans le sud-ouest de l'Europe. L'hypothèse que ce changement de statut pourrait refléter l'établissement d'une nouvelle voie de migration, dont la fréquence d'utilisation est en augmentation dans la population reproductrice, a été proposée mais aussi considérée comme peu probable étant donné les changements majeurs de direction que cette hypothèse implique. L'hypothèse alternative correspondrait donc à une augmentation du nombre de *vagrants* (c'est-à-dire d'individus "perdus" qui ne retournent pas dans leurs zones de reproduction et ne transmettent pas leur itinéraire de migration), comme on le voit chez d'autres espèces sibériennes observées occasionnellement en Europe.

Pour le pouillot à grands sourcils, nous avons estimé l'âge d'oiseaux capturés sur plusieurs sites européens pendant la période de migration et avons démontré la présence d'oiseaux adultes notamment dans le sud-ouest de l'Europe, suggérant ainsi la présence de migrants réguliers. Pour le pipit de Richard, en capturant et marquant des oiseaux sur plusieurs sites d'hivernage sur les côtes méditerranéennes françaises et espagnoles, nous avons démontré la présence d'adultes et le retour des individus marqués au cours des hivers suivants. En utilisant également les données de la science-participative et les données de mue récoltées lors des captures, nous avons démontré qu'une partie des pipits de Richard qui hivernent dans le sud-ouest Europe sont donc des migrants réguliers, utilisant une nouvelle voie de migration, plutôt que des *vagrants* égarés. Nous avons également découvert grâce au suivi GLS que les pipits qui hivernent en Europe se reproduisent à la limite occidentale de l'aire de reproduction connue, en Asie centrale,

suggérant que ce changement de voie de migration ne résulte pas d'un changement majeur de répartition de reproduction. Cette voie de migration secondaire nécessite ainsi de parcourir une distance moyenne de 6 000 km à travers l'Eurasie, principalement en direction de l'ouest, un itinéraire très inhabituel chez les Passereaux qui se reproduisent en Sibérie. Nous avons émis l'hypothèse que ce changement d'orientation de migration et d'aire d'hivernage pouvait résulter de la survie et de la reproduction réussie des *vagrants* arrivés en Europe. En modélisant les niches climatiques de ces populations, nous avons en effet montré que les oiseaux hivernant dans le sud-ouest de l'Europe rencontrent des conditions climatiques similaires à celles de leur aire d'hivernage ancestrale, bien que certaines régions de l'aire d'hivernage européenne (sud de la France) soient différentes des conditions climatiques asiatiques.

Ces études figurent parmi les rares preuves de l'émergence de nouvelles routes migratoires chez des oiseaux migrateurs sur de longues distances. Elles présentent également deux espèces modèles pour étudier le déterminisme de l'orientation chez les oiseaux migrateurs et illustrent le potentiel sous-estimé de la *vagrancy* dans la découverte de nouvelles zones d'hivernages et dans l'émergence de nouvelles voies de migration.

[Migration, pipit de Richard, pouillot à grands sourcils, voie de migration, orientation, *vagrancy*, pression d'observation]

Note sur la participation : Ces deux projets m'ont donné l'opportunité de mettre en place et de gérer un terrain d'étude pour aborder mes propres questions de recherches, ce qui a été à la fois extrêmement formateur et épanouissant sur le plan intellectuel. Les questions de recherche ont été discutées avec mon directeur de thèse et Pierre-André Crochet et de nombreuses discussions avec des scientifiques et ornithologues amateurs ont enrichi notre réflexion.

Ce travail de terrain a pris une place importante au cours de ma thèse en se déroulant chaque hiver sur la période 2018 – 2021 pour le pipit de Richard et notamment au cours de l'automne 2020 pour le pouillot à grands sourcils. J'ai également bénéficié, pour conduire l'étude sur le pipit de Richard, d'une bourse de terrain de la SFE². La conduite de ces travaux de terrain a été rendue possible grâce à l'aide de Christophe de Franceschi (Technicien de recherche au CEFECNRS et bagueur CRBPO) et de Paul Doniol-Valcroze.

Note sur l'avancement des manuscrits : En ce début d'année 2021, nous sommes toujours en train de récupérer des GLS déployés sur des pipits de Richard au cours de l'hiver précédent. Nous déployons également de nouveaux GLS pour améliorer la connaissance des routes de

migration empruntées et affiner les limites de la zone de nidification des oiseaux hivernants en Europe. Nous pensons éventuellement attendre de récupérer un nombre de traces suffisantes avant de publier les résultats de cette étude.

Nous souhaitons soumettre le second manuscrit à la section *The Scientific Naturalist* du journal *Ecology*. Il se trouve donc volontairement en format condensé sans partie clairement délimitée. Nous sommes toujours en attente de recevoir les données d'effectifs de pouillot à grands sourcils collectées sur Fair Isle (Ecosse) au cours de la période 1950-2019. Ces données ont été collectées avec un protocole de suivi qui est resté inchangé au cours cette période. Elles permettront par conséquent de tester si l'augmentation de la pression d'observation explique ou non l'évolution des effectifs notées dans plusieurs pays d'Europe (France, Suède, Grande-Bretagne). Nous devrions également recevoir une partie des données de recaptures en Europe collectées par EURING. Enfin, nous attendons encore de recevoir les estimations d'âges de deux autres bagueurs internationaux. Les résultats et les conclusions présentés dans ce manuscrit sont par conséquent préliminaires et sont amenés à pouvoir évoluer.

Evolution of a new migratory route in an Asian passerine

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Abstract / Summary

The establishment of new migratory routes in birds is a poorly understood process, as it is rarely observable on short time scales and, at least in its early stages, easily confused with vagrancy. The Richard's pipit (*Anthus richardi*) is an obligate migratory species that breeds in open grassy habitats in Central and Eastern Asia and winters mainly in Southern Asia. The species has long been known to reach western Europe occasionally, but its occurrence there has rapidly increased during the last decades, especially in southwestern Europe. This generated the hypothesis that the species recently established a new migration route, which is now increasing in frequency in the breeding population, but this was regarded as unlikely given the major changes in direction and distance travelled that this hypothesis involved. Alternatively, this pattern could reflect an increase in the number of vagrants (i.e. "lost" individuals that do not return to their breeding grounds and transmit their migration route), as seen in other Siberian species in western Europe. By catching and marking birds in several wintering sites on the French and Spanish Mediterranean coast, we demonstrated the presence of adults among birds that winter in southwestern Europe and the return of marked individuals in subsequent winters. By also using citizen-science data and moult data from captures, we thus demonstrated that a part of Richard's pipits wintering in southwestern Europe are true migrants, using a novel migratory direction, rather than lost vagrants. We discovered through GLS-tracking that birds wintering in Europe breed at the western limit of the species' known breeding range in Central Asia (southern Russia), suggesting that this change in migration route did not result from a major change of breeding distribution. Their migration requires an average 6000-km journey across Eurasia in a mainly westerly direction, a route that is highly unusual among Siberian-breeding species. We hypothesised that this change in migratory direction and wintering range originated from the survival and successful reproduction of vagrants after they reached southwestern Europe. Climatic niche distribution modelling showed that birds wintering in southwestern Europe did so in conditions that are broadly similar to those of their ancestral wintering range, although parts of the European wintering range were not predicted to be suitable based on climatic conditions in Asia. This study documents one of the few directly observable changes in migration route in a long distance migratory bird and sheds lights on the underestimated role of vagrancy in promoting the evolution of new wintering areas and new migratory routes.

Introduction

Why and how new migration routes emerge remains a fundamental question in ecology, particularly in the context of current global changes. Drastic contemporary changes in migration routes of birds, involving major changes in the migration orientation and/or distance, have been documented in two species only (Blackcap *Sylvia atricapilla* in Western Europe: Berthold et al. 1992, Plummer et al. 2015; Barn Swallow *Hirundo rustica* in South America: Martinez 1983, Winkler et al. 2017, but see Sutherland 1998). Probable causes of these changes were the increase in food resources in winter supplied by humans (Plummer et al. 2015) and the fortuitous colonization of a new breeding site (Martinez 1983) helped by the increase of man-made breeding habitats availability (Winkler et al. 2017). Because in passerines migration routes are genetically encoded (e.g. Helbig 1991, Delmore et al. 2016) and migratory behaviour is highly constrained (see Barlein et al. 2012), such changes must be genuinely rare and so unlikely to be observable by modern scientists. In addition, “atypical” migratory movements such as those involved in the establishment of new migratory routes can also be confused with other movements undertaken by migratory birds outside the breeding period, increasing the difficulty to detect the initial stages of the emergence of new migration routes.

Vagrancy in particular, defined as birds that appear far outside their normal breeding, migration or wintering grounds (Kot et al. 1996, Veit 2000) can be difficult to tell apart from a regular migration route adopted by a small fraction of a population. Vagrancy typically involves young birds that adopt an atypical direction during migration or dispersal; they are rarely able to survive and return to their breeding grounds (Gilroy & Lees 2003). Vagrancy and rare seasonal migration can thus be distinguished because 1) migrants are made of young and adult birds while the vast majority of vagrants are young birds prior to their first reproduction and 2) migrant individuals typically return to the same wintering area (e.g. Blackburn & Cresswell 2016, van Wijk et al. 2016) while very few vagrants are expected to return several winters in a row, at least in passerines (which have a low annual survival rates). The role of vagrancy in allowing the colonization of new wintering areas and emergence of novel migration routes has been proposed in the past (Alerstam 1990, Sutherland 1998, Gilroy & Lees 2003) but has never been empirically demonstrated to our knowledge.

In Western Europe, several Siberian passerine species occur each autumn in low numbers (see Rabøl 1969). These species normally winter in southern and Southeast Asia and none of these are known to migrate towards Western Europe and North Africa on a regular basis. Over the last few decades, the number of sightings of these vagrant species has increased, probably because observation pressure increased as well (Lees & Gilroy 2009). However, a few

species stand out from this pattern because they have increased much more than the baseline trend of Siberian vagrants and/or they also occurred in areas where the observation effort has not varied markedly. They also involve records in winter in addition to the “typical” pattern of autumn vagrancy. For these species, Gilroy & Lees (2003) proposed the hypothesis that vagrants and regular migrants co-occur in southwestern Europe and North Africa, named the ‘pseudo-vagrant’ theory. However, this hypothesis was regarded as unlikely given the major changes in direction of migration and the increase in distance travelled that this hypothesis involved.

Among the Siberian species that have been observed with increasing frequency in Europe, the Richard's Pipit (*Anthus richardi*) is considered to be the most likely ‘pseudo-vagrant’ (Gilroy & Lees 2003). This passerine breeds in the Siberian plains from eastern Kazakhstan to eastern China, and typically overwinters in open habitats from India to Southeast Asia (Figure 1; Alström et al. 2003). Small numbers have long been known to reach Western Europe (e.g. Gätke 1895, Alström et al. 2003) and North-Africa (Cramp & Simmons 1983) in autumn (and possibly in winter, Cramp & Simmons 1983) but the first instances of complete overwintering were not properly documented until twenty years ago in southern Europe (Dulau 1997, Biondi & Grussu 2004). Thus, if the Richard's pipit winters and migrates to southern Europe, this represents a new migration route in a completely different direction from its ancestral wintering grounds in Southeast Asia.

In this study, we wanted to test if Richard's pipit established a new migration route between Central Asia and Europe. We first checked whether the number of Richard's pipits occurring in Europe actually increased more than other Siberian passerines over the last decades, as suggested by Gilroy & Lees (2003). We then initiated a capture-recapture program at several sites on the French and Spanish Mediterranean coast that regularly host the species during the autumn and winter periods to test if some of these birds were returning seasonal migrants rather than lost vagrants using several lines of evidence. The first line of evidence is indirect: we caught birds to age them in the hand and check if some of the birds wintering in Europe were adults, which would suggest that they are returning regular migrants rather than lost vagrants (see Ralph 1981, van Wijk et al. 2016). We also directly tested for the return of individuals in subsequent winter by colour-ringing and recapture or resighting. By combining information on moult obtained from captures and photographs in the field from citizen-science database, we tested if regular migrants also occur in the rest of Europe and North Africa. We also deployed Global Location Sensor data loggers to document the journey of some of these birds and test if the emergence of the westward migration route was linked to the colonisation

of still unmapped breeding areas or emerged from birds breeding in the known breeding range. Last, we used niche-base distribution modelling to investigate if vagrants may have benefited from encountering similar wintering conditions to those experienced in their normal wintering ranges to survive the winter (i.e. niche conservatism hypothesis; Wiens & Graham 2005).

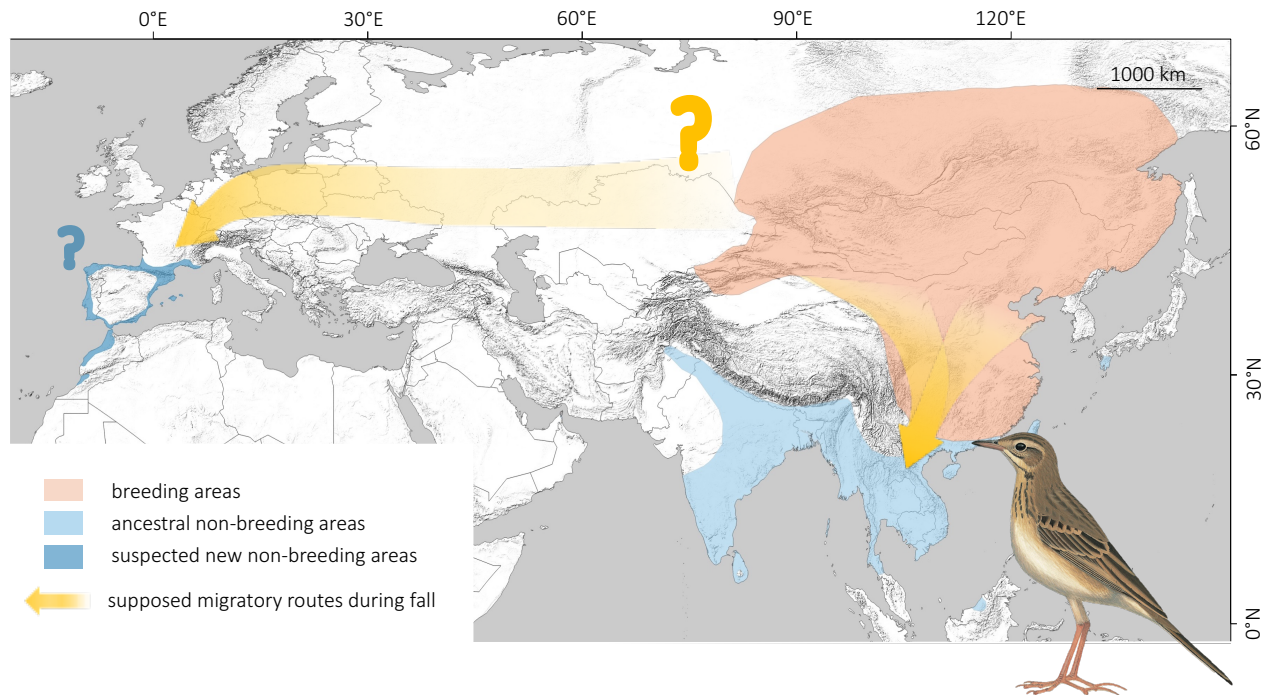


Figure 1. Distribution ranges and migratory movements of Richard's Pipit. Breeding and ancestral non-breeding ranges are taken from BirdLife International (2020). Suspected new non-breeding areas are based on occurrences collected from the Global Biodiversity Information Facility (GBIF) for countries that regularly host the species during the winter period and from information in Alström et al. (2003; see the Material and Methods section). The yellow arrow (left) illustrates the potential migratory routes that birds undertake to reach Europe and North-Africa. The double yellow arrows indicate suspected migratory flyways that the species use to reach his ancestral non-breeding ranges (right). Note that there is no evidence that the species migrates through the Himalayas or even west of the Himalayas (see Delany et al. 2017). Illustration © Bill Zetterström.

Materials and methods

Estimating trends in Richard's pipit occurrence

To check whether the number of Richard's pipits occurring in Europe actually increased over the last few decades, we studied the trend in occurrences in France between 1981 and 2019. We focused on France because the country hosted the first documented wintering record (Dulau 1997) for Europe and because data have been meticulously collected over a period of about 30 years. The French Birds Rarities Committee collected data between 1981 and 2005 when the species was still very rare. Then, from the 1990s onwards, numbers of occurrences started to increase and data on the species were collected by another committee between 2005 and 2010, when the citizen-science databases took over. To avoid double-counting, we used the maximum number of individuals simultaneously recorded on a given site on a given year. Since wintering cases mostly occur in the regions of the French Mediterranean coast, we studied the trends for these regions on the one hand and for the entire France on the other hand over the same period.

To test if the species' increase is entirely driven by an increase in observer effort, we compared linear regression coefficients of number over time for Richard's Pipit and other vagrants of eastern origin. As these data have always been collected using the same methodology by the French Rarities Committee, we assumed no reporting bias over time and we considered these data as an approximation of observer effort. We excluded the rarest species from the dataset (typically less than 5 records over the 1981-2019 period; the list of species considered can be found in Table S1). We analysed separately southern France and the entire France to test for potential geographic variations. Finally, we report the number of sites frequented by the species in winter between 1981 and 2019. By gridding the whole France territory in cells of 10 x10 kilometres, we evaluated the number of new grid cells frequented each year between 1981 and 2019. We studied this trend for the winter period (December-February) and the migration period (September-November and March-May).

Ringling campaigns

Richard's pipits were caught over the course of three wintering periods between 2018 and 2021 on several locations along the Mediterranean coast of France and Spain (see details in Table S2). These sites were chosen because they frequently hosted the species during autumn and winter. With the exception of one site that hosts several dozen birds during migration (Crau Plain in southern France, own data), numbers of birds at the other sites fluctuated between 3 and 7 individuals per winter. Birds were handled with permission from MNHN-CRBPO (reference program # 989) for France and SEO-BirdLife (reference program # SF/0106/2019)

for Spain. Since the success of the capture sessions was strongly dependent on weather, the effort of capture was heterogeneous between sites and between wintering seasons. Birds were attracted with conspecific call playback and caught using vertical monofilament mist nets or spring traps. All captured birds were measured, ringed with a metal (left leg) and a coloured band (marked with an identification number; right leg), photographed, and a feather sample (one greater covert) was taken before birds were released after ca. 5 min of handling.

Birds ageing and moult scoring

First-winter Richard's pipits that retain some juvenile feathers can be aged from field observations or photographs since juvenile coverts can be easily recognised as they show a characteristic thin whitish edge (Figure S1). In contrast, second-generation (post juvenile) coverts are indistinguishable from adult feathers and the only way to separate first-winter birds with advanced moult (i.e. having replaced all wing coverts) from older birds is to examine the shape and colour of their primary coverts (P. Alström *pers. com.*; Alström et al. 2003; Figure S1). As a consequence, it is usually necessary to handle those birds that have moulted all wing coverts, tail feathers and tertials to age them. Birds that were caught were thus separated into adult and first winter birds and we measured the moult extent in the latter age class. Since birds were caught mostly between November and February, they had already achieved their autumn moult (no birds in active moult, *pers. obs.*). We assessed the moult extent considering feathers that are apparent when a bird is perched (i.e. with the wing closed). We thus counted the number of moulted feathers in median coverts (from 0 to 8), in greater coverts (from 0 to 10) and in tertials (from 0 to 3) on the right wing. The moult score scaled from 0 (no moulted feathers) to 21 (completely moulted; adult birds logically had a score of 21; Figure S2 & S3).

Based on the moult phenotypes observed during captures, we considered that a first winter bird with a moult score above 18 cannot be distinguished from an adult bird from field observations or photographs. We thus defined an *adult-type* phenotype for this type of individuals and identified, in total, three phenotypes that we called *full-juvenile*, *extensive* and *adult-type* moult phenotypes. The first moult phenotype called *full-juvenile* corresponded to first-winter that had not performed a post-juvenile moult (score of 0-1). The *extended post-juvenile* moult phenotype concerned birds that replaced most of their median coverts (from 0 to 8) and tertials (from 0 to 3), and up to eight greater coverts (score of 6-18). The *adult-type* moult phenotype gathered adults and young birds performing a very extensive post-juvenile moult and which may retain a maximum of one tertial and some greater coverts (score of 19-21; see Figure S3).

Assessing the geographical distribution of moult phenotypes from photos

To test if *adult-type* birds also occur in other European localities, we collected georeferenced pictures on citizen-science databases across different European and North-African countries. We only collected data associated with pictures and obtained between 08/2013 and 02/2019, which corresponds to six successive wintering seasons and retained countries which regularly host the species in autumn and/or during the wintering period. After February, some first-winter birds are likely to finish the moult started in the autumn and cannot be distinguished from adult birds even in the hand (*pers. obs.*). We selected pictures of perched birds of sufficient quality showing the secondary coverts and tertials correctly. When several photos were available for a place and date where several birds were reported, we ensured no individual entered the data set more than once by comparing photos (individual birds usually differ in details of moult or plumage); in case of doubt, only one picture was selected from the available sample. We obtained a total of 344 pictures from 326 individuals (presumably all different from the birds we caught ourselves) from 17 European and North-African countries. Details on picture collections and websites consulted are available in Table S3. We assigned each bird to one of the three moult phenotypes identified during captures based on its moult score, *adult-type* moult phenotype including adult birds and first winter birds that had undergone an extensive post-juvenile moult.

We tested for the effect of latitude and longitude on the distribution of moult phenotypes by using ordinal logistic regression models (*MASS* package; Venables & Ripley 2002) with moult phenotype as a response ordinal variable, with a larger distance between *full-juvenile* and *adult-type* moult phenotype than between *full-juvenile* and *extended*. Since birds can move between seasons and since we expected vagrants to occur mostly during autumn, models were replicated for the autumn period (September – November) and the winter period (December – February). To evaluate the latitude and longitude effects, we calculated p-values by comparing the t-value against the standard normal distribution and 95% confidence intervals (CI) for the parameter estimates.

Tracking the breeding range of Richard's pipits with archival light loggers

We deployed Global Location Sensor loggers (GLS hereafter) to locate the breeding sites of Richard's pipits wintering in Southern France. GLS are small electronic devices that record time and light intensity, enabling the calculation of the approximate position of the logger given the duration of the day and the time of solar noon, both depending on latitude and longitude for a

given calendar day (Lisovski et al. 2019). GLS do not remotely transmit positions and have to be retrieved to download the data. Due to the equivalent day length, everywhere on Earth at the autumnal and spring equinoxes, latitudinal positions within 15 days on each side of the 2 equinox dates cannot be estimated accurately (see Phillips et al. 2004). The error of GLS locations during migration is known to vary up to 200 km (Phillips et al. 2004) but the precision is larger (in the order of a few dozen kilometres) when birds spend a long time at the same location (see Rakhimberdiev et al. 2016).

During the 2019-2020 winter period, seven INTIGEO P65C2-7 GLS (Migrate Technology, 0.74 g) were deployed (Covid-19 lockdown stopped the fieldwork season in early 2020) on 4 adults and 3 first-winter birds caught as explained above (see Table S4). We used leg-loop harnesses made from rubber bands to attach the loggers. The device and fitting material represented less than 3% of a bird's weight, since birds we caught weighted on average ($\pm$ SD) 30.5 ± 2.2 g ($n=64$). We retrieved three devices the next winter, containing data from at least one complete migration (Table S4). Return rates of GLS-equipped birds did not differ obviously from those that have been coloured-ringed during winter 2018-2019 and re-sighted during winter 2018-2019 (42% of returning GLS-equipped bird and 33% of returning colour-ringed individuals, but note small sample sizes).

We followed the method described in Lisovski et al. (2020) to analyse the light data. We used the *TwGeos* R package (Lisovski et al. 2015) to define twilights with the *preprocessLight* function, using a threshold of 2.5 lux. We manually removed obviously erroneous twilights and applied an additional automated screening using the *twilightEdit* function (settings were window = 4, outlier.mins = 45 and stationary.mins = 25). We then used the *FLightR* package (Rakhimberdiev et al. 2017) to determine migration timing. Since, the package requires calibration periods during which the bird is stationary in a known location, we ran the model a first time using the month of March as calibration period and with a particle filter of 10^4 particles (colour-ringed birds were observed throughout March on their wintering site, *pers. obs*). We then refined the calibration period using the *plot_lon_lat* function (plot of latitude and longitude in horizontal layout). We defined the *FLightR* search grid between 35° S and 65° N latitude and 0° W and 100° E longitude and ran the particle filter with the recommended 10^6 particles. We estimated the breeding location, migration timing, potential stationary periods and their locations using the *stationary.migration.summary* function by defining a minimum duration of stationary period of 24 hours and testing different values of minimum probability of movement (*prob.cutoff*). We estimated the migratory route and the

distance travelled via the shortest route (i.e. a great circle route; *distHaversine* function in the *geosphere* R package, Hijmans et al. 2015) between these different stationary locations.

Wintering niche comparison

To compare environmental niches of birds wintering in their ancestral Asian areas and birds wintering in Europe, we collected occurrences of Richard's pipit from the Global Biodiversity Information Facility (<https://www.gbif.org/>). We selected occurrence data for the wintering period alone (between December and February, included) and from countries known to host the species regularly during this period (see details of the countries considered in Table S5). We retained verified and georeferenced occurrences, resulting in 1,268 occurrences for Europe and North-Africa and 6, 717 occurrences for Asia. Data were then thinned prior to analyses using the *spThin* package (Aiello-Lammen et al. 2015) with a thinning parameter of 0.5 kilometres, leaving a total of 1,638 occurrences.

Since environmental conditions seem to play a key role in the selection of species' wintering grounds, particularly for finding the resources necessary for winter survival (Thorup et al. 2017), we collected several climatic and habitat variables related to the species preference (Alström et al. 2003). We downloaded the temperature and precipitations of the winter months (between December and February), an aridity index (corresponding to the ratio of the mean annual precipitation on the mean annual potential evapo-transpiration) and a discrete habitat variable separating open and closed habitats. The climatic data were collected from the CHELSA database v1.2 (<http://chelsa-climate.org>) at a resolution of 30 arc seconds, with monthly mean temperature and precipitation averaged over the period 1979– 2013 (Karger et al. 2017). The aridity index was collected from the CGIAR-CSI Database (<http://www.cgiar-csi.org>) at a resolution of 30 arc seconds for the period 1970–2000 (Zomer et al. 2008) and habitat variable from the Global Land Cover Map (GlobCover; Arino et al. 2012). The habitat variable was coded as “open” and “closed” habitats based on GlobCover categories; crop and mosaic habitats with more than 50% of cropland or grassland were considered as open habitats whereas mosaic habitats with less than 50% of cropland or grassland and more than 50% of forest or scrubland were considered as closed habitats. We checked that variables were not collinear (correlation coefficients < 0.50) using occurrences in both European and Asian regions, resulting in five variables to represent environmental variation among regions: PRW (precipitation during winter months), TW (temperature of winter months), AR (aridity), OH (open-habitats) and CH (close-habitats).

Environmental niche variation was evaluated using principal component analysis (PCA) implemented in the *ade4* package (Chessel et al. 2004). We assessed the variation between the European-North African and Asian wintering ranges by comparing the coordinates of occurrences in a two-dimensional environmental space (PC1 x PC2). We then calculated three niche metrics using occurrence densities along the two first axes of PCA (Broennimann et al. 2012; Petitpierre et al. 2012) in the *ecospat* package (Di Cola et al. 2017). We then evaluated the niche overlap between the Asian and the European niches using Schoener's D (Schoener 1968). We also evaluated the percentage of inclusion of the European niche in the Asian niche by measuring the intersection between each convex hull defined from 100% of locations.

To identify areas in Europe and North Africa that are suitable to the species but where it is not known to winter and thus is possibly overlooked, we performed niche distribution models with the *BIOMOD* package (Thuiller 2003; Thuiller et al. 2009) implemented in the *biomod2* package v3.3-7.1 in R (Thuiller et al. 2019). For each region, an ensemble of projections from four statistical models was obtained, including random forest (RF), generalized linear models (GLM), generalized additive models (GAM) and general boosting method (GBM; Araújo & New 2007, Marmion et al. 2009). Models were calibrated for the baseline period using 70% of observations randomly sampled from the initial data and evaluated against the remaining 30% data using the true skill statistic (TSS; Allouche et al. 2006) and the area under the curve (ROC; Swets 1988). For each model, the relative importance of each environmental variable was assessed by calculating the Pearson's correlation between the standard predictions (i.e. fitted values) and the predictions after randomly permuting the values of the variable. The ensemble forecasting was then built by assigning weight to each individual model depending on its quality (TSS) and taking the weighted sum of probabilities. Both calibrated models were projected under current conditions over Europe – North-Africa and Asia.

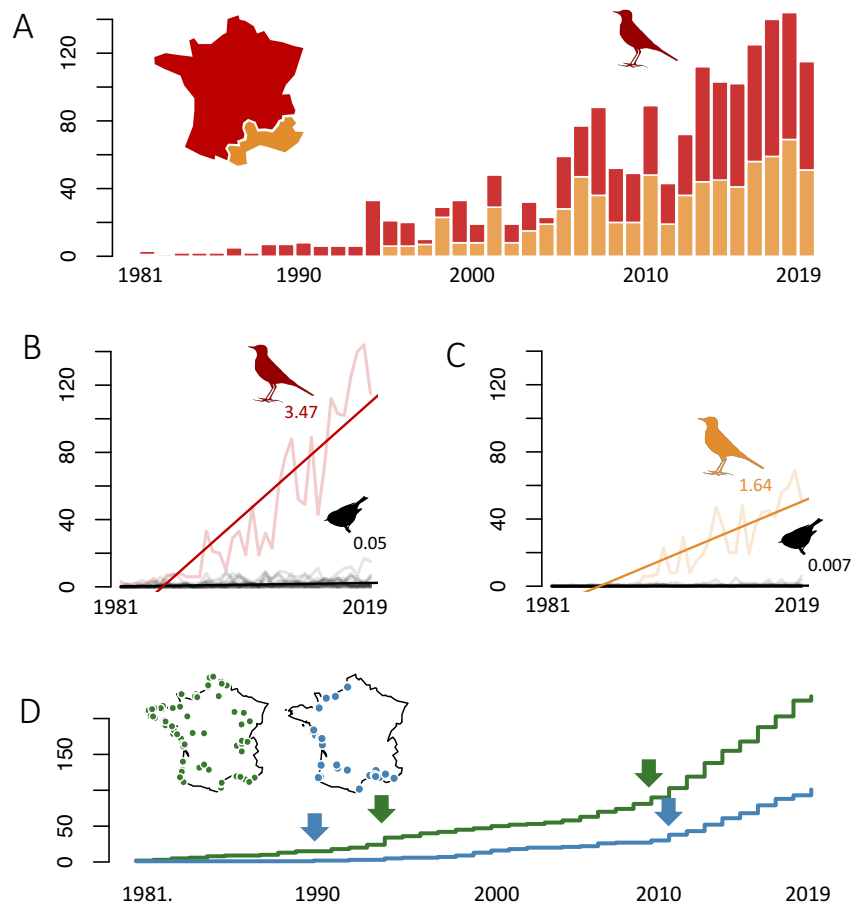


Figure 2. Trends in Richard's pipit occurrences in France during the last decades

(A) Evolution of the number of Richard's pipits observed in the Mediterranean regions (orange) and in other French regions (red) between 1981 and 2019. Barplots (orange + red) thus indicate the number of birds observed in the entire France. Comparison of trends in the number of Richard's pipits (red and orange) versus other vagrant species of eastern origin (black) regularly observed in the entire France (B) and in the Mediterranean regions of France (C) over the same period (1981-2019). Regression lines and coefficients are shown on each graph. See the Materials and Methods section regarding the choice of other Siberian species. (D) Evolution of the number (cumulative) of locations frequented by Richard's pipits during the migration period (green; September-November and March-May) and the winter period (blue; December-February) over the period (1981-2019). Approximate locations are indicated on the two schematic maps. The first case of wintering recorded in southern France in 1991 is indicated by the first blue arrow (left; Dulau 1997). Other arrows indicate main changes in the trends of locations frequented.

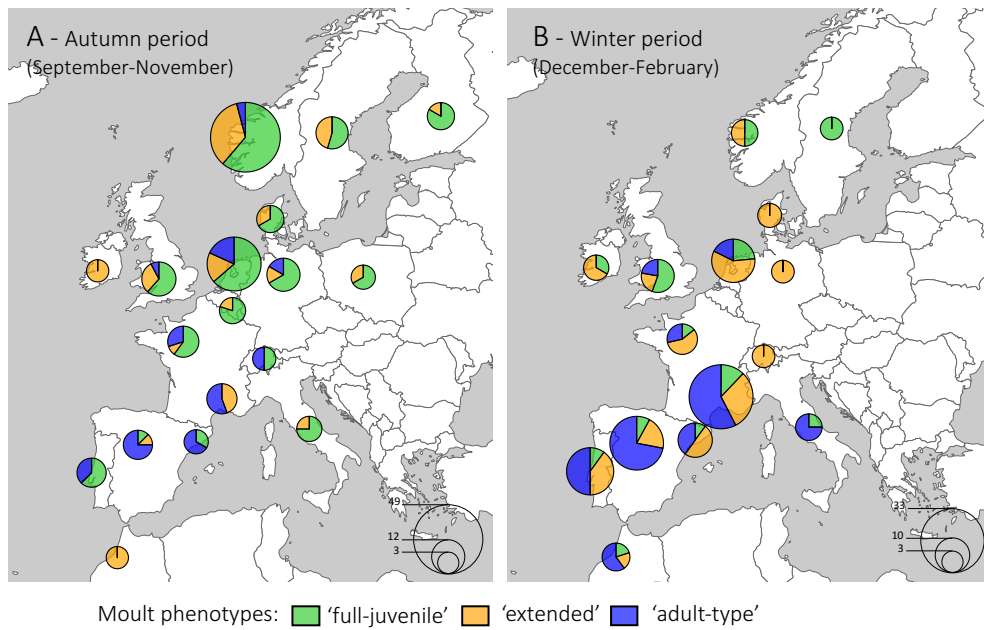


Figure 3. Variation in moult phenotypes in Richard's pipits observed in Europe

Geographical variation in moult phenotypes of Richard's pipits photographed in European and North Africa between 2013 and 2019 in autumn (A) or during winter (B). Moult phenotype is a proxy for age, with *full juvenile* + *extended* entirely made of young birds while *adult-type* is a mixture of adult and young birds (we found 17% of young birds within the adult-type birds in our captures). The size of the pie charts depends to the number of data collected per country (see inset). France is divided between the Mediterranean coast and the rest of the country.

Results

Trends in Richard's pipit occurrences

We found an unequivocal increase in the number of Richard's pipits observed in France between 1981 and 2019 both in the Mediterranean regions and in France in general (Figure 2A). While the numbers fluctuated between 3 and 6 birds in France between 1981 and 1993, they increased almost linearly from 1994 onwards with a maximum of 144 birds noted in 2018. The numbers of other vagrant species of eastern origin clearly did not increase as much with time as those of Richard's pipits in France between 1981 and 2019 (average and standard deviation of r^2 calculated for each vagrant species of 0.050 ± 0.057 and 0.009 ± 0.013 against 3.47 and 1.63 respectively for Richard's Pipits in France and the Mediterranean regions; Figure 2B-C). We also found that the number of wintering sites slowly increased from the 90s before rising considerably faster from 2010 onwards, like the number of sites occupied during migration periods (Figure 2D).

Returning individuals

We caught a total of 72 birds in southern France and northeast Spain during the course of the three ringing seasons; numbers varied from 21 birds in La Crau, representing a small fraction of the all birds there (based on numerous sightings of unringed birds, *pers. obs.*), to 1 or 4 birds in Fréjus, representing all birds present there. Indeed, most sites are used by a small number of individuals that remain all winter, but in La Crau we recaptured or re-sighted only 3 individuals out of the 42 ringed, indicating that this area either holds very large number of birds or is used as a migration and staging site and not only a wintering site (see Table S2). We caught 24 (33 %) adult birds among the 72 different individuals. This number varies between sites (Table S2) and between periods (62.5% of adult birds were caught over the December-March period). Compared to other sites, a very large proportion of first-winter birds (82 %) were caught in La Crau during the three ringing seasons. Among the 25 birds colour-ringed or equipped with GLS over the December-March period, 9 (36 %) have been re-sighted during subsequent winters, including four birds ringed during the 2018-2019 winters that have returned in 2019-2020 and 2020-2021.

Geographical distribution of moult phenotypes

Among the 46 young birds (i.e. hatched in the previous summer) that we captured in southern France, 6 were of the *full-juvenile* type (13 %), 35 belong to the *extended* type (76 %) and 5 to the *adult-type* (11 %). We thus estimated that first-winter birds having completed an extensive

post-juvenile moult thus only represented a small fraction of adult-type birds in our captures since 83% of *adult-type* birds were true adult birds (24 out of 29 *adult-type* birds).

Among the 326 individuals examined, we identified 115 *full-juvenile* (35%), 115 *extended* (35%) and 96 adult-type (30%). We found that the distribution of moult phenotypes varied greatly across Europe and North Africa and between the autumn and winter periods (Figure 3) with notably high proportions of *full-juvenile* birds in autumn in northern Europe and high proportions of *adult-type* birds in southern and southwestern Europe and North Africa in winter. Ordinal logistic regression analysis confirmed these results with significant p-values for a latitudinal effect for the winter (p-value < 0.001) and the autumn (p-value = 0.002) periods but we did not find any significant effect of longitude.

According to the capture results, a part of *adult-type* birds estimated in Iberian Peninsula, North-Africa (Morocco), southern and Western France and Italy were likely true adult birds. However, in localities where the proportions of *adult-type* birds during winter were relatively low (i.e. less than 20% in United Kingdom, the Netherlands), we did not exclude that they were first-winter birds having completed an *extensive* post-juvenile moult.

Breeding locations of Richard's pipits wintering in Europe

We tracked the migration of three Richard's pipits equipped in 2020: an adult (BW367) in Labruguière (southern France), an adult (BW376) and one first-winter (BW372) in Lespignan (southern France; Figure 4; Table S4). The BW372 logger stopped recording in the end of July 2020. The three loggers, retrieved in November 2020 (BW272 and BW376) and in January 2021 (BW367) enabled us to identify the breeding location used by these birds. These two birds breed in a small area at the western edge of the known breeding distribution of the species, in the Novosibirsk Oblast, Russia (BW367 around 55°21' N, 77°32' E; latitude SD $\pm$ 1.3 longitude SD $\pm$ 2.1; BW376 around 54°08' N, 79°48' E; latitude SD $\pm$ 0.8 longitude SD $\pm$ 1.3; BW372 around 55°21' N, 79°54' E; latitude SD $\pm$ 0.4 longitude SD $\pm$ 0.6). Since tracked-birds made their autumn migrations close to the equinox period, the tracks are difficult to interpret and we only present here the spring migration tracks.

Both adult individuals stopped on three different stopover locations for more than 24 hours during their spring migration. The first individual even made a fourth stopover further east before moving a likely breeding site where it did not move from mid-June until the end of the summer period (Figure 4A). The first-winter individual first headed north and stopped around Sweden before redirecting eastward. It thus made three stopovers of more than 24 hours and two stops of about two weeks before reaching a likely breeding site where it did not move

until the GLS stopped recording data (Figure 4C). We estimated that the distance travelled by these individuals during their spring migration was respectively of 7320 km (BW367), 5750 km (BW376) and 7045 km (BW372).

Wintering niche comparison

The PCA of the 1,638-thinned occurrences revealed two significant axes of environmental variation (Figure 4A). The first axis (PC1, 39.6% of total variance) differentiated the environmental spaces between wintering ranges with warmer and less-humid winters in Asia than in Europe. The second axis (PC2, 26.4% of total variance) was mostly associated with the opening of the habitats with Asian niches having more often closed habitats than in Europe. The European wintering niche showed overlap with the Asian wintering niche with Schoener's D of 0.31 ($D = 0$: no overlap, $D = 1$: complete overlap). We found that 68.8% of the European niche was included within the Asian niche without considering occurrence densities.

The quality of distribution models was high for both areas and both TSS and ROC values (Figure S4). The most relevant environmental variables in the prediction of Richard's pipit distribution were the temperature of the winter months (TW) for both areas and the aridity index (AR) for Europe – North-Africa (Figure S5). Projection of the Asian calibrated model under current conditions over Europe did not predict wintering in the Mediterranean basin (southern France, Catalonia), suggesting that the species winters, at least in these areas, outside its Asian climatic niche. Projections under current conditions over Europe – North-Africa and Asia of both calibrated models showed many areas in North Africa where the species could find suitable conditions for wintering (Figure 4B-D) but has rarely been reported yet. These include the coastal plain in North-West Morocco and the coastal plain area between Alger and Tunis (in Algeria and Tunisia).

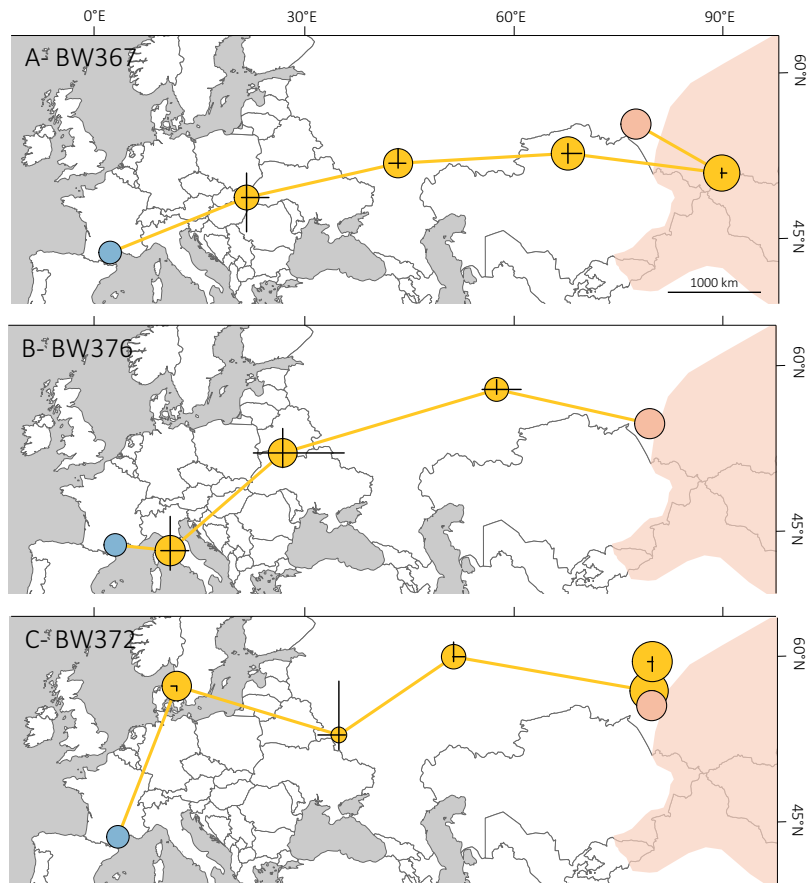


Figure 4. Migration routes, stopovers and breeding site of three GLS-tracked Richard's pipits Spring migration of the individual BW367 in (A), individual BW376 in (B) and BW372 in (C). All birds were tracked in 2020. Blue dots indicate the wintering location (Labruguière in (A), Lespignan in (B) and (C); southern France) where the GLS was deployed. Pink dots indicate the estimated breeding location, at the limit of the known breeding distribution (BirdLife International 2020). Other dots with standard error indicate estimated stopovers sites where the bird stayed more than 24h. The sizes of these yellow dots are proportional to the length of the stopover.

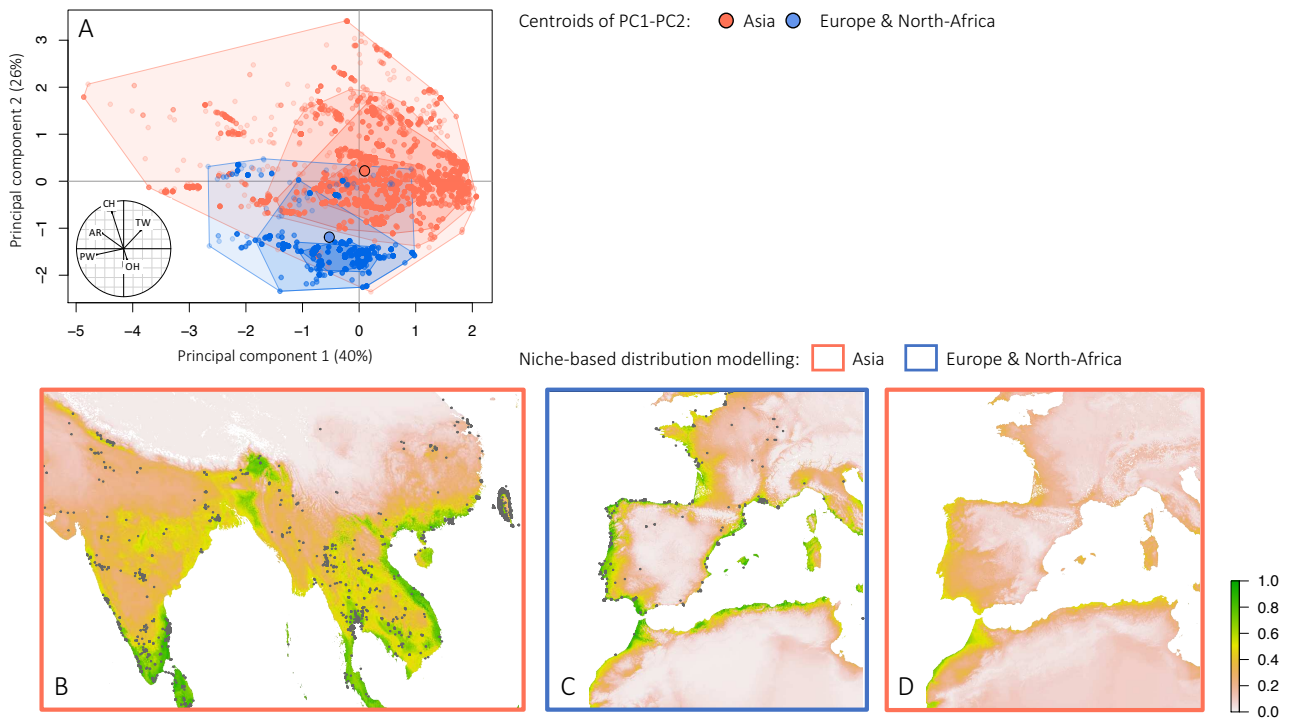


Figure 5 Wintering niches comparisons and niche-based distribution modelling.

(A) Niche comparisons between birds wintering in Europe and North-Africa (blue) and birds wintering on their ancestral wintering area in Southeast Asia (red). The convex hulls indicate the prevalence (25%, 50%, 75%, and 100% of locations included) of the environmental conditions. Small dots indicate GBIF occurrences and big black-circled dots indicate the centroids. The correlation circle (inset) indicates the importance of environmental variables on the two first axes of the PCA: PRW (precipitation during winter months), TW (temperature of winter months), AR (aridity), OH (open-habitats) and CH (close-habitats). Maps (B) and (C) figure predicted areas from models calibrated respectively in Asia (B) and in Europe and North-Africa (C). (D) Habitat suitability from models calibrated in Asia and projected over Europe and North Africa; grey dots are GBIF records (see Table S4 and the Material & methods section).

Discussion

Richard's pipits migrate from Asia to spend winter in Europe and North-Africa

This study demonstrates for the first time that some Richard's pipits, a complete migrant whose breeding range lies entirely in Asia, winter in western Europe (Gilroy & Lees 2003). This is based on the presence of a significant proportion of adult birds on European wintering sites and on the return of marked birds during consecutive winters, some of which have been tracked to their breeding grounds by GLS loggers. The presence of adult birds in wintering sites implies that these individuals have already made the journey to Europe during previous migrations, since most complete migrant passerines use the same migration route and wintering areas in successive years (e.g. van Wijk et al. 2016). It is thus highly improbable that individuals migrating to Southeast Asia during their first migration would migrate to Europe the following year (see Helbig 1991). The geographic distribution of moult phenotypes shows that adult birds are also present in winter in the Iberian Peninsula, North Africa (Morocco), Western France and Italy. The GLS tracking data confirmed that Richard's pipits wintering in Europe breed at the western margin of the known breeding distribution in Asia (Alström et al. 2003, BirdLife International 2020). They migrate 6,000 km in average between southern Europe and Central Asia/southern Siberia to the border with Russia, Kazakhstan and Mongolia.

Richard's Pipit's migration to Europe clearly represents a secondary evolution since the main wintering grounds of the species are in southern (India, Nepal, Sri Lanka, Bangladesh) and Southeast Asia (Myanmar, Thailand, Laos, Vietnam; Alström et al. 2003). No other migratory passerine that breeds entirely in Asia winters regularly in Europe (Yong et al. 2015) and all these species winter in southern and Southeast Asia. In addition, its sister species, the Blyth's pipit *Anthus godlewskii*, breeds in Central Asia and also winters exclusively in southern and Southeast Asia (Alström et al. 2003). We are thus confident that the ancestral migration route is towards southern and Southeast Asia, and that the migration towards Europe is a secondary evolution. Determining when the westward migration route evolved is currently not possible but several lines of evidence suggest that this is recent. Firstly, while the species has long regarded as regular during winter in Arabia and the Middle East (see Cramp & Simmons 1983, Hollom et al. 1988, Alström et al. 2003), the wintering of the species in Europe had not been properly documented before 1991 (Dulau 1997, Biondi & Grussu 2004). Cramp & Simmons (1983) reported the species as wintering in southern Spain and some areas of Northwest Africa but this was based on very scant data. Secondly, in spite of a recent upsurge of records in Europe and a clear increase in both the number of birds and number of sites used in winter in Europe, the species remains a scarce visitor here. Our preferred scenario is thus that

a few birds have been using a westward migration route for decades and that this route has recently been selected more strongly, resulting in an increase of the population using it. As it seems highly improbable that this route would have been used for a very long time while remaining very rare, we hypothesize that migrating to Europe evolved recently in ecological times.

This new migration route now implies that Richard's pipit has disconnected wintering grounds in both South/Southeast Asia (west to the Middle East) and southwestern Europe / northwestern Africa, which is not known in any other Eurasian passerine breeding exclusively in Asia. The only known examples of somewhat similar routes are Northern wheatear *Oenanthe oenanthe* from Alaska (USA, Barlein et al. 2012) and Willow warbler *Phylloscopus trochilus yakutensis* from northeast Russia (Sokolovstki et al. 2018) that migrate in a westerly direction through Siberia to reach east African wintering quarters. However, these two populations represent the margins of the breeding distribution of species that breed across Eurasia to Western Europe and their migration is interpreted as evolutionary conservatism of ancestral migration routes as a result on constraints on the evolution of migration (Sokolovstki et al. 2018). In terms of evolution, they are thus the opposite of the Richard's Pipit: their migration is the consequence of the conservation of their ancestral wintering areas, while in Richard's Pipit the migration route to Europe results from the colonisation of new wintering areas.

Selection and inheritance of this migration route

It is now well established that numerous small passerines genetically inherit a migratory distance and direction that determines the general area of their wintering grounds (e.g. Helbig 1991, Delmore et al. 2016) and that learning only allows individuals to repeat their routes (see Thorup et al. 2007, Chernestov et al. 2017). Several studies suggest that multiple chromosomal regions are typically involved in the determinism of the migration orientation (e.g. Lundberg et al. 2017, Delmore et al. 2016). If we assume a polygenic determinism of orientation in Richard's Pipit, effective selection of this novel migratory direction between Central Asia and southern Europe requires some forms of reproductive isolation between individuals migrating west and east, as panmixia would prevent the stability of migration to Europe (see Bearhop et al. 2005). Barriers to reproduction have been documented in most case where there is intraspecific variation in migration orientation (Lievogel & Delmore 2018, Turbek et al. 2018); these barriers can be prezygotic, when differential timing of arrival on the breeding site can lead to assortative mating (Bearhop et al. 2005) or post-zygotic, when hybrids undertake inferior migratory routes and experience suboptimal life conditions (Rohwer & Irwin 2011,

Delmore & Irwin 2014). In birds, barriers to reproduction are mainly found in migratory divides where parapatric populations using two distinct migration orientations are in contact (Irwin & Irwin 2005, Moller et al. 2011). We suggest that a migratory divide could exist in Richard's Pipit, with individuals at the western margin of the species' range all having a westerly migration route. Of course, this is entirely speculative and will need to be tested by deploying data loggers on birds breeding in this part of the range. If this hypothesis is validated, the next step would be to identify the geographic location of the divide.

The positive selection of this new migratory route seems counter intuitive as it leads to a much longer journey (at least in straight line) to the wintering grounds: direct flight from the western edge of the breeding range to the closest wintering grounds are 3000 km, against 6000 km to Europe. However, Delany et al (2017) suggested that the species sometimes occur at high altitudes in the Himalaya but not west of the Himalaya. If the species really crosses through the Himalaya or goes around the east of the Himalaya to reach Southeast Asia, then individuals breeding at the western margin of the distribution might fly comparable distance or need a comparable amount of energy to reach southern Europe or southern Asia. Although a better understanding of the migratory routes of this species would be necessary, it suggests that migrating to Europe might not be as costly as one would imagine by looking at straight-line distances on a map. Avoiding the difficult conditions that crossing the Himalaya imply (see Alerstam & Lindström 1990, Delmore & Irwin 2014) might be especially important. It would also be interesting to investigate whether the species suffer from present or past modifications of its ancestral wintering habitats, which could provide a further advantage to wintering in Europe (e.g. Dolman & Sutherland 1995, Taylor & Stutchbury 2016).

Vagrancy may promote the discovery of new wintering areas and changes in migration routes
As suggested by Rabøl (1969, 1978), the study of vagrant birds and the origin of their occurrences could help to understand better the orientation mechanisms used by migratory birds. We still poorly understand why some species exhibit vagrancy behaviour and how it is determined, whether by genetic changes or phenotypic plasticity. If vagrancy has some genetic basis, it is an obvious candidate mechanism for the emergence of new migration routes. In Richard's Pipit, it is entirely possible that the emergence of the new western migratory route results from the survival and successful reproduction of vagrants arriving in Europe which transmitted this orientation to their offspring. Indeed, the migration route followed by Richard's pipit between Central Asia and southern Europe corresponds with what has been described as large angle misorientation, also known as reverse migration (Rabøl 1969) or mirror-image

migration (DeSante 1983). This hypothesis had been proposed to explain the appearance of Siberian vagrants in Europe, particularly for populations breeding in the western part of the distribution of these species (see Thorup 1998).

The hypothesis that survival vagrants arriving in Europe may have enabled the evolution of this migration route is also supported by the large proportion of first-winter birds, especially birds with a *full-juvenile* moult phenotype, in northern Europe in autumn. While we cannot exclude that some of these birds are regular migrants on their way to their wintering sites further south, it is likely that the majority of these birds are vagrants because this moult phenotype is very rare at this time of year in the normal range of the species (see Alström et al. 2003). The higher proportion of birds with retarded moult in northern Europe compared with southern Europe or Asia supports the idea that a large proportion of the birds seen in Northwest Europe in autumn are indeed vagrants.

The role of vagrancy in colonisation of a new breeding range has been witnessed in several species (e.g. Holt 1933, Veit & Lewis 1996, Massa et al. 2014, Dufour et al. 2017). Our study supports the hypothesis that vagrancy may also promote the establishment of new wintering areas and the establishment of new migration routes, as suggested by Gilroy & Lees (2003), even if most vagrants undoubtedly fail to reorient and die before reproduction. Indeed, misorientation has usually dramatic consequences on fitness (e.g. Delmore & Irwin 2014), especially in passerines where the energy cost of flights of several thousand kilometres is very high (Alerstam 1991). The ability of vagrants to survive will depend crucially on the wintering conditions they encounter, and encountering conditions similar to their usual wintering conditions will likely increase their probability of survival. Accordingly, our niche modelling results identified several areas in North-Africa and west Iberia where the climate is suitable to the species in winter based on similarity with the winter conditions of their Asian range. However, part of the wintering range in Europe lies outside the climatic envelop of the Asian wintering range, suggesting that the climatic variables we used do not entirely explain the realized niche in Asia. Nevertheless, the global increase in temperature may have also made the south of France and the Iberian Peninsula more suitable for the wintering of the species over the last decades and thus favoured the wintering establishment of the species and the selection of this migration route.

In addition, Richard's pipit would encounter similarly suitable climatic conditions in winter in large areas of North Africa, suggesting that the low coverage by ornithologists and birders in these areas explains why they are currently rarely recorded there. Dedicated field work would be desirable to check if Richard's Pipit, but also other species of Siberian origin

that have also increased in recent decades in Europe (notably Yellow-browed warbler *Phylloscopus inornatus* or Little bunting *Emberiza pusilla*; Thorup 1998, Gilroy & Lees 2003), could also be found in these areas in winter.

Conclusion

This study demonstrates the recent selection of a migration route leading Richard's Pipits breeding in Central Asia to new wintering areas in southern Europe and North Africa, instead of reaching their ancestral wintering areas in South East Asia. This type of event reveals the complexity of predicting change in migratory habits and on how to consider them in dispersion models (Kot et al. 1996). Such an event also shows how difficult it can be to predict adaptation and changes in the distribution of migratory birds and animals in the context of global changes. Finally, this study calls for more consideration of the vagrancy behaviour and its underestimated evolutionary role in the discovery of new breeding locations or new wintering sites (therefore in the establishment of new migration routes).

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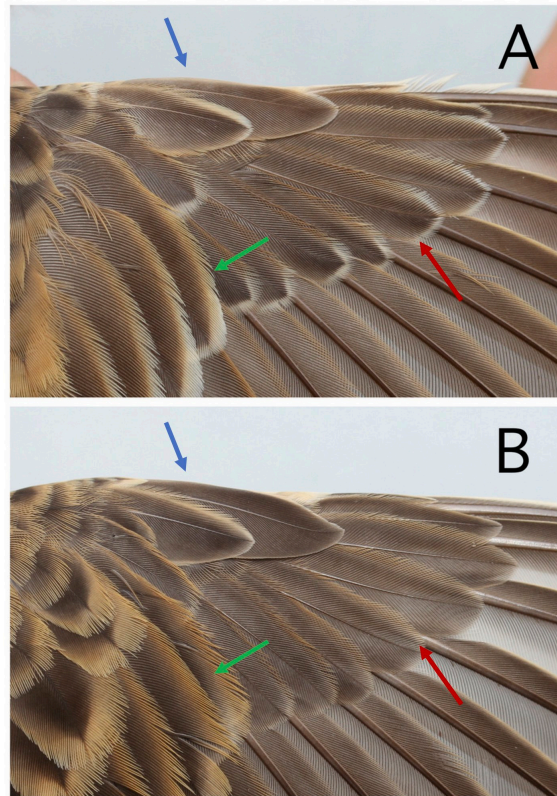
Supplementary information

Figure S1. Illustration of the difference in shape and colour between juvenile (first-winter, A) and adult feathers (B). Blue arrows indicate alula, green arrows indicate greater coverts and red arrows indicate primary coverts. Juveniles feathers are mostly thinner, browner and white-surrounded than adult feathers. Examination of primary coverts in hands remains the only manner to ensure ageing in Richard's pipit (P. Alström *pers. com.*). Photos Paul Dufour.

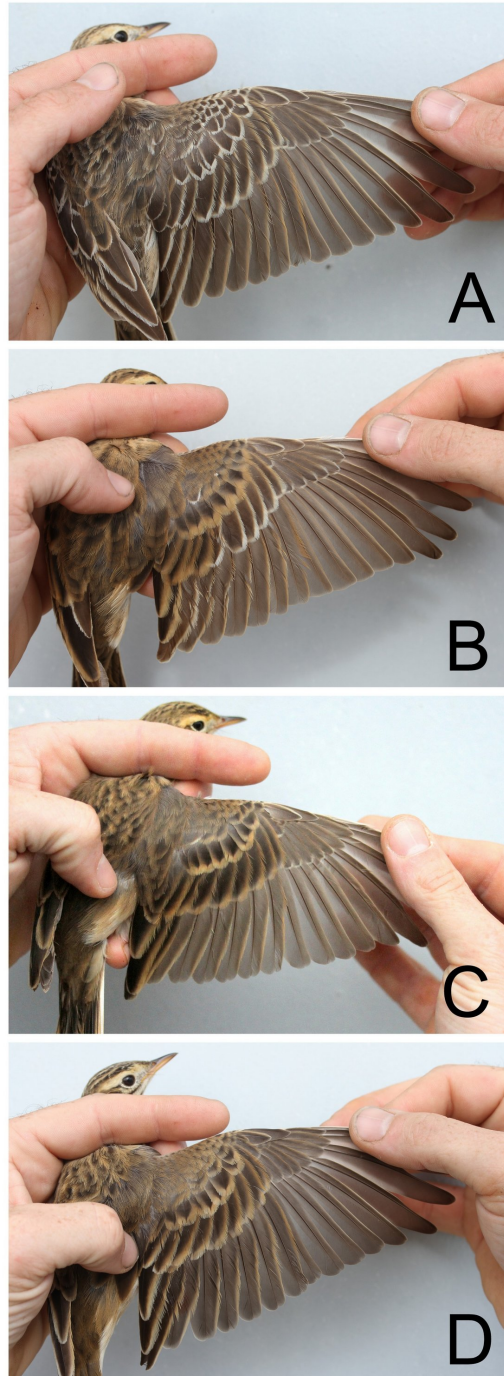


Figure S2. Illustration of the different moult phenotypes observed in captured Richard's pipits and described in this study. A: '*full-juvenile*', B: '*extended*', C: '*adult-type*' and D: adult bird for comparison. Photos Paul Dufour.

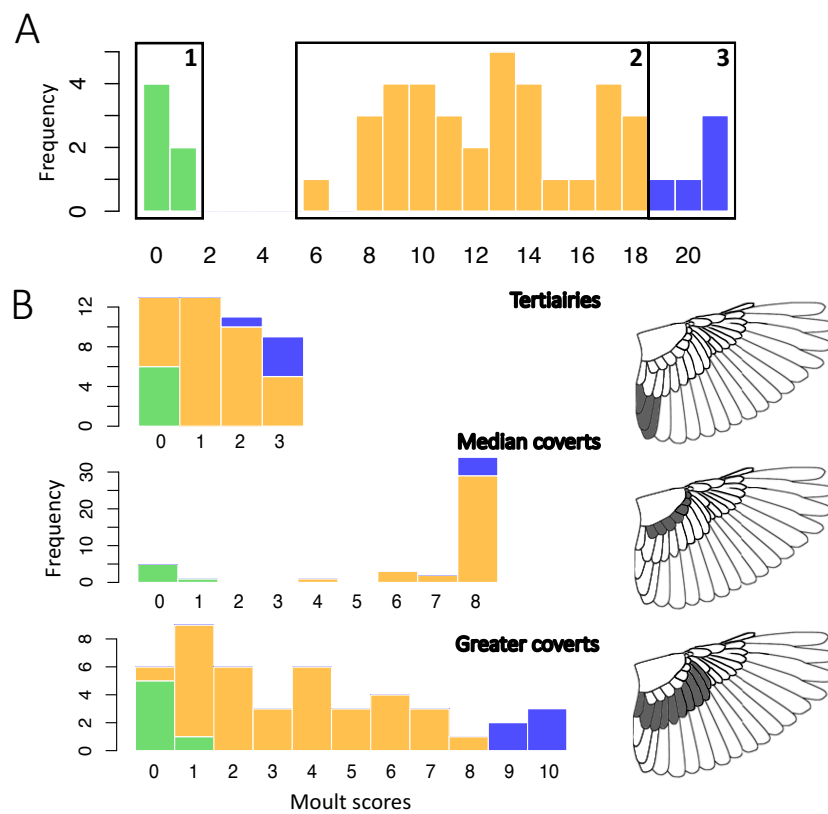


Figure S3. (A) Barplots representing the total number of moulted feathers in first-winter birds caught in this study. Colours and the three boxes represent the three moult phenotypes estimated: (1) *full-juvenile*, (2) *extended* and (3) *adult-type*. (B) Barplots representing the number of moulted feathers in tertialries, median and greater coverts scored from first-winter birds caught in this study.

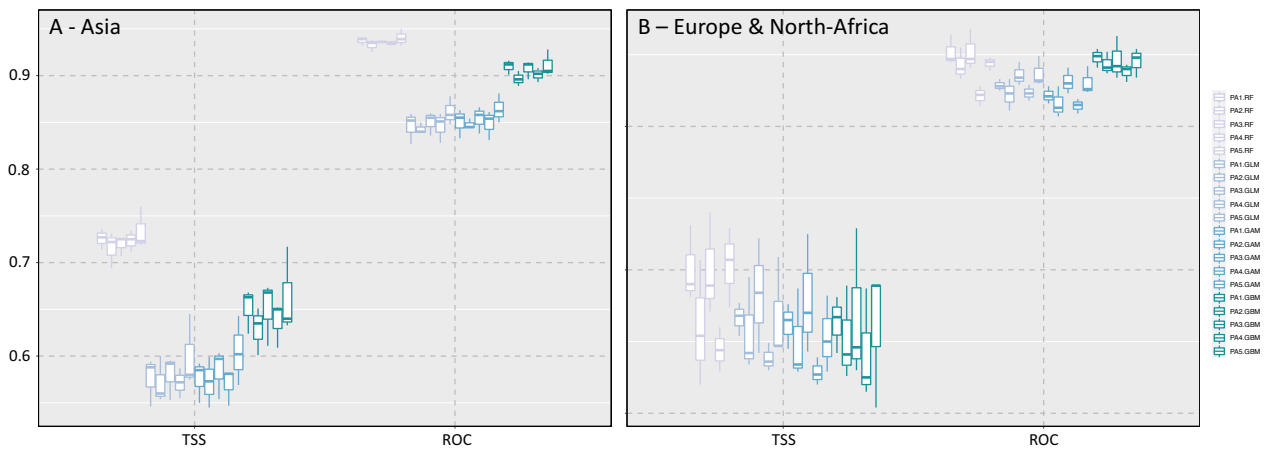


Figure S4. True skill statistic (TSS) and area under the curve (ROC) values obtained for the four statistical models tested. Models tested are random forest (RF), generalized linear models (GLM), generalized additive models (GAM) and general boosting method (GBM).

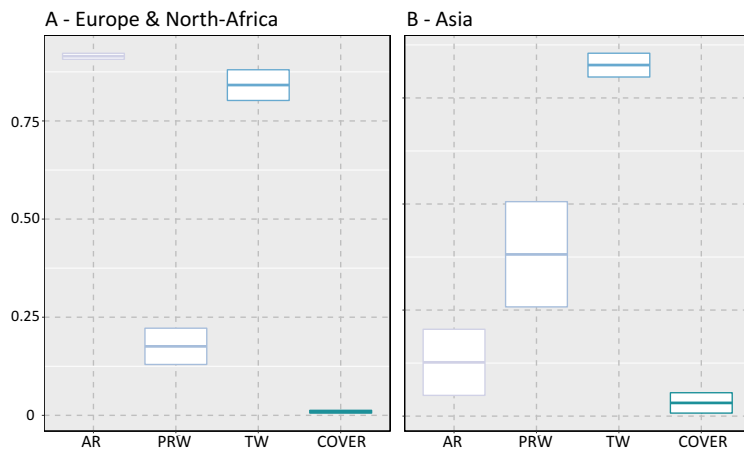


Figure S5. Relative importance (Pearson's correlation) of the four environmental variables used to project the potential distribution of Richard's pipit and obtained from calibration in Europe and North-Africa (A) and in Asia (B). PRW (precipitation during winter months), TW (temperature of winter months), AR (aridity), COVER (open and close habitats).

Table S1. List of species from eastern origin and total number of birds recorded in France and Mediterranean regions between 1981 and 2019.

Siberian species	Total record	
	France	Medit. Regions
<i>Acrocephalus agricola</i>	62	18
<i>Acrocephalus dumetorum</i>	22	1
<i>Anthus godlewski</i>	18	3
<i>Anthus hodgsoni</i>	40	1
<i>Emberiza leucocephalos</i>	55	8
<i>Emberiza pusilla</i>	205	29
<i>Emberiza rustica</i>	33	0
<i>Iduna caligata</i>	14	0
<i>Lanius isabellinus/phoenicuroides</i>	13	3
<i>Luscinia luscinia</i>	9	0
<i>Motacilla citreola</i>	62	26
<i>Phylloscopus borealis</i>	17	1
<i>Phylloscopus fuscatus</i>	87	6
<i>Phylloscopus humei</i>	38	3
<i>Phylloscopus proregulus</i>	133	18
<i>Phylloscopus schwarzi</i>	19	0
<i>Phylloscopus trochiloides</i>	30	3
<i>Saxicola maurus</i>	36	3
<i>Sylvia nisoria</i>	82	5
<i>Tarsiger cyanurus</i>	19	3

Table S2. Locations of the spots where Richard's pipits were captured during the different winters. The total numbers of birds captured, the number of adult birds among birds captured and the number of ringed birds re-sighted or recaptured in following winters are indicated. Numbers between brackets indicate the number of birds ringed during the 2018-2019 winters that have returned in 2019-2020 and 2020-2021. (-) indicates that no capture was made on the spot.

Sites	Country	GPS (lat, lon)	Winter 2018/2019			Winter 2019/2020			Winter 2020/2021		
			Total	Adult birds		Total	Adult birds	Control	Total	Adult birds	Control
Crau plain	France	43.57°N, 4.87°E	21	2		21	4	2	3	2	2 (1)
Fréjus	France	43.41°N, 6.73°E	4	2		1	1	1	-	-	1 (1)
Alenya	France	42.65°N, 3.00°E	2	1		1	0	2	4	3	1 (1)
Labruguières	France	43.54°N, 2.28°E	3	1		2	1	2	1	1	1 (1)
Lespignan	France	43.27°N, 3.15°E	-	-		3	2	-	1	0	2
Vilanera	Spain	42.11°N, 3.11°E	1	1		-	-	-	-	-	-
Camp Turies	Spain	42.23°N, 3.11°E	4	3		-	-	-	-	-	-

Tables S3. Details on number of pictures collected per websites and per countries to assess the distribution variation in moult phenotypes.

Countries	Websites	Pictures collected
France	https://www.faune-france.org/	59
Belgium	https://waarnemingen.be/	4
	https://www.trektellen.nl/	1
Holland	https://waarneming.nl/	44
	https://www.trektellen.nl/	6
Germany	https://www.ornitho.de/	13
Poland	http://www.clanga.com/	3
Denmark	https://dofbasen.dk/	9
Norway	https://www.artsobservasjoner.no/	53
Finland	https://www.tiira.fi/	6
Sweden	https://www.artportalen.se	11
	https://ebird.org/	1
Britain	https://www.birdguides.com/	22
Ireland	http://www.irishbirding.com/	2
	https://www.birdguides.com/	2
Italy	https://www.ornitho.it/	8
Switzerland	https://www.ornitho.ch/	3
Spain	https://www.reservoirbirds.com/	13
	https://www.ornitho.eus/	7
	https://ebird.org/	14
Catalonia	https://www.ornitho.cat/	13
Portugal	https://ebird.org/	32
Morocco	https://maroc.observation.org/	2
	https://ebird.org/	5

Table S4. Locations of the spots where seven Richard's pipits were GLS-equipped during the 2019/2020 winter season. The total numbers of birds equipped and retrieved the following winter are indicated.

Sites	GPS (lat, lon)	Deployed: 2019/2020		Retrieved: 2020/2021	
		Total	Adult birds	Total	Adult birds
Fréjus	43.41°N, 6.73°E	1	1	0	0
Alenya	42.65°N, 3.00°E	1	0	0	0
Labruguières	43.54°N, 2.28°E	2	1	1	1
Lespignan	43.27°N, 3.15°E	3	2	2	1

Table S5. Number of occurrences per countries collected in GBIF (<https://www.gbif.org/>). We considered verified and georeferenced occurrences within the wintering period (between December and February, included) for countries known to host the species during this period.

	Country	Nb of occurrences
<i>Europe and NA</i>	France	366
	Spain	440
	Portugal	439
	Italy	19
	Morocco	4
	Taiwan	3510
<i>Asia</i>	Thailand	977
	Hong-Kong	564
	China	215
	India	1098
	Myanmar	45
	Vietnam	41
	Laos	46
	Cambodia	107
	Sri Lanka	114

Siberian bird vagrants occurring in Europe may have become regular migrants

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With billions of individuals traveling twice a year, sometimes over tens of thousands of kilometers between their breeding and wintering grounds, birds are arguably the most vagile group of terrestrial organisms. Migratory birds also frequently engage in surprising long-distance movements, far off their normal breeding ranges, migration routes or wintering ranges. Such individuals are often referred to as vagrants (Kot et al. 1996, Veit 2000) and thus differ from seasonal migrants by the non-regularity of their movements. Vagrant birds generally encounter unsuitable environmental conditions and are rarely able to survive and return to their breeding grounds (Gilroy & Lees 2003). Thus, vagrants are young birds prior to their first reproduction, while seasonal migrants are logically young and adult birds that will regularly return to the same wintering area (van Wijk et al. 2016). Long considered to be of little or no biological interest, these vagrants nevertheless attracted the attention of naturalists, who have meticulously collected their annual occurrences for several decades (Booth et al. 2011). In some cases, the regular increase in the number of annual occurrences would suggest that some vagrants may have survived their misorientation of the preceding year, managed to return to their breeding sites, transmitted their migration route and become regular migrants (see the ‘pseudo-vagrant’ theory in Gilroy & Lees 2003). Yet, the role of vagrancy in the discovery of new suitable wintering areas and therefore in the evolution of new migration routes has rarely been investigated and tested empirically.

The Yellow-browed warbler (*Phylloscopus inornatus*) is a small passerine which breeds in a wide range extending from Urals to East Siberia (Anadyr region) and overwinters from Northeast Indian Subcontinent to Southeast Asia and Taiwan (Figure 1a). Like other Siberian species, vagrants Yellow-browed warbler have been noted in small numbers during autumn in Western Europe since the 1950s, while the species is not known to undertake seasonal migration to Western Europe and North Africa (Thorup 1998, Thorup 2004). Over the last few decades, occurrences of this species remarkably increased in autumn and winter, more than the increasing observation and ringing pressures would suggest (see Figure 2 and Appendix 3, Tonkin & Perea 2019). It has been proposed that this change in occurrences may result of the presence of regular migrants using a newly selected migration route to reach newly established wintering areas in southern Europe (Gilroy & Lees 2003). But this hypothesis has also long been regarded as unlikely because of the major change in direction involved (Figure 1a).

Recently, the recovery of a ringed Yellow-browed warbler the winter following its capture in Andalusia (Spain) has shed light on the possibility of returning migratory individuals (Tonkin & Perea 2019). However, given the poor knowledge of the wintering sites used and the average weight of the species of 5g, it was not possible to set up color-ringing or individual

tracking to assess whether this returning case was anecdotal or not. To test if a significant proportion of Yellow-browed warblers observed in Europe were truly migrating individuals (and not only “lost” vagrants), we evaluated the presence and distribution of adult birds among birds captured during autumn in Europe. Since migratory individuals generally repeat the general route and migration direction that had been proven successful in the previous year (van Wijk et al. 2016), we hypothesized that it is very unlikely that individuals migrating to Southeast Asia during their first migration would then migrate to Europe the following year. Thus, adult birds have most likely already been to Europe in their previous migrations and can be considered as regular migrants. To do so, we set up a standardized-picture protocol that we distributed to several ringing stations in Europe regularly capturing this species (see Figure 1b and Appendix 1 & 2). Pictures were collected, randomized and evaluated by three observers, used to handling this species, to propose an age estimation for each individual. Since estimating the age of this species is very challenging (Norevink et al. 2020), observers were asked to assign to each individual as: first-calendar (1A), possible first-calendar (1A?), possible adult bird (+1A?), adult bird (+1A) or indeterminate (i.e. when the observer judges that pictures do not allow an accurate estimate of age). Then, we examined whether the distribution of the age ratio varies across Europe. Assuming that regular migrants would likely pass through Europe to reach wintering areas located in the Iberian Peninsula and North Africa (see Tonkin & Perea 2019), we expected that adult birds will most often be observed on the most direct flyway, commonly used by other European migratory birds (Nilsson et al. 2019). This would correspond of passing through continental Europe and approaching the Mediterranean or Atlantic Ocean & Channel sea coasts to avoid the Alps and cross the Pyrenean barrier (Nilsson et al. 2019, see Figure 1a). We also suspected that birds observed outside this flyway would be most likely young birds on their first migration (see “coastal effect” in Ralph 1981) or vagrants flying in the wrong direction (see Thorup et al. 2012). We therefore expected to find a negative effect of latitude and longitude on the age distribution, with more adult birds estimated in southwestern Europe. To test the effect of latitude and longitude on age distribution, we fit a linear model with age as the response variable (coded as 1: 1A, 2: 1A?, 3: +1A?, 4: +1A), latitude, longitude and observers as fixed effects and individuals identity as a random effect. By compiling data from all observers, we wanted to give more weight to individuals that received the same age estimations. To support our assumptions on bird movements within Europe, we also collected intra-annual recapture data of Yellow-browed warblers from the EURING database (see Figure 1c).

We collected standardized pictures for 291 individuals coming from seven European locations (Figure 1b). Most pictures were taken during the last two years (39 individuals in 2019, 14%; 167 individuals in 2020, 57%) or between 2014 and 2018 in Messanges (Southwest France) and in Ottenby fågelstation (Sweden) where standardized pictures have been taken since 2014 (respectively 54 and 22 individuals between 2014 and 2018, 19% and 8%). An average number of 2.31 % (SD ± 1.16 , N=6.75) adult or 7.64 % (SD ± 2.53 , N=22.25) possible adult birds has been estimated by the observers, varying according to locations (see Figure 1b and Appendix 4). Consistently among observers, age estimations showed that adult birds were most likely captured in southwestern Europe, especially in western and southwestern France (Figure 1b). In smaller numbers, adult birds have also been estimated in the Netherlands, Spain and southern France. Conversely, almost only juvenile birds were estimated in Scotland and Sweden. The statistical test showed consistency between observers and a negative and significant effect of longitude on age distribution (p-value < 0.001), but failed to find an effect of latitude (p-value = 0.120, see details in Appendix 4).

In this study, we demonstrated the likely presence of a small proportion of adults Yellow-browed warblers in Europe during the autumnal migration period which must have already come to winter in Europe in previous years. A significant proportion of adult birds have thus been estimated in Southwest France before crossing the Pyrenean mountain range and also on the island of Ouessant (the westernmost point of France; 14.8% SD $\pm 1.3\%$ in average). Ouessant island is outside the supposedly shortest migration route, but this result may be consistent with the deportation of large numbers of migratory birds regularly observed on the island by easterly winds (see Nilsson et al. 2019 and recapture data). Furthermore, the estimated age-ratio at some locations by some observers (e.g. 11.9% SD $\pm 6.8\%$ of suspected adult birds in Southwest France) is similar to what can be expected for other migratory passerine species migrating across Western Europe (see Ralph 1981).

Even if the results concern small number of adult individuals and invite to repeat these analyses over several years, they suggest that the Yellow-browed warbler may be a regular migratory species in Western Europe among the usual procession of European migratory species. The rapid increase in occurrences observed in recent decades also supports the evolution of a new migratory route, used by an increasing number of birds (Figure 2). Even if the species seems to be better known from observers and observation pressure may have increased over the last few decades, it is unlikely that it alone explains such an increase in occurrences. Indeed, counting protocols have not changed for several decades on some sites

where comparable increases in occurrence have been noted (e.g. in Fair Isle, Scotland; Mark Bolton *pers. comm.*).

Yellow-browed warbler's migration to Europe would represent a secondary evolution since the wintering grounds of the species are only known from Southeast Asia. Apart from the recovery data in Andalusia (Spain), the regular wintering of the species is not known in Europe (or not properly documented; Tonkin & Perea 2019). Thus, the lack of regular wintering occurrence of the species outside Southeast Asia (see <https://ebird.org/>) strongly indicates that the ancestral migration route is towards Southeast Asia. Moreover, isotopic analyses carried out on Yellow-browed warblers captured in Finland suggest that birds seen in Europe likely originate from the western part of the species' distribution (i.e. western Urals; de Jong et al. 2019), and not from an unknown breeding location. A migration route from Siberia to Europe would represent a secondary evolution in a novel migratory orientation for the species, likely resulting from the colonisation of new wintering grounds somewhere in southern Europe or North-Africa. If the recovery data (Tonkin & Perea 2019) suggest that the species can winter in the Iberian Peninsula or North Africa, it would now be interesting to find the regular wintering grounds of the species, possibly using a niche-based modelling approach.

Vagrancy is an obvious candidate mechanism for the emergence of new migration routes (Thorup et al. 2012) and for Yellow-browed warbler, it is entirely possible that the emergence of this western route results from the survival and successful reproduction of vagrants arriving in Europe, which transmitted this orientation to their offspring (see Berthold et al. 1992, Gilroy & Lees 2003). Indeed, the occurrence of this species in Europe copes with what has been described as large-angle misorientation, also known as reverse migration (Thorup 1998, Thorup 2004), to explain the appearance of Siberian vagrants in Europe. This pattern of vagrancy is particularly relevant to explain the appearance of populations breeding in the western part of the distribution of these species (Thorup 1998), which is consistent with the results of the isotopic analyses of de Jong et al. (2019). In addition, Veit (2000), proposed the idea that vagrants may be more numerous as the expanding fringe of a growing population. Even though we have no information on the evolution of populations west of the Urals Mountains, this is also consistent with the results of de Jong et al. (2019). Last, the hypothesis that vagrants may have promoted the evolution of this new migration route is also supported by the presence of many juvenile birds in northern Europe (e.g. Scotland, Sweden). Even if we cannot exclude that some of these birds are regular migrants located at the margin of the most direct flyway, it is likely that the majority of these birds are vagrants because juvenile birds deviate more frequently from the main migration routes (Ralph 1981). Moreover, intra-annual recaptures in

Europe showed that birds ringed in northern Europe (i.e. Finland) seem to continue their journey westward without changing direction. This is consistent with the migration orientation of vagrant individuals of diverse Siberian species observed in the Faroe Islands (including a Yellow-browed warbler; Thorup et al. 2012). These arguments support the hypothesis that vagrants Yellow-browed warblers are still occurring in Europe (maybe as a result of reverse migration; Thorup 2004), while regular migrants might now be migrating to south-western Europe.

Although there is some evidence of flexibility in bird migration, such drastic changes in migratory routes have only been reported in very rare cases (e.g. in Eurasian Blackcap in Berthold et al. 1992) and raise question about their rapid selection. Indeed, in the case of Yellow-browed warbler's migration to Europe, the rapid increase in occurrences observed over the last decades suggest that it should provide a selective advantage to the individuals making this journey (Åkesson & Hedenström 2007). The positive selection of this new migratory route might be explain by a reduce journey to the wintering grounds. Direct flight from the western edge of the breeding range to the closest wintering grounds (in straight line) are rather similar for Asia and Europe (i.e around 5000 km; considering the location of Tonkin & Perea 2019). However, historical surveys (Delany et al. 2017, Cramp 1992) as well as current observations (in citizen-science database; <https://ebird.org/>) suggested that species' migration routes to Southeast Asia are mostly concentrated east of the Himalayan mountain range. Assuming that regular migrants of Yellow-browed warbler seen in Europe breeds at the limit of the western species distribution (de Jong et al. 2019), it can be hypothesized that there is a selective advantage in terms of distance travelled to winter in Europe rather than migrating to Southeast Asia by bypassing the Himalayas from the east. Of course, this is entirely speculative and would deserve a better understanding of the migratory routes of this species in Asia.

This natural history illustrates the presence of adult Yellow-browed warblers in Europe which suggest the evolution of a new migration route in a completely different direction from the species' ancestral wintering grounds, pending evidence that they transmit the westward migratory orientation to their offspring. This study also introduces an excellent model for understanding migration route selection and the genetic determinism of migration orientation. Finally, it reveals the complexity of predicting changes in the distribution of migratory birds (Kot et al. 1996) and sheds light on the underestimated role of vagrancy to discover new wintering areas and promote the evolution of new migration routes.

Article 6

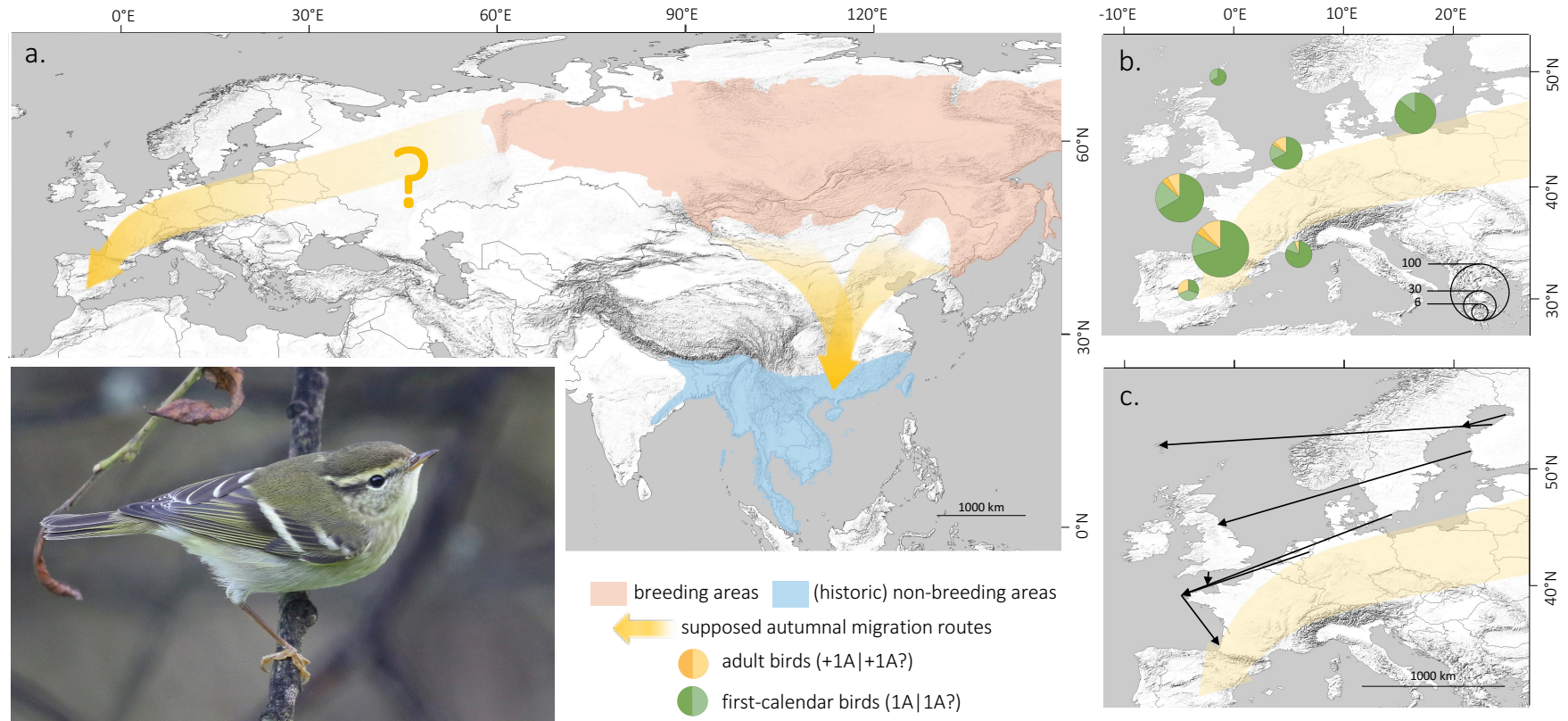


FIGURE 1. (a) Distribution ranges and supposed migratory flyways of the Yellow-browed warbler (*Phylloscopus inornatus*). Breeding and ancestral non-breeding ranges are taken from BirdLife International (2020). Asian migratory routes are supposed from BirdLife International information (2020) and citizen-science data (<https://ebird.org/>; see also Delany et al. 2017). The arrow to Europe indicates the potential migratory routes that regular migrants would undertake to reach Europe. (b) Age-ratio variations of birds caught in different ringing stations. Close ringing stations were gathered under the same point for visualization purpose (see Appendix 2). The size of pie-charts depends to the number of birds caught (see insert). (c) Intra-annual recapture points of YBW ringed in Europe (EURING data). According to the ringers' estimation, recapture data only concern juvenile birds. The photo shows a Yellow-browed warbler observed during 2020 fall on Ouessant Island (Photo Frédéric Veyrunes).

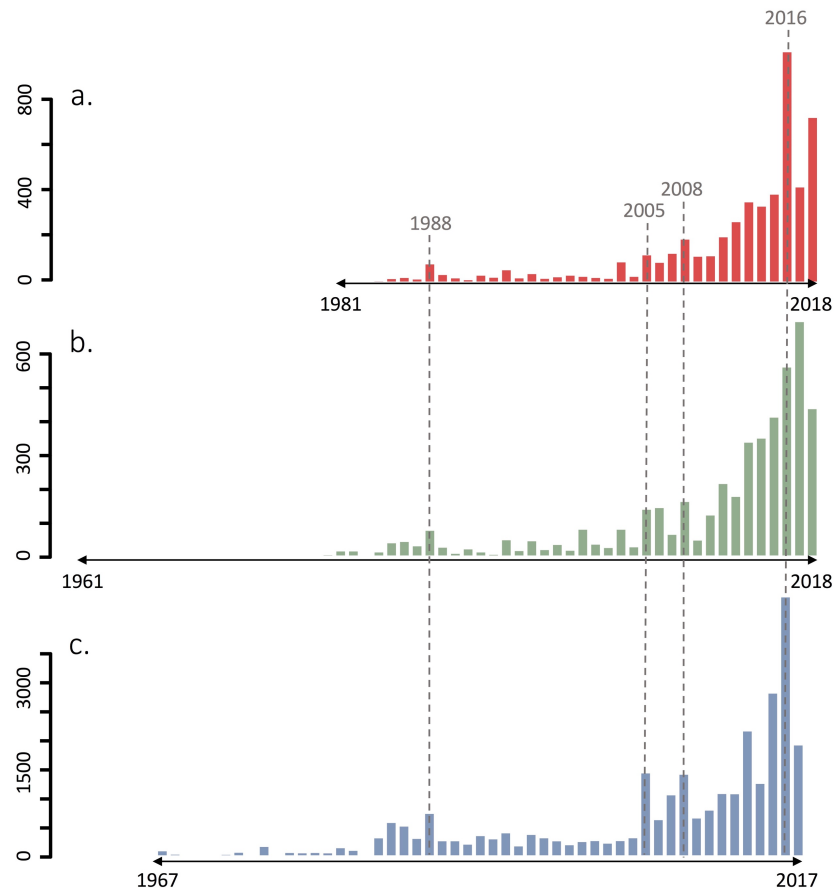


FIGURE 2. Trends in Yellow-browed warbler occurrences in France (a), Sweden (b) and Britain (c) during the last decades. The dashed lines show years with large numbers of birds recorded simultaneously in all three countries (excepted for 2016 in Sweden). See the count details in Appendix 3.

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APPENDIX

1: Standardized-photo protocol

The following protocol has been sent to several ringing stations in Europe. We asked ringers:

- to be particularly attentive to the quality of the photos and the availability of all requested images
- to take to photos away from the sun (hence in the shade if the weather is sunny), preferably using a grey background and with a caution utilization of the flash (at the lowest intensity and only if necessary)
- to use a camera rather than phone and to use large file formats
- to zoom in or get close enough to have full frame pictures and to make sure to focus on the requested part of the bird (with a speed high enough to avoid blurred photos).

The full series of pictures to take on each bird correspond to the plates below :

Pictures © Ottenby fågelstation



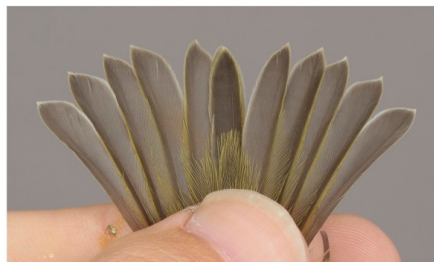
1. Side view of the bird



3. Details of undertail coverts



5. Details of greater, median, primary coverts and alula



2. Open tail



4. Details of uppertail coverts



6. Open wing

2: Location of ringing stations

Country	Location	Coordinates (Latitude, Longitude)	Number of birds
France	Ouessant island ^a	48.458, -5.122	61
	Sein island ^a	48.035, -4.852	3
	Messanges ^b	43.805, -1.394	90
	Saint-Martin de Seignanx ^b	43.513, -1.407	7
	Hyères ^c	43.044, 6.133	10
	Porquerolles ^c	42.988, 6.203	6
	Camargue ^c	43.626, 4.523	2
	Agde ^c	43.313, 3.528	2
	Other locations		12
Netherlands	Castricum aan Zee	52.549, 4.616	31
United-Kingdom	Fair Isle Bird Observatory	59.536, -1.609	6
Spain	Lerida ^d	42.406, 0.944	6
	Other locations ^d		9
Sweden	Ottenby fågelstation ^e	56.196, 16.398	45
	Falsterbo fågelstation ^e	55.383, 12.816	1

Precise locations of ringing stations that took part in this study. Other locations indicate stations where less than two birds have been caught and photographed in the purpose of this study. Small letters indicate close stations that have been grouped together on Figure 1b for visualization purpose.

3: Trends in Yellow-browed warbler occurrences

To illustrate the significant change in Yellow-browed warbler occurrences, we collected data from France, Sweden and Britain during the last decades (Figure 2). For Sweden, occurrence data were compiled annually by the Swedish Rarities Committee from 1961 to 2017 and are available in their annual reports. For Britain, annual occurrences were compiled and published annually in the reports on scarce migrant birds of Britain in *British Birds* from 1985 to 2017 (e.g. White & Kehoe 2018). Annual data from 1965 to 1985 have been collected and published in Baker and Catley (1987). For France, Zucca (2017) compiled annually occurrences from 1995 to 2016. From 1981 to 2005, data were compiled annually by the French Rarities Committee in their annual reports (e.g. Dubois & le CHN 1989). The Scarce Migratory Birds Committee then compiled the data between 2006 and 2008 (e.g. Zucca & le CMR 2009). For this study, data from 1981 to 1994 were collected from the French Rarities Committee reports and data from 2017 to 2019 were collected from the national ringing center and citizen-science databases (<https://www.faune-france.org/> and <https://observation.org/>). Following the method used by Zucca (2017), we added a new bird to the count as soon as it was seen after at least one day without data on the same location on islands, where the observation pressure is the highest during autumn. On the continent, we considered a period of two days without data to add a new bird to the count, since the observation pressure is less important, especially during autumn. From mid-November to mid-March, birds that were observed on the same location (on islands or on the continent) were counted only once.

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4: Supplementary results

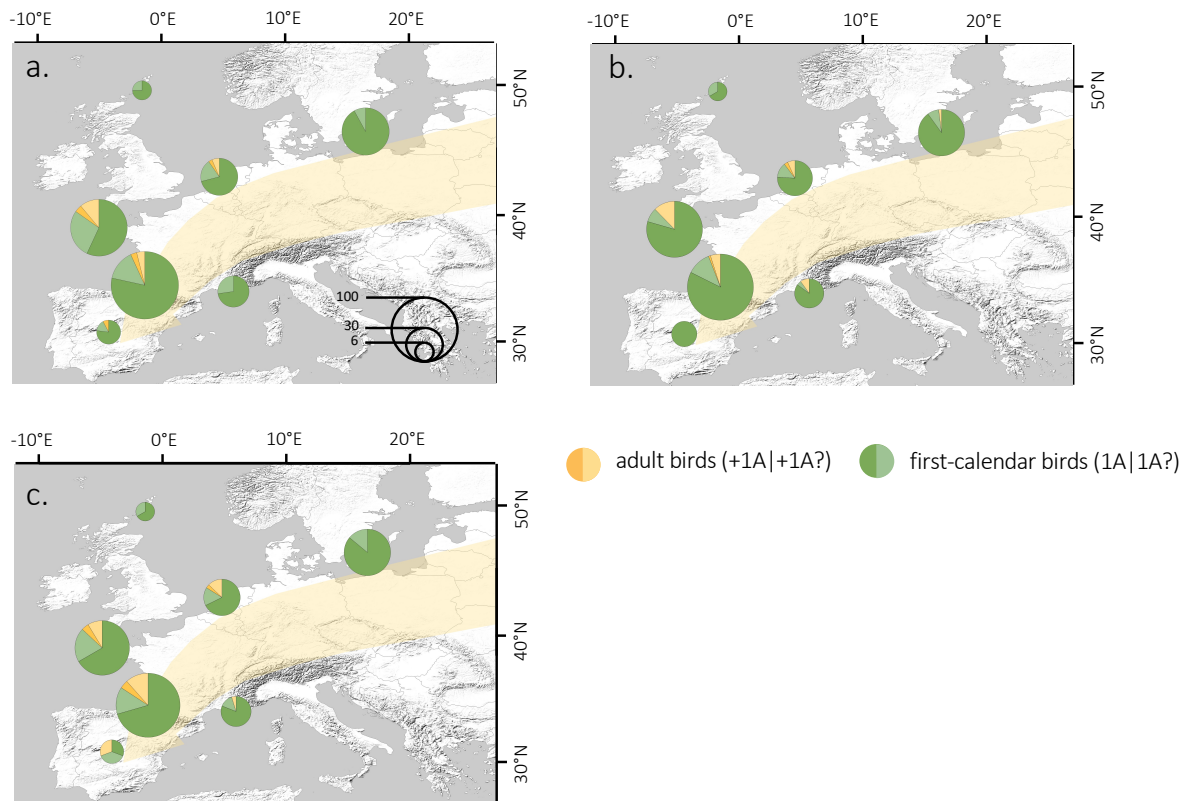


FIGURE. Results of the age estimations for different observers. (a) Paul Doniol-Valcroze, (b) Marc Illa, (c) Christophe de Franceschi. The size of pie-charts depends to the number of birds caught (see insert).

Variables (fixed)	Estimate	SE	t-value	p-value
Intercept	1,28	0,36	3,60	<0.001
Latitude	0,01	0,01	0,89	0.120
Longitude	-0,02	0,01	-3,45	<0.001
Observer1	-0,31	0,05	-6,16	<0.001
Observer2	-0,13	0,05	-2,49	<0.001

TABLE. Results of the linear model testing the effect of latitude, longitude, observers as drivers of age distribution (fixed effects) with individuals identity as a random effect. The concordance in the estimate value of the three observers indicates that their estimates were substantially identical to those of the observer 3. The variance of individuals identity is 0.17 (SD± 0.42) and 0.35 (SD± 0.59) for residuals.

Variables (fixed)	Estimate	SE	t-value	p-value
Intercept	1,12	0,36	3,11	<0.001
Latitude	0,01	0,01	0,89	0.022
Longitude	-0,02	0,01	-3,45	<0.001

TABLE. Results of the linear model testing the effect of latitude and longitude as drivers of age distribution (fixed effects) with observers and individuals identity as random effects. The variance of individuals identity is 0.17 (SD± 0.42), 0.02 (SD± 0.12) for observers and 0.35 (SD± 0.59) for residuals. The effect of latitude becomes a bit more detectable but is contrary to our assumptions, suggesting that adults are more regular in high latitudes.

DISCUSSION GENERALE

1 – Aperçu général de la thèse et de ses principaux enseignements

J'ai étudié au cours de cette thèse l'évolution du comportement de migration à longue distance chez les oiseaux, à différentes échelles temporelles et taxonomiques. Dans une première partie, nous avons notamment montré que la migration saisonnière est apparue il y a plusieurs dizaines de millions d'années, en étroite relation avec l'apparition des cycles saisonniers. Nous avons estimé que plusieurs scénarios biogéographiques complémentaires tendent à expliquer l'émergence de ce comportement en lien avec la saisonnalité (Chapitre 1 et 2). Ces reconstructions ancestrales ont également montré que la migration est un trait labile qui est apparu et a disparu à de nombreuses reprises au cours de l'histoire évolutive des oiseaux. L'émergence de la migration saisonnière semble avoir été une innovation évolutive majeure ayant permis la colonisation de régions et d'habitats nouveaux, au moins chez les Charadriiformes et les Ansériformes (Chapitre 1 et 2). Et cela bien que la migration à longue distance soit apparue visiblement à des périodes différentes : au Miocène supérieur (11.3–5.3 Ma) chez les Ansériformes et à l'Eocène moyen (47.8–38 Ma) chez les Charadriiformes. Chez les Passeriformes, l'apparition de la migration chez leur ancêtre commun (ou chez une lignée proche de cet ancêtre) a vraisemblablement joué un rôle prédominant dans le succès évolutif de cet ordre. En effet, il représente l'une des radiations évolutives les plus remarquables du règne animal où seules quelques familles se sont largement diversifiées sur l'ensemble des continents (sauf l'Antarctique) à travers de multiples routes biogéographiques (Fjeldså et al. 2020). Ceci explique aussi la diversité des scénarios d'apparition secondaire de la migration que nous avons trouvés (Chapitre 1) et qui avait été suspecté par Winger et al. (2014) chez les *Emberizoidea*. Chez les Charadriiformes, nous avons montré que l'apparition de la migration a notamment permis la mise en place d'un gradient de diversité atypique en période de reproduction, biaisé vers les latitudes tempérées et arctiques (Chapitre 2). Nous avons ainsi mis en évidence une influence positive du comportement de migration sur les taux de spéciation, soit en permettant la reproduction dans des zones très saisonnières, soit en permettant la colonisation de nouvelles zones de reproduction par des mouvements de migration longue distance (Chapitre 2).

Il est aussi intéressant de noter que ces migrateurs à longue distance passent généralement une majeure partie de leur cycle annuel en dehors des sites de reproduction et que

par conséquent, ils subissent pendant cette période des pressions de sélection vraisemblablement importantes et sous-estimées. Notre travail sur la coloration des Laridae illustre parfaitement ceci et montre que leur phénotype, notamment la coloration du plumage, est principalement déterminé par des pressions de sélections subies pendant la période d'hivernage et la période de migration (Chapitre 3).

A une échelle taxonomique plus fine, mon travail illustre aussi la variabilité des routes migratoires empruntées et aborde la question des déterminants de ces évolutions. En s'intéressant à une espèce d'Alcidés de l'Arctique présentant des coûts de vol élevé, nous avons montré que des destinations d'hivernages très différentes n'avaient pas d'effet apparent sur la reproduction et ce malgré une ségrégation importante des individus en hiver selon leur taille et leur sexe (Chapitre 4). Nous avons ainsi discuté de l'hypothèse de destinations d'hivernages ancestrales en lien avec les voies de recolonisation postglaciaire pour expliquer cette différence de destination d'hivernage. Par ailleurs, dans le dernier chapitre de cette thèse, nous avons également montré chez deux espèces de passereaux d'origines asiatique et sibérienne que des changements très importants de distribution géographique (ici une partie de l'aire d'hivernage) et par conséquent de routes migratoires empruntées peuvent avoir lieu en quelques dizaines d'années (Chapitre 5). Nous ne sommes pas en mesure de savoir si ces modifications de distributions seront viables (et/ou s'étendront) sur le long terme, mais elles illustrent la rapidité avec laquelle ces évolutions peuvent avoir lieu et suggèrent que des migrants égarés (*vagrants*) peuvent vraisemblablement permettre la découverte de nouvelles aires d'hivernages.

Ces différents résultats montrent ainsi la difficulté de prédire comment les mouvements de migration à longue distance vont évoluer face aux changements globaux. Ils démontrent également que les études de cas et les approches macro-écologiques et -évolutives restent très importantes et complémentaires pour comprendre l'évolution de ce comportement. Tandis que les études à grandes échelles aident à fournir des généralisations valables pour des grands groupes taxonomiques, les études de cas permettent des tests plus approfondis des mécanismes évolutifs opérant sur l'évolution de la migration. Cette complémentarité des approches utilisées est d'autant plus importante que nous vivons dans une période charnière où nous pouvons commencer à confronter les résultats des études prédictives aux effets visibles du changement climatique.

2 – Perspectives dans la compréhension du comportement migratoire

a) Importance du comportement de migration partielle

Nous avons montré dans plusieurs études l'importance de considérer le comportement de migration partielle (i.e. lorsqu'une partie de la population est résidente et l'autre migratrice) pour catégoriser le comportement de migration et étudier son évolution. Si de nombreuses études ont considéré un trait binaire (migrateurs versus résidents) pour estimer l'évolution de ce comportement (ex. Rolland et al. 2014) et que cette dichotomie continue d'être utilisée dans des études récentes (ex. Soriano-Redondo et al. 2020), nos résultats montrent pourtant le rôle d'intermédiaire obligatoire entre l'état de résidence et l'état de migration stricte que représente ce comportement et la nécessité de le prendre en compte. Dans cette même perspective, une étude récente simulant l'évolution de la résidence chez une population migratrice de fauvette à tête noire (*Sylvia atricapilla*) a démontré la persistance du comportement de migration partielle, même dans le cadre d'une forte sélection directionnelle (de Zoeten & Pulido 2020). Il a été montré que la baisse de l'activité migratoire s'explique principalement par une très forte sélection directionnelle, dans laquelle les individus résidents ont une plus forte valeur sélective et avec une valeur sélective des individus migrateurs qui diminue de façon exponentielle avec la distance de migration. Les auteurs de cette étude projettent ainsi qu'une population migratrice stricte deviendra alors migratrice partielle en 6 générations et totalement résidente en 98 générations (de Zoeten & Pulido 2020).

Dans le cas de cette thèse et des Chapitres 1 et 2, nous avons utilisé les cartes de distributions (BirdLife International and Handbooks of the birds of the World 2018) et les informations contenues dans la littérature (Birds of the World 2020) pour catégoriser le comportement de migration. Cette catégorisation reste cependant complexe, notamment lorsqu'il s'agit de définir si une espèce est migratrice partielle ou migratrice stricte. En effet, si cela ne pose pas de problème lorsque les aires de distribution de reproduction et d'hivernage sont disjointes (= migrateur strict), cela devient plus complexe lorsque ces deux aires sont séparées par une aire de présence annuelle de l'espèce. De fait, la présence annuelle de l'espèce au sein d'une aire de distribution ne signifie pas forcément que les populations y soient toutes résidentes. Dans un contexte européen, beaucoup d'espèces montrant ce type de distributions sont en réalité des migrateurs stricts, avec par exemple des migrations en « saute-mouton » (*leap-frog migration*) où les populations les plus nordiques effectuent des mouvements de migration plus importants que les populations méridionales (voir aussi les migrations en chaîne, ex. Akesson et al. 2020). Dans beaucoup de cas, il est donc indispensable d'utiliser une

information complémentaire pour connaître les mouvements entrepris à l'intérieur de ces aires de présence annuelle (Birds of the World 2020). Les données de baguage notamment sont très utiles, si l'effort de capture est homogène sur l'ensemble de l'aire de distribution, pour détecter des populations résidentes ou migratrices strictes à l'intérieur de ces distributions. Nous avons ainsi considéré qu'une espèce était migratrice partielle, si une population résidente était connue au sein d'une aire de présence annuelle (Birds of the World 2020). Mais on peut donc se demander si cette stratégie de migration partielle n'a pas été sous-estimée dans nos analyses, vu que la connaissance des mouvements entrepris reste limitée pour certains groupes taxonomiques et certaines régions géographiques. Ainsi, pour les espèces que nous avons catégorisées en tant que résidentes dans le Chapitre 1 mais dont nous ne disposons pas d'informations concrètes sur l'existence ou non de mouvements migratoires, il serait intéressant de modéliser si un élargissement de la catégorie de *migrateurs partiels*, prenant en compte ces incertitudes, pourrait modifier les estimations des temps d'apparition de la migration saisonnière chez les grands ordres d'oiseaux.

b) Migration et dispersion

J'avais déjà discuté en introduction de la difficulté de faire le lien entre la migration saisonnière et la dispersion (dispersion juvénile et de reproduction ; Ronce 2007, Clobert et al. 2009). D'une part sur le lien entre propension à se disperser et stratégie de migration (résident, migrateur partiel ou strict) mais également sur le lien entre capacité de dispersion (distance de dispersion juvénile et de reproduction) et distance de migration parcourue. Cette relation dispersion / migration reste une grosse interrogation et pourrait permettre de comprendre comment certains clades, comptant aujourd'hui de nombreuses espèces migratrices, se sont largement dispersés et diversifiés sur l'ensemble des continents et sous toutes les latitudes. Chez les Charadriiformes par exemple, nous avons estimé que plusieurs mouvements de dispersion indépendants ont vraisemblablement permis à plusieurs lignées de quitter les latitudes tropicales et d'évoluer ensuite vers un comportement migrateur (Chapitre 2). De même, chez les Passeriformes, l'existence d'un comportement de migration précoce au sein de ce clade pourrait expliquer comment quelques familles se sont largement dispersées de l'Asie du Sud-Est vers l'Amérique du Nord et l'Ouest Paléarctique au cours de leur histoire évolutive (Chapitre 1, Ericsson et al. 2002, Fjeldså et al. 2020).

L'étude de Paradis et al. (1998) avait notamment testé chez 75 espèces d'oiseaux terrestres d'Angleterre les relations entre capacité de dispersion et diverses variables géographiques et traits d'histoires de vie parmi lesquels la stratégie de migration. Ils avaient

montré que les espèces migratrices se dispersent davantage par rapport aux espèces résidentes et ce indépendamment de leurs tailles corporelles (Paradis et al. 1998). On peut s'interroger sur le nombre d'espèces et sur le choix de celles-ci pour tester une telle hypothèse. Même s'il ne s'agit pas de remettre en question les résultats obtenus, j'aimerais avoir l'opportunité de reproduire ce type d'étude avec les jeux de données plus conséquents dont nous disposons aujourd'hui pour estimer les mouvements de dispersions (juvénile et de reproduction), chez un plus grand nombre d'espèces notamment. Ainsi, si les données de baguage du British Trust for Ornithology avaient été utilisées dans ce papier, il serait aujourd'hui possible d'utiliser l'ensemble de la base EURING (centre de coordination des reprises d'oiseaux bagués) pour l'Europe en incluant également d'autres systèmes de migration avec les bases de données de baguage des continents américains et asiatiques (voir par ex. Bonnet-Lebrun et al. 2020). Au-delà d'utiliser la stratégie de migration, il pourrait également être intéressant d'utiliser les données de suivi télémétrique pour obtenir des données précises sur la distance de migration parcourue. Cette donnée devrait même être, dans le cas d'espèces bien suivies, disponibles pour plusieurs populations réparties en différents endroits de la distribution de l'espèce. Avec de telles données, il devrait être possible d'affiner l'étude des relations dispersion / migration pour certains groupes taxonomiques où certains traits d'histoires de vie et de tester si ces variables de migration et de dispersion évoluent selon la localité des populations au sein de la distribution des espèces. Par exemple, tester si les distances de dispersion deviennent plus importantes à mesure qu'on se rapproche des limites de l'aire de distribution (voir Ronce 2007) en le lien avec les mouvements migratoires effectués (voir Sheard et al. 2020). Le martinet noir (*Apus apus*), par exemple, pourrait être une de ces espèces modèles pour lesquelles on dispose de données de suivi télémétrique et de baguage pour une grande partie de son aire de distribution (au moins pour la sous-espèce *apus*, voir par ex. Akesson et al. 2020).

De plus, une étude récente a également mis en évidence grâce à un système de radio-télémétrie (de l'initiative « MOTUS wildlife tracking system ») des mouvements entrepris pendant la période de reproduction qui pourraient s'apparenter à des mouvements de prospection d'habitats de nidification favorables à utiliser en cas d'échec de reproduction ou lors des saisons de reproduction à venir (chez la paruline de Kirtland *Setophaga kirtlandii* ; Cooper & Marra 2020). Ces mouvements sont vraisemblablement étroitement liés au comportement de dispersion (de reproduction). Ces résultats illustrent encore une fois la complexité du comportement de dispersion mais également l'apport des nouvelles technologies pour mieux évaluer et comprendre l'origine de la dispersion.

c) *Etudier l'origine du comportement de vagrancy*

Si nous avons vu que la *vagrancy* (i.e. l'apparition d'animaux migrateurs très loin de leurs aires de présence habituelle) pouvait permettre, dans de rares conditions, la colonisation de nouvelles aires de distributions et à terme permettre l'évolution de nouvelles espèces, l'origine de ce comportement reste extrêmement peu comprise (Chapitre 5). On s'interroge sur un déterminisme génétique de ce comportement lié à une ou plusieurs mutations sur des gènes impliqués dans le déterminisme de l'orientation (ex. Berthold et al. 1992, Delmore et al. 2016, Toews et al. 2019) ou sur de la plasticité comportementale des mouvements de migration.

Les travaux que nous avons réalisés sur les pipits de Richard hivernant dans le sud de l'Europe montrent que ces derniers migrent selon une orientation radicalement différente de celle les menant sur leurs zones d'hivernages ancestrales en Asie du Sud-Est (voir Alström et al. 2003). Nous avons ainsi fait l'hypothèse que ces zones d'hivernages ont été découvertes par des oiseaux égarés en Europe qui s'étaient égarés au départ de leur première migration (voir Thorup 2004). L'augmentation croissante du nombre d'oiseaux utilisant cette voie de migration laisse également supposer à une héritabilité de cette orientation de migration. Dans ce contexte, l'hypothèse d'un déterminisme génétique semble plus probable et en accord avec les résultats obtenus chez d'autres espèces (ex. Delmore et al. 2016, Toews et al. 2019). Identifier les régions chromosomiques, les gènes et/ou les anomalies chromosomiques impliquées dans cette orientation pourrait nous permettre de mieux comprendre l'origine du comportement de *vagrancy*. Pour cela, une possibilité serait de comparer les génomes d'individus utilisant chacune des voies migratoires (en direction de l'Europe versus en direction de l'Asie du Sud-Est) pour chercher des signatures de sélection dans certaines portions du génome. Mais sachant que les variations génétiques peuvent également dépendre des caractéristiques de l'environnement de nidification (latitude, altitude, voir Lundberg et al. 2017), il s'agirait de réaliser un échantillonnage le plus homogène possible (i.e. dans un espace géographique restreint par rapport à la distribution de l'espèce ; Turbek et al. 2018). En pratique, cela nécessiterait de se rendre sur la zone de nidification des oiseaux hivernants en Europe (identifiée dans le Chapitre 5) et d'identifier, à l'aide de géolocalisateurs ou de traceurs isotopiques, les individus qui migrent en direction de l'Asie du Sud-Est. Ces prospections pourraient également permettre de chercher s'il existe une discontinuité géographique dans la distribution de l'espèce qui pourrait expliquer la sélection de cette voie de migration occidentale et le maintien d'un isolement pré-zygotique (i.e. mettre en évidence la présence d'un *migratory divide*). Cette espèce offre de nombreuses perspectives aussi bien dans l'étude de la *vagrancy* que dans le déterminisme et la sélection des voies de migration. J'aimerais pouvoir continuer à travailler sur

cette espèce dans le futur et aborder de nouvelles approches de microévolution au cours de mes recherches.

De façon plus générale sur l'étude de la *vagrancy*, j'aimerais à travers un papier d'opinion proposer une définition plus claire de ce comportement, permettant 1) de mieux identifier les différences par rapport aux mouvements de dispersion et de migration saisonnière et 2) de mettre en avant le rôle sous-estimé de ce comportement dans l'évolution des distributions géographiques. En effet, il serait intéressant d'identifier et de définir les différents types de mouvements qui par définition se révèlent être de la *vagrancy*. Les patrons d'apparition de ces « oiseaux égarés » laissent supposer qu'il existe deux grands types de mouvements : 1) des mouvements au-delà de l'aire habituelle mais dans la « bonne direction » et 2) des mouvements dans des directions drastiquement différentes des orientations de migrations ancestrales. Dans le premier cas, cela peut se référer aux mouvements dit d'*overshooting* lorsqu'une espèce migratrice dépasse son aire de distribution habituelle (ex. espèce méditerranéenne apparaissant dans le nord de l'Europe) ou aux mouvements d'erratisme juvénile bien au-delà de l'aire habituelle (ex. jeunes rapaces méditerranéens apparaissant dans le nord de l'Europe). Dans l'autre cas, cela peut se référer aux mouvements de migration « à image miroir » lorsqu'un individu s'oriente dans la mauvaise direction au départ de sa première migration (*reverse migration* ; voir DeSante 1983, Thorup 2004 ; mouvements qui tendent à expliquer l'apparition d'espèces sibériennes en Europe). Il conviendrait également de savoir si la limite de ce qu'on considère comme étant un *vagrant* doit être définie sur la base de la distance où de la fréquence d'apparition de celui-ci. Il semble en effet que l'expression de ce comportement soit plus régulière chez certaines espèces plutôt que d'autres. Par exemple, plusieurs espèces d'oiseaux nicheuses sur îles méditerranéennes apparaissent fréquemment sur le continent à plusieurs centaines (ou milliers) kilomètres de leurs sites habituels lors de la migration printanière et pourraient ne pas être considérées comme *vagrants* en raison de la fréquence régulière de leur apparition. A l'inverse, l'engoulevent à collier roux (*Caprimulgus ruficollis*) est d'apparition extrêmement occasionnelle dans le sud de la France alors qu'il ne niche qu'à quelques dizaines de kilomètres en Catalogne (Cleere et al. 2020). Ce travail pourrait même être généralisé aux animaux migrateurs de façon générale puisqu'il existe d'autres groupes taxonomiques qui apparaissent fréquemment en dehors de leurs aires de présence habituelle, colonisant dans certains cas de nouveaux habitats de reproduction. Il existe plusieurs exemples chez les insectes (ex. des Lépidoptères dans Rose & Polis 2000), chez les mammifères (ex. des chauves-souris dans Stansfield 1966) et chez les reptiles (ex. des tortues marines dans McAlpine et al. 2004).

3 – Vers une utilisation de nouveaux jeux de données

Cette thèse a été réalisée sur une période charnière pendant laquelle l'évolution des jeux de données utilisés a été très importante, qu'ils s'agissent de nouvelles découvertes fossiles ou d'une arrivée massive de données de science participative. Même si l'utilisation de ces données est encore limitée à cause d'un manque d'exhaustivité spatiale, cela montre que la recherche en écologie et en évolution pourra bientôt bénéficier de données d'une plus grande précision pour approfondir ces mêmes thématiques.

a) Données de science-participative et dynamisme des cartes de distribution

Une grande partie des études réalisées au cours de cette thèse se sont basées sur l'utilisation des cartes de distribution de toutes les espèces d'oiseaux du monde mises à disposition par BirdLife International and Handbooks of the birds of the World (2018), que ce soit pour l'étude des scénarios biogéographiques de l'évolution de la migration que comme référence pour comprendre l'apparition des espèces sibériennes en Europe. Si ces cartes représentent un atout considérable pour l'étude de la classe aviaire, elles peuvent être incomplètes pour certaines régions du monde ou simplifiées pour certains groupes taxonomiques pour lesquels la distribution est seulement partiellement connue. Ce manque de connaissances dans la distribution géographique des espèces (également appelé *Wallacean shortfall* ; et vraisemblablement plus important pour les zones d'hivernages ; Lomolino 2004, Whittaker et al. 2005) semble aujourd'hui pouvoir être réduit à l'aide des données de science participative (Chandler et al. 2017). L'ornithologie a en effet la chance d'être une discipline naturaliste facilement accessible à tous, avec un nombre d'espèces relativement restreint par rapport aux autres groupes taxonomiques (plantes, insectes, et ce surtout dans les pays les plus développés des régions tempérées). Si bien que l'engouement pour l'utilisation des interfaces de science participative est rapidement devenu viral chez les ornithologues amateurs au cours des dernières années.

Parmi ces bases de données de science participative où des observateurs bénévoles saisissent les observations d'oiseaux à partir de n'importe quel endroit et à n'importe quel moment de l'année, eBird représente l'interface la plus utilisée dans le monde (Sullivan et al. 2014). eBird a déjà permis aux chercheurs d'explorer un large éventail de questions (Sullivan et al. 2014, La Sorte et al. 2017), y compris l'estimation des distributions et d'abondance des espèces d'oiseaux (Fink et al. 2014, 2020). Des études récentes ont évalué les zones géographiques les mieux fournies en données eBird pour évaluer la possibilité d'affiner les

distributions des oiseaux à échelle globale (La Sorte & Somveille 2020a, voir aussi Sorte & Somveille 2020b). Ces études montrent que 84% des données d'occurrences sont concentrées en Amérique du Nord, Europe, Inde, Australie et Nouvelle-Zélande, alors les zones les moins représentées dans ces bases de données se situent dans le centre de l'Amérique du Sud, l'Afrique du Nord et centrale et dans le Nord de l'Asie (La Sorte & Somveille 2020a). Mais l'augmentation progressive des données sur la période 2002-2018 dans toutes les régions du monde laisse supposer qu'une couverture géographique pourrait devenir rapidement devenir suffisante pour affiner les cartes de distributions de l'ensemble des oiseaux du monde. L'obtention de cartes dynamiques de distribution et d'abondance (évolution de la distribution et de l'abondance au cours du cycle annuel des espèces, voir Fink et al. 2020) pour l'ensemble des oiseaux du monde marquera assurément un tournant dans l'étude de ce clade charismatique et déjà bien étudié, que ce soit pour répondre à des questions d'écologie, d'évolution ou de conservation.

b) Avancées technologiques des méthodes de suivi

Si les données de baguage se sont longtemps imposées comme l'unique source de savoir pour connaître les mouvements entrepris par les oiseaux migrants, les avancées technologiques des dernières dizaines d'années ont permis de mettre en évidence des mouvements insoupçonnés jusque-là (l'incroyable migration des phalaropes à bec étroit *Phalaropus lobatus* par exemple, van Bemmelen et al. 2019) et d'améliorer notre vision globale de l'utilisation des systèmes migratoires (voir la plateforme Movebank qui regroupe l'ensemble des suivis d'oiseaux dans le monde, mais voir aussi Ruegg et al. 2017). Au cours de cette thèse, nous avons utilisé des géolocalisateurs pour déterminer deux types d'information. D'une part, pour suivre les mouvements entrepris en dehors de la période de reproduction chez une population d'espèce d'oiseau marin de l'Arctique pour laquelle nous ne connaissions que quelques reprises de bagues sur les côtes Islandaises et Groenlandaises (Isaksen & Bakken 1996, mais voir aussi Fort et al. 2013). D'autre part, pour à l'inverse identifier les zones de nidification de passereaux d'origine sibérienne hivernants en Europe. Si obtenir un suivi précis d'oiseaux aussi petits aurait pu paraître impensable il y a quelques dizaines d'années, il n'est toujours pas possible d'équiper des oiseaux de très petites tailles (ex. le pouillot à grands sourcils *Phylloscopus inornatus*) et il est toujours nécessaire de récupérer ces appareils pour accéder aux informations.

Il est aujourd'hui possible d'équiper des espèces d'une vingtaine de grammes seulement avec un géolocalisateur d'un poids minimal de 0.32g (en supposant que l'équipement ne doit pas dépasser 3% du poids de l'oiseau ; Rutz & Troschianko 2013). Si ces appareils nécessitent

d'être retrouvés, l'initiative Icarus (International Cooperation for Animal Research Using Space ; Wikelski et al. 2007) a été créée dans le but de développer un système satellitaire permettant d'observer les mouvements des petits animaux sans nécessité de recapture. Ce système a notamment permis au cours des dernières années d'équiper des oiseaux de moins d'une centaine de grammes (ex. le merle noir *Turdus merula*) avec une transmission directe des données. Ces deux informations, tirées parmi de nombreux exemples, montrent le potentiel croissant des méthodes de suivi pour identifier les mouvements des petits animaux. Il est probable que nous disposions dans quelques années de la possibilité d'équiper des oiseaux de très petites tailles et avec une transmission des informations en temps direct. Cela nous permettra sans doute d'avoir une vision précise et globale de l'utilisation des routes migratoires, permettant notamment de mieux appréhender les problématiques de conservation.

c) Nombreuses et récentes découvertes fossiles

Les données fossiles sont généralement utilisées comme points de calibration pour estimer les temps de divergence des phylogénies et sont également utiles pour calibrer les mouvements biogéographiques passés (Morlon et al. 2011). Il est en effet possible de paramétrer les reconstructions d'aires géographiques ancestrales à partir de la distribution des données fossiles (ex. Rolland et al. 2015, Moyle et al. 2016). Dans le cas de notre étude sur les Charadriiformes, nous avons utilisé plusieurs fossiles dont certains récemment découverts pour estimer les temps de divergence de la phylogénie de ce clade. Par contre, nous n'avons pas utilisé les données fossiles dans nos analyses de reconstructions biogéographiques, risquant d'induire un biais à cause de la distribution de ceux-ci (voir Mayr 2017). En effet, la distribution des fossiles de Charadriiformes, datant du Paléogène (66-23 Ma), représente notamment les zones où la pression de fouille a été la plus importante (voir Fountaine et al. 2005, Mayr 2017). Cependant, de nombreuses découvertes et descriptions de fossiles ont été réalisées au cours des dernières années (voir le Tableau 1 ci-dessous). Ces découvertes pourraient progressivement combler les variations de distribution géographique du registre fossile.

Nom fossile	Clade	Période	Pays	Références
<i>Cherevychnavis umanskae</i>	Charadrii, Charadriiformes	Miocène supérieur	Ukraine	Bochenski et al. 2019
<i>Gallinago azovica</i>	Scolopaci, Charadriiformes	Miocène supérieur	Ukraine	Zelenkov & Penteleyev 2015
<i>Hakawai melvillei</i>	Thinocoridae, Charadriiformes	Miocène inférieur	Nouvelle-Zélande	De Pietri et al. 2016a
<i>Becassius charadrioides</i>	Glareolidae, Charadriiformes	Miocène inférieur	France	De Pietri et al. 2020
<i>Oligonomus milleri</i>	Pedionomidae, Charadriiformes	Oligocène inférieur	Australie	De Pietri et al. 2015
<i>Priscaweka parvales</i> , <i>Litorallus livezei</i>	Rallidae, Gruiformes	Miocène inférieur	Nouvelle-Zélande	Mather et al. 2018
<i>Miohypotaenidia tanaisensis</i>	Rallidae, Gruiformes	Miocène supérieur	Russie	Zelenkov et al. 2017
<i>Teviornis gobiensis</i> , <i>Wilaru tedfordi</i>	Anseriformes	Crétacé supérieur, Oligocène supérieur	Mongolie, Australie	De Pietri et al. 2016b
<i>Chenoanas asiatica</i> , <i>Cheonoanas sansaniensis</i>	Anseriformes	Miocène moyen	Mongolie, Chine	Zelenkov et al. 2018

Tableau 1. Liste (non-exhaustive) de fossiles décrits au cours des dernières années. Ces fossiles datent notamment du Paléogène (environ 66 - 23 Ma) et correspondent à des clades qui sont aujourd'hui composés d'espèces majoritairement migratrices.

Ces découvertes, réalisées dans de nombreuses localités et pour plusieurs clades d'oiseaux notamment migrateurs (Charadriiformes, Gruiformes et Anseriformes notamment), pourraient permettre d'affiner les reconstructions phylogénétiques et biogéographiques pour ces clades. De plus, pour les fossiles datant du Miocène et de l'Oligocène, ce qui correspond à la période de baisse des températures terrestres et d'apparition des rythmes saisonniers, ils pourraient permettre de mieux comprendre l'apparition du comportement migratoire au sein de ces groupes. Enfin, on peut imaginer que la découverte de fossiles de bonnes qualités puisse permettre de directement étudier l'évolution du comportement migratoire à partir des caractéristiques phénotypiques relevés sur les fossiles eux-mêmes (voir Kiat et al. 2020 et Claramunt et al. 2012, Sheard et al. 2020). C'est par exemple ce qui a été fait récemment par Kiat et al. (2020) à partir de l'observation d'une mue séquentielle sur un fossile de dinosaure (*Microraptor*) de la fin du Crétacé.

La macroévolution et la paléontologie sont deux domaines de recherche qui ont souvent été abordés séparément malgré des complémentarités évidentes. Des papiers récents montrent les possibilités de fusion de ces domaines, à la fois d'un point de vue conceptuel et méthodologique (ex. Saupe et al. 2019, Sayol et al. 2020). Ils ouvrent de nouvelles perspectives pour tester de grandes hypothèses biogéographiques, profondément ancrées dans la littérature

Discussion générale

scientifique et c'est typiquement vers ce type d'approche que je souhaite placer mes futures recherches en macroévolution.

4 - Bibliographie de la discussion

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ANNEXES

Ces annexes correspondent à deux articles publiés, ou en cours de publication, sur lesquels j'ai pu collaborer. Ils résultent des stages de Master de Louis Bliard et de Raphael Mossion, encadrés respectivement par Claire Doutrelant (CEFE-CNRS) et Jean-Yves Barnagaud (CEFE-EPHE).

Research



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Evolutionary biology

Examining the link between relaxed predation and bird coloration on islands

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Insular ecosystems share analogous ecological conditions, leading to patterns of convergent evolution that are collectively termed as the 'island syndrome'. In birds, part of this syndrome is a tendency for a duller plumage, possibly as a result of relaxed sexual selection. Despite this global pattern, some insular species display a more colourful plumage than their mainland relatives, but why this occurs has remained unexplained. Here, we examine the hypothesis that these cases of increased plumage coloration on islands could arise through a relaxation of predation pressure. We used comparative analyses to investigate whether average insular richness of raptors of suitable mass influences the plumage colourfulness and brightness across 110 pairs of insular endemic species and their closest mainland relatives. As predicted, we find a likely negative relationship between insular coloration and insular predation while controlling for mainland predation and coloration, suggesting that species were more likely to become more colourful as the number of insular predators decreased. By contrast, plumage brightness was not influenced by predation pressure. Relaxation from predation, together with drift, might thus be a key mechanism of species phenotypic responses to insularity.

1. Introduction

Islands are fascinating systems to study biological evolution as they are replicates of geographically isolated systems that share similar ecological characteristics. Their reduced area and simplified biota, including impoverished predator and parasite communities, are usually associated with repeated patterns of convergent evolution [1,2] grouped under the name 'island syndrome' [3]. In birds, this syndrome includes changes in coloration, with many insular species exhibiting less colourful and duller (i.e. less bright) ornamentations [4–6]. This decrease in coloration has been proposed to result from a relaxation of two selective forces: selection for species recognition [4–6] and intersexual selection [4,7].

However, not all species respond to insularity in a similar way. Some species living on small islands show a 'reversed island syndrome', with increased coloration [4], sexual dimorphism and aggression [8]. Why does coloration increase more often on small islands wherein the decrease should be more marked, given a stronger relaxation of mate choice and need for species recognition?

Changes in other selection pressures like predation, as well as changes in the intensity of drift [9], could explain the cases of a reversed island syndrome. Here, we conducted a study to investigate how variation in insular predation relates to island birds' coloration while controlling for the coloration and predation faced by their mainland relatives.

With the exception of aposematism, predation is usually thought to select for inconspicuous signals [10–12, but see 13]. This effect is further supported by the observation that many birds tend to display a conspicuous plumage coloration on their ventral part (hidden to aerial predators) and a cryptic coloration on their back (exposed to predators) [14]. In insular ecosystems, where predator richness is reduced [15], a relaxation from predation pressure could be associated with an increase in conspicuousness. In agreement, the relaxation from predation pressure on small islets influences coloration traits of a lizard species, which evolved towards poorer background matching, hence higher conspicuousness [16].

We studied 110 pairs of endemic insular bird species and their mainland closest relatives and examined whether insular coloration is associated with the number of predator species on islands while controlling for mainland coloration and predation. If predation is an important driver of bird colour evolution on islands, we predict a negative relationship between insular predator richness and insular coloration, so that island species facing more predators are more prone to show a decrease in plumage coloration. Secondly, under the hypothesis that the dorsal part of birds is more likely to be under a predation-driven selection for crypsis [14,17] than the ventral part, we expect the dorsal area of birds to be more influenced by changes in predation.

2. Methods

(a) Data collection

The dataset is composed of 220 bird species (electronic supplementary material, appendix S1), corresponding to 110 endemic insular species from 46 different archipelagos and their closest mainland relatives from a similar latitude [4]. For the present study, we selected only bird species that are not themselves birds of prey. We used spectrometry measurements of plumage coloration for three males and three females of each species (see electronic supplementary material, appendix S2 for details regarding plumage variation) from a previous study by Doutrelant *et al.* [4] (excepting four new pairs measured in 2018). Reflectance spectra were converted to bird-specific photoreceptor excitations with the Goldsmith model of tetrahedral colour space for a violet sensitive vision [18,19], using the R package *pavo* [20]. Indeed, predators considered in this study are raptors, which only have limited ultraviolet vision [21,22].

The intensity of coloration was estimated by the brightness, which describes the intensity of the achromatic component of a signal, and the colour volume, defined as the minimal convex volume in the tetrahedral colour space that contains all the patches measured. It quantifies the diversity of colours and is used to describe colourfulness [18].

To estimate predation pressure, we collated data on the average specific richness of sympatric avian predators across the range of each species [23–29] and computed predator–prey mass allometry relationships to exclude some predators based on size mismatch with potential preys [23,30] (electronic supplementary material, appendix S3). Predator densities or species-specific estimates of raptor-driven mortality would provide additional resolution but are not available for such a large-scale study. Predators included were all species from the Accipitriformes and Falconiformes orders, which are known predators of adult birds. Indigenous

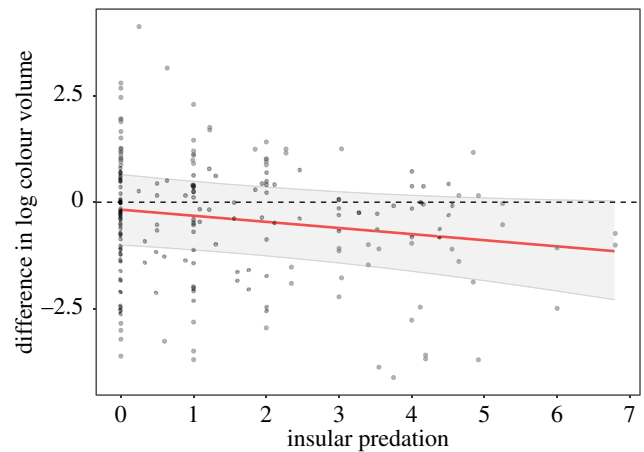


Figure 1. Difference in log colour volume between insular species and their continental counterpart in relation to the number of sympatric predators. A positive value indicates a larger colour volume for the insular species compared to its mainland relative. The regression line and its associated 95% CI are those predicted by the BPMM, accounting for continental predation. The mean log continental colour volume was subtracted to the intercept, and insular predation was transformed back to its original scale. (Online version in colour.)

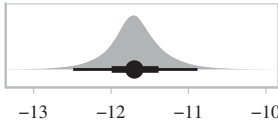
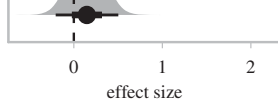
terrestrial mammals are scarce or lacking on islands, representing a marginal predation pressure on adult birds compared to avian predators [23,31]. Moreover, mammals are mostly blind to ultraviolet and possess a poorer colour vision as they only have two types of photoreceptors (versus four in birds). We did not include snakes because they likely represent a less important predation pressure as only a small number of species specialize on adult birds, even though a few of them are known to be present on some of the islands considered (e.g. *Boiga irregularis* [32]). Nocturnal avian predators (Strigiformes) were excluded, as their eyes are mostly composed of rod cells, resulting in a poor colour vision [33]. Resident, breeding, and wintering ranges of all bird species considered in this study were retrieved from BirdLife International and NatureServe [34] and HBW [35], using a 10-min resolution grid. For polytypic species, we used only the geographical range of the subspecies that was measured by spectrometry, as subspecies usually differ in coloration. When the range of a subspecies was too complicated to delimitate, the whole range of the species was used. All species range maps from Accipitriformes and Falconiformes ($n = 309$) were collected at the same spatial resolution, and the number of grid cells shared between each focal species and each raptor species was calculated.

(b) Statistical analyses

We tested the effect of predator richness on the coloration of insular birds while controlling for the coloration and predator richness of their mainland closest relative [7,15,36,37]. The dependent variables were the estimates of coloration of the insular species: colour volume and brightness, which were averaged for males and females of each species. Colour volume was log transformed prior to analyses. Analyses were performed with the R software, v. 3.5.1 [38].

We first investigated how colour volume and brightness of insular species were influenced by predation, considering the whole body of birds, using 107 pairs of species with known colour volumes (three species were excluded as at least four distinct colour patches are needed to compute a volume) and 110 pairs with known brightness. Explanatory variables were sex, insular predation, continental predation, the interaction of both terms with sex, and the absolute value of latitude of the insular species. We also included as covariate the coloration of the continental species of the pair. Island size was not included in the model to avoid collinearity due to its positive correlation with insular predation ($r = 0.51$; $p < 0.001$).

Table 1. Results of the BPMM exploring the relation of different factors with the log insular colour volume ($n = 107$ insular species). All continuous covariates were z-transformed to get standardized effect sizes.

log insular colour volume				
model estimates		95% credible intervals		
predictor variables	estimate	lower 2.5% CI	upper 2.5% CI	
intercept	-11.692	-12.488	-10.883	
fixed effects				
log continental colour volume (z-transformed)	1.823	1.533	2.075	
insular predation (z-transformed)	-0.241	-0.513	0.030	
continental predation (z-transformed)	-0.061	-0.357	0.231	
latitude (z-transformed)	-0.105	-0.319	0.113	
sex male ^φ	0.088	-0.260	0.430	
sex male * insular predation ^φ	0.071	-0.281	0.425	
sex male * continental predation ^φ	0.147	-0.205	0.503	

effect size

^φ Reference category is “sex female”

marginal $R^2 = 0.598$
 conditional $R^2 = 0.713$
 phylogenetic heritability = 0.873

We then tested the influence of predation pressure on insular brightness for different body parts separately. The ventral parts and the head are assumed to be more prone to sexual selection compared to other body parts. The dorsal parts (i.e. tail, outer wing and back), more likely to be seen from above by avian predators, are potentially selected for crypsis [14]. The colour volume has not been calculated for different body parts as at least four measurements are needed to compute a volume in a tetrahedral colour space and not all species displayed enough visually distinct colour patches within each body part. Explanatory variables were the same as in previous models, and ‘body part’ was included as a two-level factor (ventral patches/dorsal patches), along with interactions with insular and continental predation.

As species do not represent independent data points due to shared ancestry, all models accounted for the phylogenetic dependence between species using Bayesian phylogenetic mixed models (BPMMs). BPMMs were done using the R package *MuTree* [39], with a species random effect linked to the phylogeny. All simulations were performed on 100 alternative trees from the most recent known phylogeny [40] instead of a consensus tree, to account for phylogenetic uncertainty [41] (electronic supplementary material, appendix S4).

3. Results

Most islands present decreased average predation richness (electronic supplementary material, appendix S5, figure A1). Following our expectations, we found a likely negative effect of insular predator richness on insular colour volume while accounting for continental colour volume and predation (estimate: −0.241 [95% CI: −0.513; 0.030]; figure 1 and table 1; negative effect of insular predation estimated from the posterior distribution in 95.9% of the cases). Insular species are on average as colourful as their mainland counterparts in the absence of avian predators but are more likely to be less colourful as the number of insular predators increased (figure 1). Similarly, insular species facing a large decrease in predation pressure compared to their mainland counterparts tend to display an increased coloration (electronic supplementary material, appendix S5, table A1 and figure A1). Latitude, sex and the interaction between sex and predator richness did not have any clear effect (table 1).

We did not find any clear effect of insular predator richness on insular brightness at the scale of the whole body (estimate: −0.003 [95% CI: −0.011; 0.006]; electronic

supplementary material, appendix S5, table A2 and figure A2) or on the dorsal and ventral parts (estimate for the dorsal parts: 0.004 [95% CI: -0.004; 0.013], for the ventral parts: -0.004 [95% CI: -0.013; 0.006]; electronic supplementary material, appendix S5 and table A3).

The phylogenetic heritability was high for both colour volume and brightness of insular birds (respectively, $\lambda = 0.873$ and $\lambda = 0.992$) [42,43].

4. Discussion

We found a trend suggesting a negative relationship between insular predator richness and insular coloration while accounting for mainland coloration and predation, as well as controlling for a strong phylogenetic signal. These results tend to support the hypothesis that island species facing less predators are more prone to an increase in colour volume. To our knowledge, this is the first comparative study testing the effect of predation on colour evolution on islands. Below, we discuss two non-exclusive hypotheses to explain the response of colour volume to predation.

Species colonizing islands face reduced selection pressures from mate choice and/or the need for efficient species recognition [4], and thus should face a strong effect of genetic drift [9]. The lower predation found on islands represents a reduction of an important selective pressure, thus increasing further stochasticity in plumage colour evolution. Accordingly, about half of the species facing low predation (i.e. left side of figure 1) displayed an increased colour volume, which is consistent with stochastic dynamics. In addition, island size also affected bird coloration (electronic supplementary material, appendix S6). While this effect is likely to be linked to reduced predation pressure, stochasticity is also thought to be stronger on smaller islands due to more pronounced genetic bottlenecks. However, species colonizing islands wherein predation pressure is high are more prone to evolve towards duller coloration because the selective pressure imposed by predation is maintained, while the strength of mate choice and need for efficient species recognition are lowered.

Another possibility, independent of island living, is that predation could act on coloration through colour-dependent predation [44,45], where a decrease in predation pressure is associated with diminished costs of being colourful, and indirectly through changes in sexual selection. Indeed, predation is known to affect prey population size, and the removal of predator species tends to enhance population size and thus prey densities [46]. Higher population densities in birds have been linked to higher rates of extra-pair paternity [47], hence stronger sexual selection [48]. This mechanism would indirectly favour colourfulness when predation is lowered.

Why plumage brightness, either at the scale of the whole body or on different body parts, decreases on islands [4] but

does not covary with predation pressure remains unclear. However, even though brightness is expected to be important for long-distance prey detection [49,50], thereby generating a viability cost for brighter individuals by enhancing predation risk, this may not always be the case. Unlike high colour volumes, which make species conspicuous in whichever environment [51], high plumage brightness might render species inconspicuous if it effectively matches the brightness of the environment. A proper evaluation of the link between brightness and predation pressure might thus require a detailed knowledge of the brightness of the visual environment specifically used by each bird species.

Since this study is correlational, additional factors covarying with insularity or predation may influence the results. For instance, availability in dietary resources such as carotenoids at the basis of some pigmental colours may vary between locations inhabited by species within pairs. Furthermore, the use of spectrometry only measures coloration while ignoring colour patterns and ornament sizes that may also be subjected to evolutionary changes, depending on predation pressure and following island colonization.

Islands represent natural laboratories for studying the factors governing evolution at large evolutionary scales [2]. While general patterns of evolution on islands are well documented [1], studies of the underlying mechanisms are still rare. The present study contributes to our understanding of these mechanisms and suggests that predation is one of the factors influencing the evolution of bird plumage coloration on islands worldwide.

Data accessibility. Data are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.mw6m905tc> [52].

Authors' contributions. C.D., R.C., P.-A.C., A.G. and A.R. designed this study. R.C. collated the database. C.D. and A.R. measured plumage coloration. J.P.R. and L.B. performed visual models. P.D. and L.B. collected predation data. L.B. performed analyses with the help of M.P. L.B. wrote the first draft. All authors contributed to revisions of the manuscript, approved its final version and accept to be held accountable for its content.

Competing interests. We declare we have no competing interests.

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Trait-habitat associations explain novel bird assemblages mixing native and alien species across New-Zealand landscapes

RUNNING TITLE: Trait-habitat associations in New-Zealand birds

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ABSTRACT

Aim: Species introductions in islands are continuously reshaping insular faunas, often threatening native biodiversity. In New Zealand, native and alien birds occur in balanced proportions, but show distinct habitat use. Antagonistic interactions, habitat affinities or legacies of introduction history may explain this segregation along habitat gradients. To separate these hypotheses, we investigated the respective effects of habitat, ecological traits and introduction history on the current composition of New Zealand bird assemblages.

Location: New-Zealand

Taxon: Birds

Methods: We analysed 917 bird point counts spread along habitat and elevation gradients in the Canterbury region, South Island, and related 10 ecological traits to landscape composition using a RLQ analysis accounting for spatial autocorrelation and phylogeny. We tested whether alien species' scores in the RLQ were related to introduction history (date of first introduction, number of introduction events and total number of individuals released).

Results: Eighteen endemic, 11 native and 19 alien species were distributed along a gradient from forest to open-habitat assemblages, in relation with foraging mode, nesting site and body size. A second gradient segregated species between native and exotic forests according to territoriality, sedentarity and diet. Traits accounted for the separation of native and alien bird species in forests, but not in open habitats. Phylogenetic signals emerged from the separation of native and alien species by forest type, and spatial structures suggested a landscape-level, rather than regional or local determinism. These patterns were mostly independent from introduction history, although open-habitat assemblages tended to host alien species introduced later in time.

Main conclusions: Habitat or resources, rather than competitive exclusion, appear to drive the spatial partitioning of native and alien species among bird assemblages in New Zealand. We conclude that trait-mediated ecological differences among species has contributed to shape novel insular species assemblages, while maintaining original endemic bird assemblages in native forests.

Keywords: ecological traits, island, birds, species introductions, land-cover, native habitats, RLQ, species assemblages, phylogenetic analysis

INTRODUCTION

Avifaunas on oceanic islands are amongst the most spectacular in the world, with disproportionate rates of endemism and narrow distributions (Newbold et al., 2018). Island bird species and assemblages bear unique combinations of ecological traits and evolutionary pathways with few equivalents on continents (Pavoine et al., 2017). These unique features make them sensitive to small changes in their abiotic or biotic environment, and ultimately more prone to extinctions as compared to mainland species (Blackburn et al., 2004; Sanchez-Ortiz et al., 2019).

Worryingly, insular bird assemblages face the synergistic impacts of climate change, habitat loss and man-mediated introductions of alien species – including predators, pathogens and competitors (Blackburn et al., 2004; Parlato et al., 2015; Walker et al., 2019). The latter threat is exacerbated on oceanic islands where long-term isolation has limited native species' capacity to accommodate novel biotic interactions (Traveset et al., 2013). As a consequence, introductions of alien species, usually paralleled with modifications of insular habitats for human land use, have dramatically altered native insular avifaunas and disrupted irreplaceable ecosystem processes and services provided by island endemic birds, such as seed dispersal, pollination and pest control (Anderson et al., 2011; Foster & Robinson, 2007; Şekercioglu et al., 2016). In New Zealand, for instance, the predation of endemic bird species by introduced mammals led to the extinctions of obligate bird-pollinated or bird-dispersed plant species and contributed to the impoverishment of plant assemblages on top of direct habitat destruction (Carpenter et al., 2018; Kelly et al., 2010; Wotton & Kelly, 2012).

Current bird assemblages on islands could result from species' idiosyncratic responses to habitat, land use and abiotic features, but may also arise from niche-based exclusion between native and alien species. Experimental tests or dedicated monitoring hardly separate these processes for more than a few well-identified species : as a result, the impact of alien species on insular avifaunas remains poorly known (MacFarlane et al., 2016; Williams, 2006). Alternatively, studying how alien and native species' ecological traits are segregated among species assemblages offers a correlative, yet comprehensive approach (Allen et al., 2013; Kennedy et al., 2010; Vandewalle et al., 2010). Ecological traits encompass species' characteristics, such as diet, mobility or reproductive traits, organized into syndromes that emerge from evolutionary strategies in response to environmental conditions (Díaz et al., 2016; Jeliaskov et al., 2020). Directional variations of these syndromes along environmental gradients allow inference on species co-occurrences or exclusions patterns over regional extents, although the exact processes involved remain uncertain (Mouillot et al., 2013; Pavoine et al., 2011; Violle et al., 2014). To be robust, this approach implies that environmental gradients are well defined (e.g. elevation or forest-open habitat continuums) and traits carefully chosen to reflect species' resource use while avoiding circularity (e.g., in birds, dietary preferences, foraging modes or breeding locations ; Jeliaskov et al., 2020; Kennedy et al., 2010). With these conditions in mind, trait-based correlative approaches may help

determining whether a systematic spatial exclusion of alien and native species results from differing ecological requirement (no trait overlap) or from heterospecific competition.

Anthropogenic alteration of native insular habitats favours alien species coping well with urban areas, cultivated fields or planted forests (Barnagaud et al., 2014; Cardador & Blackburn, 2019; Sol et al., 2017). Accordingly, many successful introductions involved species that shared ecological traits associated with synanthropy, such as dietary generalism, investment on reproduction or small size (Allen, Street, & Capellini, 2017; Capellini, Baker, Allen, Street, & Venditti, 2015; Sol et al., 2012). It is often unclear whether the success of some alien species is attributable to human-created resources or to accommodation to their novel environment. For instance, large-scale studies suggest that signals of introduction events remain prevalent long after species' establishment in many islands irrespective of local habitat suitability (Blackburn, Cassey, & Duncan, 2020; Case, 1996). However, niche-related processes also explain invasion success, especially the association between alien species and anthropogenic habitats worldwide (Cardador & Blackburn, 2019). Separating the relative roles of traits and introduction history is therefore a critical step to explain differences in habitat use between native and alien species, especially in insular ecosystems (Blackburn et al., 2020; Duncan, Cassey, Pigot, & Blackburn, 2019; Pipek et al., 2020).

No insular avifauna was reframed to the extent of New Zealand's, where the history of species extinctions since Maori and European settlement, and of species introductions since the mid-19th century, are well documented (e.g. Diamond & Veitch, 1981; Pipek et al., 2020; Veltman et al., 1996). Today's bird assemblages in mainland New Zealand are typically novel, mixing native and introduced species in more or less balanced proportions. In undisturbed native forests, they are however dominated by a 'wreckage' of native bird assemblages with few aliens (Barbaro et al., 2012; Clout & Gaze, 1984; Deconchat et al., 2009; MacLeod et al., 2008). New Zealand bird assemblages therefore represent a unique opportunity to investigate processes underlying the habitat-related sorting of native and alien species. Contrary to other remote islands, direct competition between alien and native bird species does not seem to structure New Zealand bird assemblages. Credible explanations lie in limited niche overlap, the use of niches left vacant by extinct native species, or distinct distributions in space (Barnagaud et al., 2014; Van Heezik et al., 2008). To decide between these hypotheses, we tested whether trait-habitat relationships differed among native and alien birds along environmental gradients in the South Island of New Zealand. We used a multivariate analysis framework to decipher the link between traits, species and environment, while accounting for spatial and phylogenetic dependencies (Pavoine et al., 2011). In a second step, we investigated possible legacy effects of introduction history on trait-environment associations.

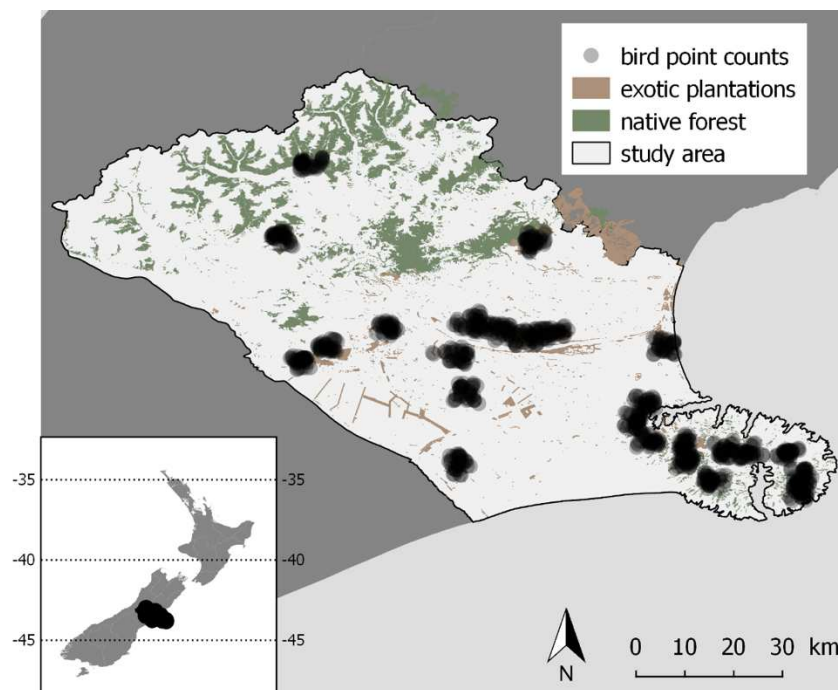


Figure 1. Study region (light grey, insert) extending from Banks Peninsula in the East to the Southern Alps in the West and the location of the 917 point counts within the study region. Points are grouped in clusters; dot density depicts the number of adjacent points.

MATERIALS AND METHODS

Study area

The study was carried out in the Canterbury Region of the South Island, New Zealand, and included Banks Peninsula in the east, the Canterbury Plains, and part of the Southern Alps in the west (Fig. 1). This area is structured by an elevation gradient ranging from 0 to 1205 m (mean 316 ± 240 m, all variation in standard deviation units). The climate is seasonal and temperate and varies with elevation under the influences of mountains and coastal areas. The landscapes are mainly composed of exotic grasslands, modified natural grasslands, some shrubland, native forest and plantations. Exotic plantation forests (57 % of total forest cover) are dominated by *Pinus radiata* while native forests account for 43 % of total forest cover, mainly in the Southern Alps and on Banks Peninsula. Together, forests account for 59% of the study area. While the native forests studied in Southern Alps are mainly old growth, those on Banks Peninsula are mainly regenerating forests after clearance had occurred since the mid-1800s (from just 1 % of native forest cover in 1900 to about 15 % in 2008, Wood & Pawson, 2008). Open habitats mainly consist of exotic grassland and mixed native and exotics grassland used as pasture, with locally substantial remnants of native tussock grasslands and occasional shrubs.

Bird sampling

A set of 917 point counts was surveyed once during two field campaigns by the same observers (austral summer 2005-06: 402 points; 2006-07: 515 points). Points were grouped into clusters (34 to 44 points per cluster) located to cover both forests and grassland areas within each cluster, but excluding urban and suburban areas (Fig.1). Forest cover within the clusters varied from a minimum of about 1% to over 90%, but high and low forest cover occurred in each of the clusters. Points were located at least 200 m apart from each other to avoid double-counting. All birds heard or seen within 100 m around each point were recorded and counted during three consecutive 5-minutes sampling events by a single experienced observer among a team of six observers; preliminary data exploration revealed no observer effect.

We retained all recorded species in our analyses to obtain the most comprehensive representation possible of bird assemblages occurring in all point counts ($n = 48$ species for 917 point counts, species list and abbreviation used in figures in Appendix S1). We classified birds according to their origin, distinguishing 18 New Zealand endemics, 11 New Zealand natives (non-endemic species that also occur elsewhere as native species) and 19 alien species mostly introduced in the 19th century from Europe and North America (Robertson et al., 2007).

Environmental variables

We characterized landscape composition in 500 m buffers centred on each point count, using the most biologically relevant classes among the 43 land use categories of the New Zealand Land Cover Database V2 (Table 1, based on Terralink International, 2004). We quantified landscape heterogeneity through a Shannon-Wiener's index based on the polygon surfaces of these classes within each buffer. We also used observers' field recordings of elevation and vegetation height within a 100 m radius around each point to obtain a more local characterization of habitats (Table 1).

Ecological traits

We compiled 10 ecological traits known to influence habitat selection in birds (Appendix S1, synthesis in Table 2). Five traits (foraging behaviour, diet, nest location, social behaviour, migration behaviour, thermal preference) represented the functional link between species and their habitat (Mac Nally, 1994; Robinson & Holmes, 1982). Five other traits represented ecological niches and interspecific interactions (Brandle et al., 2002): clutch size, brood number per year, age at fledging and body weight. In addition, we recorded three variables characterizing introduction effort for the 19 alien species: date of first introduction, number of successive initial introduction events, total number of individuals released during these events (Duncan 1997). The accessibility of other relevant variables was limited by lack of data, published literature at the time of the study and/or incomplete historical documentation (see Pipek et al., 2020).

Phylogeny

We constructed a phylogeny of the 48 species encompassed by our study (Appendix S2) with a composite of bird phylogeny established by Prum et al. (2015) and a maximum clade credibility tree computed from 10 000 iterations of the Hackett backbone (Jetz et al., 2012, downloadable at www.birdtree.org, “Stage 2 Hackett Backbone”), following Cooney et al. (2017)’s method. This approach provided more reliable divergence times and topology of the earliest branching events (especially for separating major non-passerine taxa) than previously published phylogenies (Thomas, 2015).

Trait-environment relationships

We characterized the spread of bird traits along habitat gradients with a modified version of the RLQ analysis accounting for spatial and phylogenetic dependencies among species and sampling points (Pavoine et al. 2011). The original RLQ analysis is a three-table multivariate ordination linking a sites * environment table (table R, here summarized in a principal component analysis, PCA) to a species * traits table (table Q, here a Hill & Smith analysis, HS) through a site * species table (table L, here a correspondence analysis based on the 917 point counts, CA), with appropriate weighing as described in Thioulouse et al (2018). Following Pavoine et al. (2011), we added two supplementary tables. First, we accounted for the spatial arrangement of the survey through the eigenvalues of a sites * sites binary Gabriel neighbours matrix based on point count coordinates (table S), and synthesized through a PCA (Thioulouse et al., 2018). We then concatenated the PCA axes of tables R and S to obtain table E, which thus formed a synthesis of environmental and spatial gradients. Similarly, we incorporated phylogenetic autocorrelation with a species * species square-root transformed pairwise phylogenetic distance matrix (table P; phylogenetic distance defined as the sum of branch lengths on the shortest path between two species in the phylogenetic tree), summarized by a principal coordinate analysis (PCoA). We concatenated this PCoA and the PCA axes of table Q to associate trait and phylogenetic information (table T). Following the basic structure of a RLQ analysis, we subsequently related tables E and T through the link table L. The resulting trait-environment ordinations accounted for the spatial proximity among point counts and the phylogenetic relatedness among species. For semantic simplicity, we refer to this analysis as “RLQ”.

Impact of introduction effort

We investigated the impact of introduction history on environment-trait associations through a MANOVA relating species’ coordinates in the RLQ to the three variables quantifying species’ introduction effort ($n = 19$). No phylogenetic structure appeared in the number of introduction events (Pagel’s $\lambda = 7.3 \times 10^{-5}$, $p = 1$) and total number of individual released (Pagel’s $\lambda = 6.6 \times 10^{-5}$, $p = 1$), but date of first introduction was clustered (Pagel’s $\lambda = 0.99$, $p = 4.2 \times 10^{-5}$). This structure was explained by the late introductions of two *Anatidae* (Canada Goose, *Branta canadensis* and Mallard, *Anas*

platyrhynchos, respectively introduced in 1905 and 1910) and two other non-passerines (Sulphur-crested Cockatoo, *Cacatua galerita*, in 1900 and Little Owl, *Athene noctua*, in 1906). To check whether our results were robust to this phylogenetic structure, we re-estimated the MANOVA, imposing a phylogenetic covariance matrix estimated with a linear-time algorithm, and assuming a Brownian motion model (Ho & Ané, 2014 ; a Pagel's lambda model returned similar results).

All data processing and data analyses were performed under the *ade4* (Thioulouse et al., 2018), *adiv* (Pavoine, 2020), *phylolm* (Ho & Ané, 2013) and *phytools* (Revell, 2012) packages of R version 3.6.1 (R Core Team, 2016). Maps were constructed in QGIS 3.6.

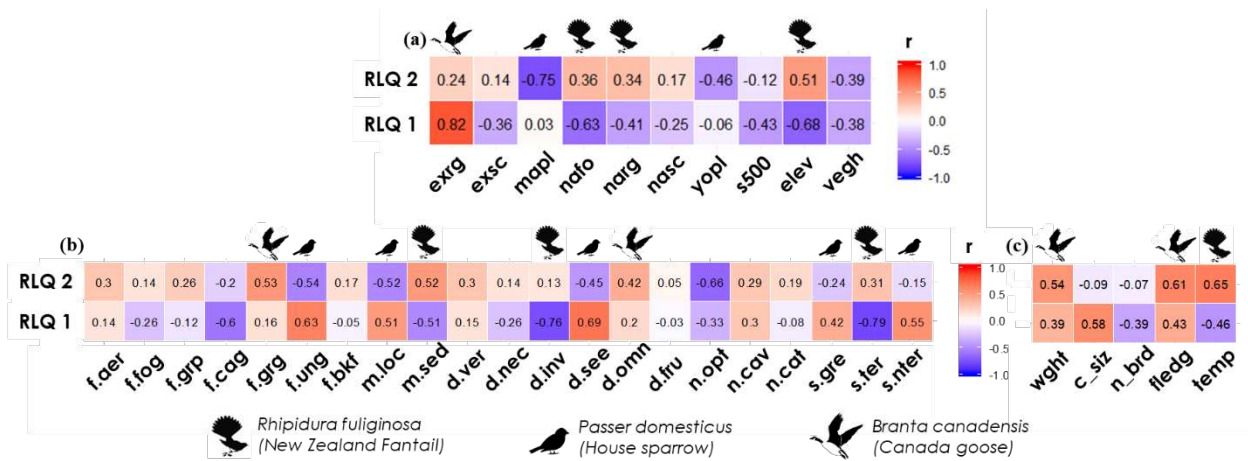


Figure 2. Pearson's correlation coefficients of the two components of the RLQ with habitat variables (a), ecological traits (b) and life history traits (c). Silhouettes depict representative species of the three main groups of trait-habitat relationships found in the RLQ.

Variable	Acronym	Resolution	Data source	Definition	Mean $\pm$ sd
% exotic grassland	exgr	Landscape	NZ Land Cover Database 2	Mainly exotic herbaceous vegetation seeded or under spontaneous dynamics; used by most open habitat species irrespective of their origin	34.53 $\pm$ 28.49
% exotic scrub	exsc	Landscape	NZ Land Cover Database 2	Shrubland of mainly exotic species that invaded modified grassland under spontaneous dynamics	3.39 $\pm$ 8.52
% young plantation forest	yopl	Landscape	NZ Land Cover Database 2	Mature planted forest of exotic trees under silvicultural management	3.14 $\pm$ 9.02
% mature plantation forest	mapl	Landscape	NZ Land Cover Database 2	Mature forest of exotic trees under silvicultural management, replacing native forest in most of the foothills and plains	17.20 $\pm$ 22.94
% native herbaceous vegetation	nagr	Landscape	NZ Land Cover Database 2	More or less native grassland under spontaneous dynamics, used by many open-habitat species	5.77 $\pm$ 15.83
% native scrub	nasc	Landscape	NZ Land Cover Database 2	Native shrubland vegetation under spontaneous dynamics, habitat used by native as well as some alien species	3.41 $\pm$ 8.26
% native forest (all stages)	nafo	Landscape	NZ Land Cover Database 2	Native forest without silvicultural management, key habitat for several native and endemic species	10.28 $\pm$ 18.62
Landscape heterogeneity	s500	Landscape	From previous variables	Shannon-Wiener's index on habitat polygon size within buffers, reflects the heterogeneity of habitats and resources	0.66 $\pm$ 0.41
Mean elevation (m)	elev	Local	Recorded on field	Elevation of a point count; key for the regional distribution of species and habitats and correlated with temperature and precipitation gradients	316.1 $\pm$ 240.1
Mean vegetation height (m)	vegh	Local	Recorded on field	Proxy of the local vegetation structure. High vegetation height is usually associated with older stands and more complex understorey	8.0 $\pm$ 7.7

Table 1. Environmental variables used in the study with description, data source and relevance to birds. Resolutions: landscape: 500 m buffer around each point; local: 100 m around each point.

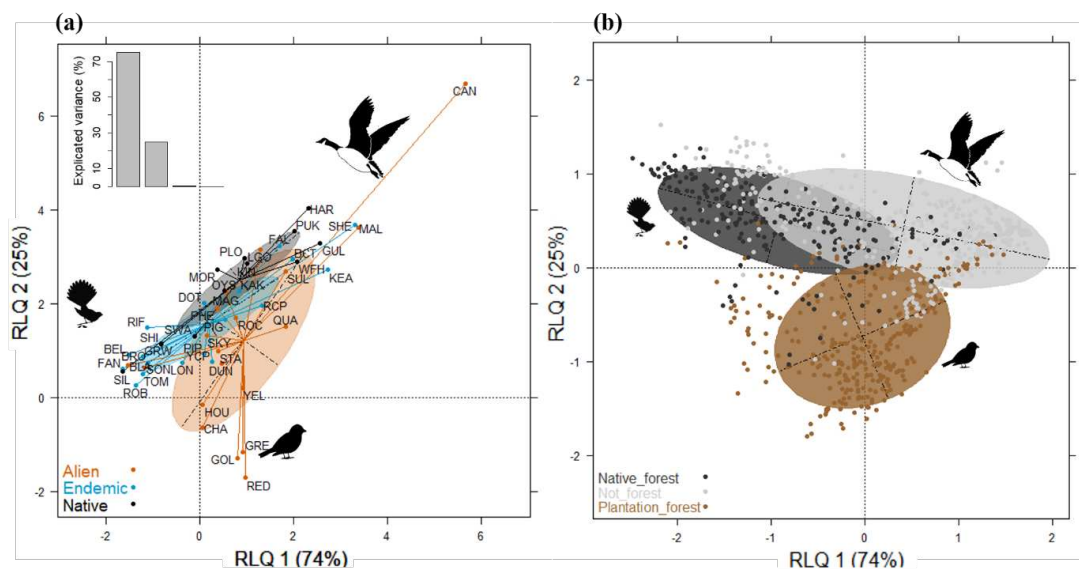


Figure 3. Projections of species (a) and point counts (b) in the bivariate RLQ space controlled for phylogeny and space (species acronyms are explained in Appendix S1, silhouettes in Fig.2). The length of empirical ellipse axes equals $1.5 \times$ the standard deviation of projection coordinates on RLQ1 and RLQ2.

RESULTS

Structure of trait-environment relationships

The two first axes of the RLQ accounted for 74 % (RLQ1) and 25 % (RLQ2) of total variance (third axis: 0.3%; not retained). The negative side of RLQ1 was dominated by native forests at higher elevations, hosting typically small-bodied species displaying invertebrate diets, canopy gleaning, high territoriality and sedentarity (Fig. 2, lower row). The positive side of RLQ1 was associated with low-elevation exotic grasslands hosting larger-bodied species, but also including a guild of granivorous, understorey-gleaning passerines. This first RLQ axis mainly discriminated high-elevation assemblages consisting mainly in native forest species from lower-elevation assemblages dominated by open-habitat species and some understorey-gleaning generalist granivores. The latter species group was tightly associated to plantation forests on the negative side of RLQ2, while the positive side encompassed both native forest birds and mixed assemblages of open-habitat natives and aliens displaying a relatively wide range of traits (Fig. 2, upper row). Consistently, the projection of species (Fig. 3a) and points (Fig. 3b) on these two axes confirmed that RLQ1 summarized a gradient ranging from birds associated with native forests at higher elevations to exotic open-habitats at lower elevations, while RLQ2 isolated alien seed-eating passerines living predominantly in plantation forests.

Three partly-overlapping assemblages emerged from this two-dimensional space. Native forest assemblages (negative side of RLQ1, positive side of RLQ2) consisted mostly in endemic and native passerines such as bellbird *Anthornis melanura* and rifleman *Acanthisitta chloris*, with the exception of two European thrushes (blackbird *Turdus merula* and song thrush *T. philomelos*, Fig. 3a). These species are territorial, sedentary and predominantly insectivorous. Avian assemblages occurring in plantation forests (positive side of RLQ1, negative side of RLQ2) were distinct on both taxonomic and functional grounds (Fig. 3b), being dominated by European finches (goldfinch *Carduelis carduelis*, greenfinch *C. chloris* and redpoll *C. flammea*, Fig. 3a), a group of abundant small tree-nesting granivorous passerines. The last assemblage (positive sides of RLQ1 and RLQ2) consisted of a less defined mixture of native and alien species exhibiting traits associated with ecological generalism and open or wetland habitats, such as gulls, introduced wildfowl or australasian swamphen *Porphyrio melanotus* (Fig. 3a). This asymmetry implies that while native/endemic and alien forest species have distinct trait suites, native and alien open-habitat or wetland species are less functionally distinct from forest bird assemblages.

Spatial distribution of trait-environment relationships

A spatial structure appeared when mapping point count scores on RLQ1: negative values were located in the northwestern, higher elevation parts of the study area and positive values were mainly in the foothills and inland Canterbury plains (Fig. 4a), with the exception of the Banks Peninsula which encompassed all the variability along this axis (Fig. 4b). Because of this elevational gradient, most open-habitat assemblages were located closer to the sea than forest ones. Intermediate assemblages, close to the centroid of RLQ1 and corresponding to mixed native-alien assemblages living in open or mosaics habitats, were located in the middle of the study area (Fig. 1). The geographic structure of RLQ2 opposed a cluster of negative values (assemblages dominated by alien species) in the plantation forests of the foothills to positive values (assemblages dominated by native species) in high-elevation native forests and in parts of Banks Peninsula (Fig. 4c). RLQ2 scores were close to 0 in most of the lower elevation lowlands, indicative of less demarcated assemblages mixing native and alien species, especially within the Banks Peninsula habitat mosaics.

The ordination of point counts on RLQ axes (Fig. 3b), their mapping (Fig. 4) and the particular pattern of the Banks Peninsula assemblages (Fig. 4b) revealed that the structure of the ordination was not a consequence of the regional elevation gradient. The alien forest species guild overlapped little with the two others, although most plantation forests were located at low or intermediate elevations, close to open habitats (Fig. 4b). Conversely, the native forest guild and the open-habitat guild overlapped substantially (Fig. 4b), although they were mainly located at the two extremes of the elevation gradient (Fig. 4a).

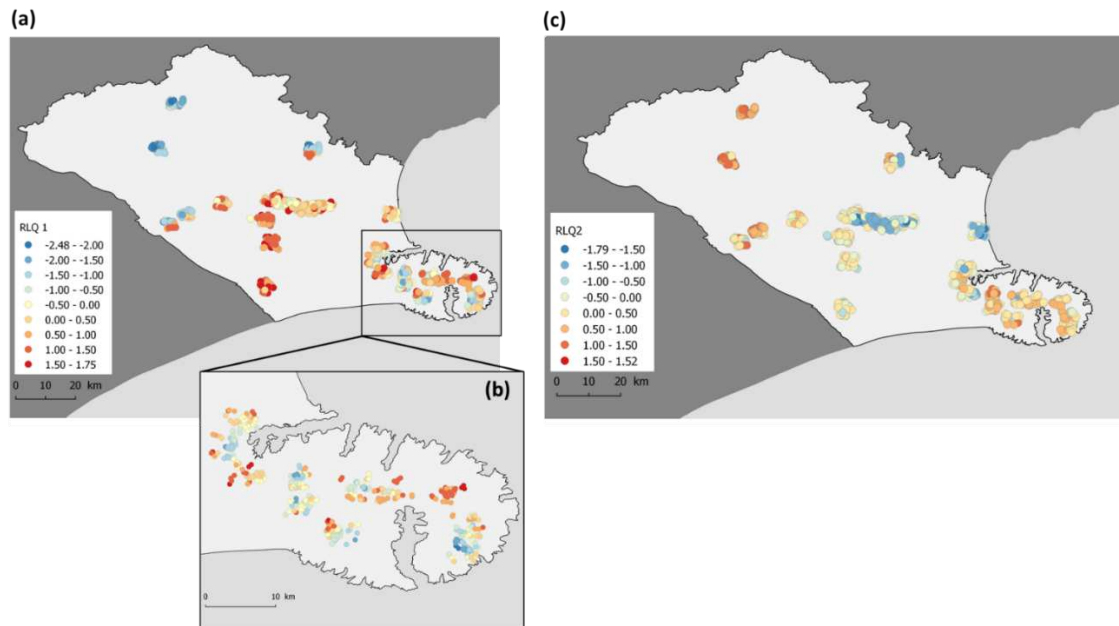


Figure 4. Spatial distribution of the scores of RLQ1 (a ; b : RLQ1 in the Banks Peninsula) and RLQ2 (c) in the study area.

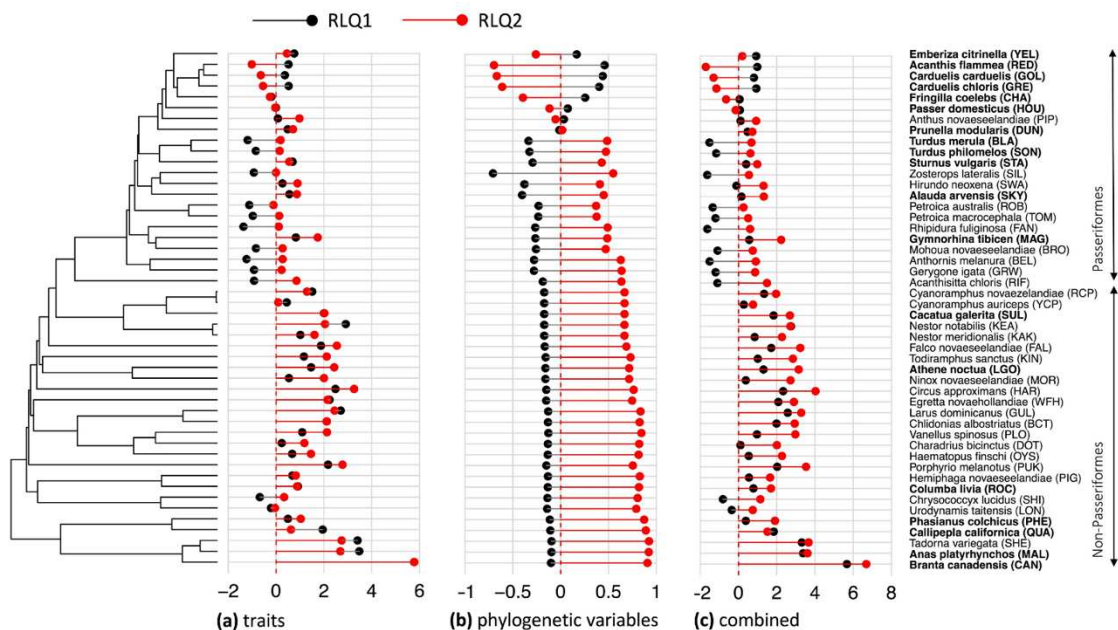


Figure 5. (a) Distribution of the RLQ scores in the phylogenetic tree of the 48 bird species encompassed by the study (alien species in bold, see Appendix S1 for acronyms). The mapping uses an interpolation of the RLQ scores along each edge following the default behaviour of the function `contMap` in the R package `phylotools`. (b) projections of trait variables (the components of a Hill & Smith analysis on the species x trait matrix) on the RLQ axes (black: RLQ1, red: RLQ2). (c) projection of phylogenetic variables (the components of a principal coordinates analysis on a phylogenetic dissimilarity matrix) on the RLQ axes. (d) combined projection of traits and phylogeny on the RLQ axes.

Influence of phylogeny

RLQ1 and 2 were phylogenetically structured (Fig. 5), as expected from the RLQ mapping in Fig. 4. Negative values of RLQ1 were mostly associated with closely related passerine families (e.g. native *Petroicidae* and *Rhipiduridae*, and the only two European *Turdidae* successfully introduced in New Zealand), revealing some evolutionary conservatism in the trait-habitat relationships of forest species (Fig. 5-6, RLQ1). The positive side of RLQ1 (open habitat assemblages) was less structured and included distant clades, including all wetland species and several passerines (Fig. 5-6, RLQ1). The main phylogenetic structure in RLQ2 was the concentration of negative values associated with exotic granivorous species living in plantations (finches, yellowhammer and house sparrow, Fig. 5-6, RLQ2), confirming that these European species share trait-habitat relationships that have no equivalent within the regional bird assemblage.

Effect of introduction history

Alien forest species (negative sides of RLQ1 and RLQ2) were introduced earlier than open-habitat ones, but this pattern was driven by the late introduction of a few large non-passerines (Fig. 6a-b, $F_{2,14} = 8.66$, $p = 0.004$; with phylogenetic correction : t value = 2.57, $df = 13$, $p = 0.021$, not shown on figure). Neither the number of introduction events (Fig. 6c-d, $F_{2,14} = 0.72$, $p = 0.50$; with correction : t -value = -1.84, $df = 13$; 0.09) nor the number of released individuals (Fig. 6e-f, $F_{2,14} = 0.39$, $p = 0.68$; with correction : t -value = 0.46, $df = 13$, $p = 0.65$) had any effect on the ordination, suggesting that the predictors used to account for introduction history had little impact on current trait-environment associations.

Annexes

Ecological traits (class)	Acronym	Sample size or mean $\pm$ sd, endemic species	Sample size or mean $\pm$ sd, native species	Sample size or mean $\pm$ sd, alien species	Justification
Foraging					vegetation strata
<i>Aerial</i>	<i>f.aer</i>	2	4	1	
<i>bark forager</i>	<i>f.bkf</i>	1	0	0	
<i>canopy gleaner</i>	<i>f.cag</i>	7	2	2	
<i>foliage gleaner</i>	<i>f.fog</i>	1	0	0	
<i>ground gleaner</i>	<i>f.grg</i>	3	4	8	
<i>ground prober</i>	<i>f.grp</i>	1	1	4	
<i>understorey gleaner</i>	<i>f.ung</i>	3	0	4	
Main diet					among species
<i>Fruits</i>	<i>d.fru</i>	1	0	0	
<i>Invertebrates</i>	<i>d.inv</i>	9	6	2	
<i>Nectar</i>	<i>d.nec</i>	1	0	0	
<i>Omnivorous</i>	<i>d.omn</i>	0	2	2	
<i>Seeds</i>	<i>d.see</i>	5	0	14	
<i>Vertebrates</i>	<i>d.ver</i>	2	3	1	
Nest location					Dependence on a specific habitat or microhabitat for reproduction
<i>rock cavities</i>	<i>n.cav</i>	3	3	4	
<i>tree cavities</i>	<i>n.cat</i>	4	0	0	
<i>Ground</i>	<i>n.ogr</i>	9	2	11	
<i>Open, in trees</i>	<i>n.opt</i>	9	9	8	
Social behaviour					Spatial distribution of individuals and pressure over resources
<i>Territorial</i>	<i>s.ter</i>	11	7	10	
<i>Non territorial</i>	<i>s.nter</i>	1	2	5	
<i>Gregarious</i>	<i>s.gre</i>	6	2	4	
Movements					Ability to cope with seasonality or unstable environments
<i>Sedentary</i>	<i>m.sed</i>	4	5	8	
<i>Local migrant</i>	<i>m.loc</i>	7	3	7	
Thermal preference	temp	11.22 $\pm$ 3.06	18.32 $\pm$ 4.68	8.77 $\pm$ 7.03	Ability to persist under a given climate or elevation band
Clutch size	c_siz	3.67 $\pm$ 1.97	3.36 $\pm$ 1.29	4.90 $\pm$ 3.21	habitat and resource during the breeding period
Brood number per year	n_brd	2.11 $\pm$ 0.90	1.82 $\pm$ 0.87	2.16 $\pm$ 0.90	Reproductive strategy and duration of habitat and resource use for breeding
Age at fledging	Fledg	21.45	15.19	20.67	Dispersal ability and colonization speed
Weight	wght	259.64 $\pm$ 399.95	400.20 $\pm$ 368.29	518.30 $\pm$ 1153.72	demands, resource use, life history, tolerance to disturbance and dispersal ability
Proxies of introduction effort					
Date of first introduction event	Date	/	/	1872 $\pm$ 19	propagules (assuming that the first event was successful)
Number of introduction events	Nb_intro	/	/	12.79 $\pm$ 4.38	Introduction pressure : recurrence of propagules arrival
Total number of individuals released	Released_tot	/	/	523.07 $\pm$ 170.98	Introduction pressure : intensity of the immigration flow

Table 2. Summary of ecological traits and proxies of introduction effort used in the study (n = 48 species).

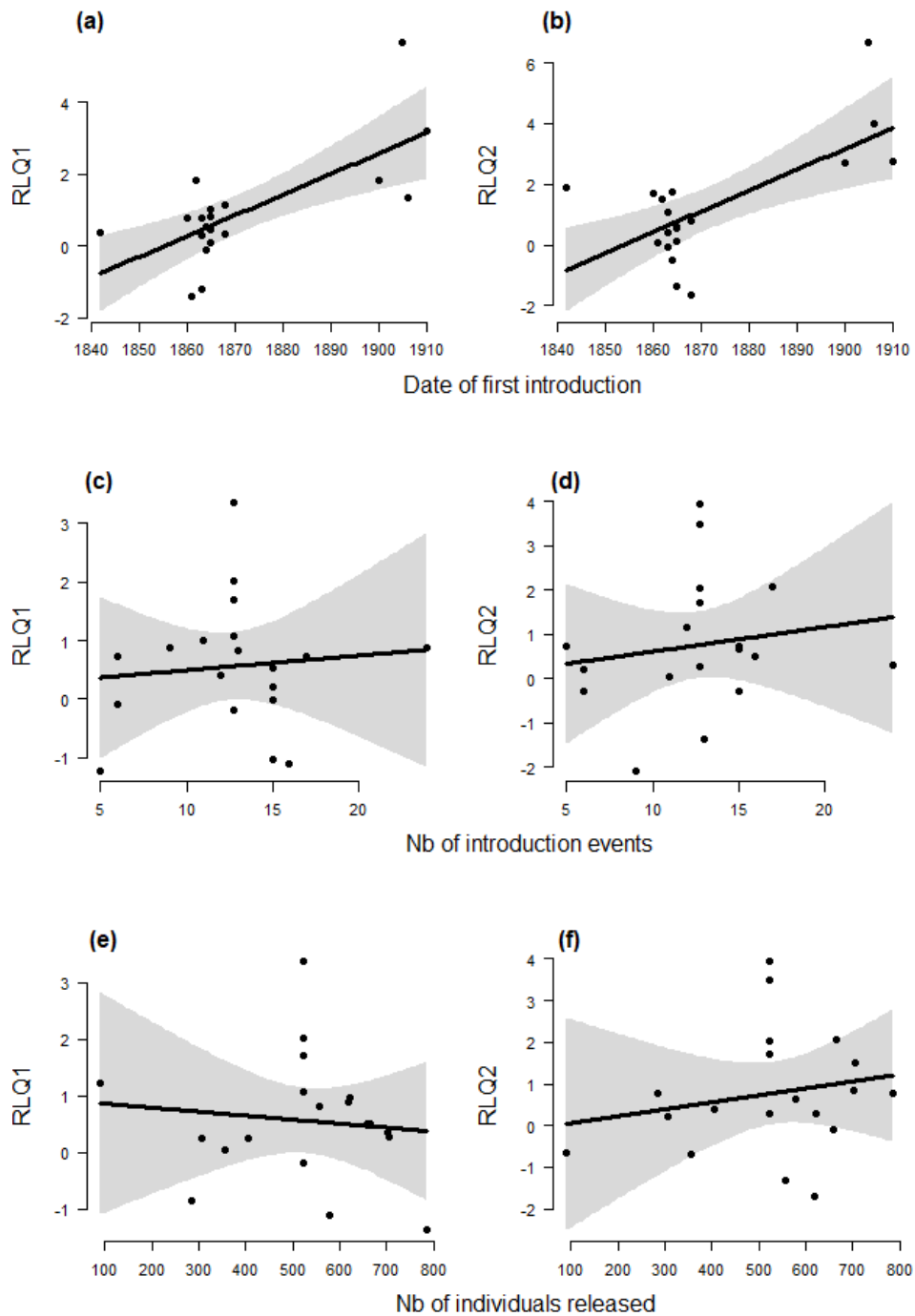


Figure 6. Relationship between proxies of the introduction effort of alien species ($n = 19$) and the two components of the RLQ ordination (estimates and 95% confidence intervals from a multivariate analysis of variance; dots depict partial residuals).

DISCUSSION

Previous studies on New Zealand bird assemblages showed that native and alien species are segregated along gradients of anthropogenic land use (Barbaro et al., 2012; Barnagaud et al., 2014; Méndez et al., 2018). In a further step, we showed in the present work that this partitioning is related with distinct trait syndromes, but mostly independent from aliens' introduction history.

Native and alien species were more clearly partitioned by their traits in forests than in open landscapes, where they exhibited more similar ecological trait suites. Prior to the clearing of forest for agriculture, many open habitats were restricted to a wetlands and small extents of scrub at low elevations. This pattern tied open-habitat native specialists to a handful of species such as fernbird (*Megalurus punctatus*) or New Zealand pipit (*Anthus novaeseelandiae*, Heather et al., 2005). Additionally, the vast majority of open habitat endemics have come extinct early after human's colonization (North and South Island goose *Cnemiornis* spp., Finsch's duck *Chenonetta finschi*, Eyle's harrier *Circus eylesi*, Haast's eagle *Harpagornis moorei*, New Zealand quail *Coturnix novaezealandiae*, adzebills *Aptornis* spp., rails *Rallus* spp., snipes *Gallinago* spp., Laughing owl *Sceloglaux albifacies*; Blackburn et al., 2004; Holdaway, 2001), as well as large-bodied forest moas (Dinornithidae, Blackburn et al., 2004; Holdaway, 2001). These selective extinctions may in turn have increased contrasts in trait composition among habitats and inflated the role of traits indirectly related with habitat preference, such as body size or diet preferences.

RLQ scores varied gradually from open coastal shores to the native forests of Southern Alps, because native species were largely relegated to well-preserved woodlands by the conversion of lowland habitats for agriculture and, subsequently, plantation forest (Deconchat et al., 2009). The overlap of native forest and open-habitat species assemblages in the RLQ space did not reflect a smooth gradient of habitat preferences – for instance, several species located close to the origin of RLQ1 were open-habitat specialists (oystercatcher *Haematopus unicolor*, New Zealand dotterel *Charadrius obscurus* or skylark *Alauda arvensis*). Furthermore, assemblages remained well differentiated in the RLQ space within Banks Peninsula, in association with a complex topography and diverse landscape mosaics where native forests and all types of open habitats were located close together. The persistence of trait partitioning across adjacent habitats within a landscape suggests that strong trait-habitat associations, rather than geographic distance, avoided the invasion of native bird assemblages by alien species in indigenous forests (Parlato et al., 2015). Larger-scale spatial and temporal data would be necessary to infer the influence of environmental filtering *per se* (Méndez et al., 2018; Ruffell & Didham, 2017), but a landscape-level determinism in trait distributions matches the separation of native and exotic species within habitat mosaics, as previously observed in the same region (Barbaro et al., 2012; Barnagaud et al., 2014). Our results are therefore consistent with the hypothesis that native and exotic species are rarely in direct interaction in these novel bird assemblages, because their trait differences (especially foraging ecology and diet) maintain a segregation across habitat patches.

Endemics of native forests were small-sized, insectivorous and territorial (e.g. tomtit *Petroica macrocephala*, rifleman *Acanthisitta chloris* and fantail *Rhipidura fuliginosa*), while alien colonizers of exotic plantations were social and granivorous (e.g. finches or buntings). This pattern is partly driven by the extinction of large forest species following the introduction of mammalian predators (Holdaway, 1989), which may exacerbate the role of body size in the RLQ. Furthermore, diet, body size and territoriality range amongst the traits that explain the winner/loser dynamics characteristic of biotic homogenization in European and Nearctic bird assemblages (Baiser & Lockwood, 2011; Devictor et al., 2008; Newbold et al., 2018). Species that cope well with anthropogenization in their area of origin are also common in the exotic planted forests of New Zealand (e.g. greenfinch *Carduelis chloris*, chaffinch *Fringilla coelebs* and goldfinch *Carduelis carduelis*), as observed in European plantation forests as well (Pedley et al., 2019). This similarity suggests that trait-based winner/loser dynamics could also have confined ecologically specialized native species in their native habitats, while generalism would have permitted some alien colonizers to invade novel man-created vegetation, which was largely free of competing species (Cardador & Blackburn, 2019).

Unique among alien species, song thrush and blackbird exhibited a strong association with native forest, and a trait suite dominated by insectivory, sedentarity and territoriality (Barbaro et al., 2012; Clout & Gaze, 1984; MacFarlane et al., 2016). As a result, they were located close to native forest specialists in the RLQ, although these two species are found in a wide range of habitats in their native areas, including old-growth forest, shrubland and various types of plantations (Samaš et al., 2013). European thrushes are ground foragers that frequently feed on ground invertebrates and breed in lower vegetation stratae (Martay & Pearce-Higgins, 2020), a niche left vacant by the extinction of native ground bird species under the pressure of mammalian predators (Duncan & Blackburn, 2004). Our results are therefore consistent with a combination of competitive release allowing alien ground-nesters and foragers to colonize lower forest stratae, and diet similarity between alien and native canopy gleaners, preventing the former from invading the higher stratae of native forests. These trait-based interpretations refine previous results which showed habitat partitioning between alien and native forest birds along a gradient of vegetation height within New Zealand forests (Barnagaud et al., 2014). However, dedicated monitoring and experimental protocols would be needed to separate the role of habitat and competition further, since they often translate into similar patterns of species distributions (Cadotte & Tucker, 2017; Germain et al., 2018).

We failed to detect any signal of introduction history on trait-environment associations, suggesting that ecological processes have taken over the initial human imprint on alien species. The proxies used here -are non-exhaustive as compared with studies investigating directly introduction effort (Pipek et al., 2020), but it they have the merit to be integrative and equally documented for all species. This result contrasts with many insular avifaunas throughout the globe, which still bear a detectable imprint of early colonization dynamics (Blackburn, Prowse, Lockwood, & Cassey, 2013; Duncan et al., 2019). A

plausible hypothesis to explain this peculiarity of New Zealand, as compared to most other islands subjected to successful bird introductions, is its position under a mainly temperate, rather than (sub)tropical climates (Foster & Robinson, 2007; Kennedy et al., 2010; Thibault et al., 2018). The constraints imposed by a seasonal climate could increase the imprint of trait-mediated environmental filters, leading to an earlier removal of initial introduction signals and lower permeability of native habitats to alien species than on tropical islands (Cardador & Blackburn, 2020). Under this climatic hypothesis, it can be predicted that discrepancies in climates, resources and habitats between native and introduction areas may lead to a stronger role of traits in explaining alien species' introduction success (Blackburn et al., 2013; Duncan et al., 2019; MacLeod et al., 2009; Redding et al., 2019).

Although introduction history played a major role in early colonization events, our results indicate that the establishment success of most alien birds in New Zealand is largely attributable to the anthropogenic conversion of habitats (Cardador & Blackburn, 2019; Veltman et al., 1996). Novel resources likely permitted the persistence of alien species even though their traits were incompatible with native forests, explaining why they remain tied to anthropogenic habitats 150 years after the introduction events. Local adaptation, the expression of behavioral plasticity or fine-grained habitat changes may still trigger future colonization of native habitats by exotic species under the influence of gradual processes or unpredictable regime shifts (Gaüzère et al., 2018). However, our results lead to conclude that trait-habitat relationships currently act as a barrier – or at least as a strong filter – to direct, competitive interactions among alien and native birds in New Zealand forests. They also pointed out the functional originality of endemic bird assemblages occupying native forests, especially when located at higher elevations and/or remote areas far from introduced predators. Since these assemblages may see their ranges restricted in the future with climate warming (Walker et al., 2019), our study urges to preserve the unique bird diversity of New Zealand mainland in the face of the multiple pressures of global change.

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DATA AVAILABILITY STATEMENT

Trait and phylogenetic data are provided as supplementary materials. Bird counts (in a partially-blinded and aggregated format to comply with the privacy policy of the owner) and environmental data will be provided in a DRYAD folder together with all scripts to replicate the analyses upon acceptance.

RESUME :

Si de nombreux animaux effectuent des migrations saisonnières, la migration des oiseaux demeure l'une des plus spectaculaires du règne animal. C'est donc d'abord parce qu'elle fascine les humains que cette migration est la plus étudiée depuis toujours. Cependant, malgré un engouement précoce de la communauté scientifique, depuis les premiers naturalistes de l'Antiquité, d'importantes interrogations persistent. Parmi celles-ci, les processus écologiques qui façonnent la distribution des espèces migratrices ou qui ont conduit des espèces ou des lignées entières à évoluer vers un comportement de migration à longue distance restent peu compris.

L'objectif de ma thèse était d'aborder ce sujet à l'aide de plusieurs approches se situant à différentes échelles taxonomiques. (1) Je me suis d'abord intéressé aux scénarios d'évolution biogéographique et climatique qui ont conduit à l'émergence du comportement de migration à longue distance chez tous les oiseaux du monde. (2) Focalisant le cadre taxonomique aux Charadriiformes, j'ai approfondi mes recherches sur la biogéographie de la migration en étudiant le rôle de ce comportement dans les processus de diversification et la mise en place des gradients globaux de biodiversité. Ces grands patrons biogéographiques décrits, j'ai ensuite cherché à mieux comprendre les mécanismes évolutifs à l'œuvre dans l'apparition et / ou le maintien des comportements migratoires à longue distance. J'ai ainsi étudié comment les pressions de sélection intervenant au cours du cycle annuel des oiseaux migrateurs influencent leur phénotype et leur valeur sélective. Je me suis en particulier intéressé, (3) à l'influence des conditions climatiques rencontrées au cours du cycle annuel sur la distribution de coloration du plumage des Laridae et (4) à l'impact des stratégies de migration sur la reproduction d'une espèce d'oiseau marin de l'Arctique. (5) Enfin, à l'échelle intra-spécifique, j'ai étudié comment de rapides changements de distribution géographiques pouvaient influencer l'évolution de nouvelles voies de migration chez deux espèces de passereaux d'origine sibérienne.

Dans l'ensemble, ces différentes études lèvent le voile sur un certain nombre de scénarios évolutifs et de pressions de sélection liés à l'émergence et aux changements du comportement de migration à longue distance. Ils montrent également l'importance de confronter plusieurs échelles taxonomiques et temporelles pour appréhender l'histoire évolutive de ce comportement. Enfin, ils soulignent la difficulté de prévoir les changements de distribution des oiseaux migrateurs dans un contexte de changements globaux, du fait que les mécanismes éco-évolutifs régissant ces changements sont encore largement inconnus et sous-estimés.

ABSTRACT :

While many animals undertake seasonal migrations, bird migration remains one of the most spectacular in the animal kingdom. Thus, it is mainly because it fascinates humans that this migration has been the most studied historically. Despite this early interest in the scientific community, since the first naturalists in Antiquity, important issues have remained unresolved. Among these, the ecological processes that shape the distribution of migratory species or that have led species or entire lineages to evolve towards long-distance migration behaviour are still poorly understood.

The aim of my thesis was to address this topic with different approaches and at different taxonomic levels. More precisely, (1) I first focused on biogeographic theories of migration evolution at a global scale, coupled with the study of the tracking of ecological niches during the annual cycle. (2) Narrowing the taxonomic framework to the Charadriiformes, I pursued my research on the biogeography of migration by also studying the role of migration in the diversification processes and in the establishment of latitudinal diversity gradients. To better understand these evolutionary mechanisms, I also studied how selection pressures experienced during the annual cycle of migratory birds influence their phenotype and fitness. To this end, I investigated (3) how the climatic conditions encountered along the annual cycle shape the distribution of the plumage colouration of Laridae and (4) how different migration strategies may impact the reproduction of an Arctic seabird species. Finally, at the intraspecific scale, I studied how rapid changes in geographic distribution could influence the evolution of new migration routes in two passerine species of Siberian origin.

Overall, these different studies reveal a number of evolutionary scenarios and selection pressures related to the emergence and changes in long-distance migration behaviour. They also show the importance of comparing several taxonomic and temporal scales in order to understand the evolutionary history of this phenomenon. Finally, they underline the difficulty of predicting changes in the distribution of migratory birds in a context of global changes, due to the fact that the eco-evolutionary mechanisms governing these changes are still largely unknown and underestimated.

Si de nombreux animaux effectuent des migrations saisonnières, la migration des oiseaux demeure l'une des plus spectaculaires du règne animal. C'est donc d'abord parce qu'elle fascine les humains que cette migration est la plus étudiée depuis toujours. Cependant, malgré un engouement précoce de la communauté scientifique, depuis les premiers naturalistes de l'Antiquité, d'importantes interrogations persistent. Parmi celles-ci, les processus écologiques qui façonnent la distribution des espèces migratrices ou qui ont conduit des espèces ou des lignées entières à évoluer vers un comportement de migration à longue distance restent peu compris.

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