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Valentin Journé

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INRA URFM

Thèse présentée pour obtenir le grade universitaire de docteur

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Spécialité : Écologie

Valentin JOURNÉ

Influence du climat lors de l'investissement des ressources dans la reproduction chez les arbres forestiers : Une approche par modélisation mécaniste

Soutenue le 17/02/2020 devant le jury :

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Avant-propos

Dans le cadre de ma thèse je me suis intéressé à l'impact des facteurs climatiques impliquées dans les variations de productions de graines en utilisant deux types d'approches : expérimentale et de modélisation. Dans les deux cas, l'apport de la thèse est de prendre en compte de façon explicite les mécanismes sous-jacents supposés être à l'origine des variations de production de graine. J'ai principalement étudié des espèces d'arbres forestiers, présentes en régions tempérée et méditerranéenne, avec l'objectif de mieux comprendre les mécanismes de leur reproduction afin de prédire leurs dynamiques futures et d'aider à guider leur gestion. Le texte qui suit est composé de parties rédigées en français, avec les articles scientifiques correspondant aux travaux menés en anglais.

Cette thèse a été financée par la région Sud-PACA et l'INRA, à partir de décembre 2016 pour une durée de trois ans. L'ensemble des données récoltées et des travaux effectués ont été financés par le méta-programme ACCAF (Adaptation de l'Agriculture et de la Forêt au Changement Climatique) de l'INRA et l'ANR (projet Mécanismes de l'Adaptation au Changement Climatique, MeCC, ANR-13-ADAP-0006).

Remerciements

Cinq pour cent, voilà le pourcentage de doctorants représentés à travers la classe sociale ouvrière. Bien que ce pourcentage soit en légère augmentation ces dernières années [1], un enfant issu de parents cadres supérieurs a plus de chances de faire un doctorat qu'un enfant de n'importe quel autre situation sociale largement sous-représentée (ouvriers, artisans, agriculteurs). À croire que les études n'ont rien de populaire, et que le doctorat n'est qu'un mythe (et encore, pour ceux qui ont déjà entendu ce mot).

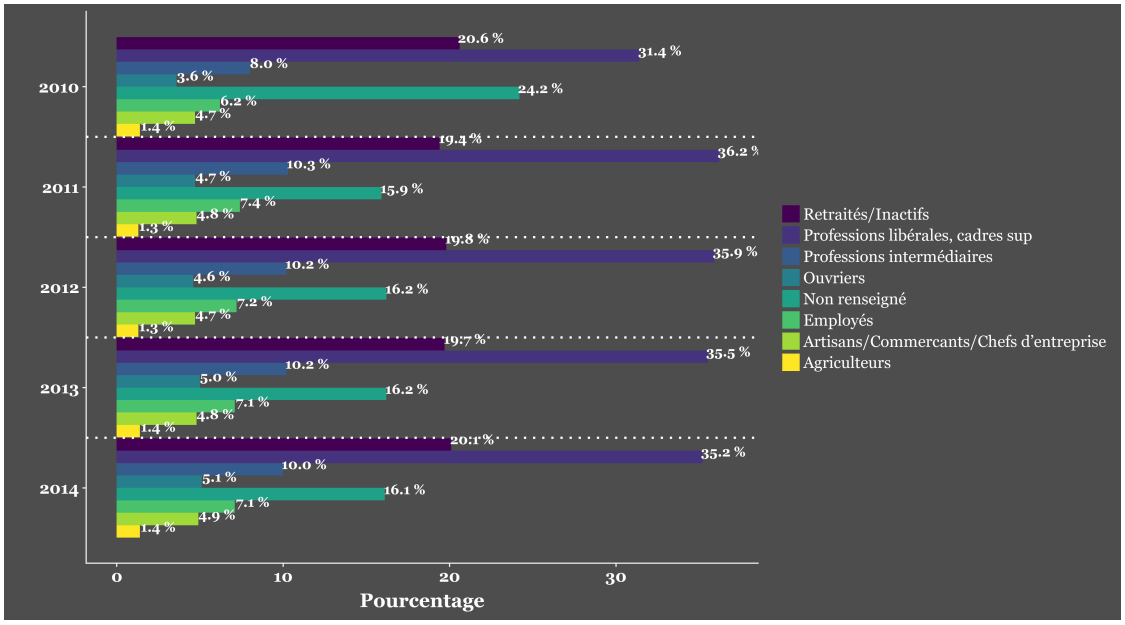

FIGURE 1: L'origine sociale des étudiants français de 2010 à 2014 en France métropolitaine en doctorat (domaines confondus). Données issues du Ministère de l'Education Nationale et de la jeunesse (consulté sur data.gouv.fr en mars 2020, `https://www.data.gouv.fr/fr/datasets/l-origine-sociale-des-etudiants-francais-00000000/`).

(1). Repères et références statistiques, 2018, 396p du Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation

Faire un doctorat, ou de la recherche, était bien loin de mes préoccupations, surtout après avoir obtenu de justesse le sacro-saint baccalauréat scientifique. Difficile de ne pas penser au concept d'égalité des chances, qui exige que le statut social des individus ne dépende plus des caractéristiques morales, ethniques, religieuses, financières et sociales des générations précédentes. En d'autre termes, nous (les humains) partons tous sur la même ligne de départ et avons tous les mêmes chances, il faut croire que **non**. Franck Lepage illustre très bien cette notion dans ses conférences ; « l'égalité des chances, soit c'est l'égalité soit c'est les chances, ça peut pas être les deux ».

Alors pourquoi avoir débuté par cette mini-section ? Simplement pour souligner que j'ai eu beaucoup de chance et surtout bien entouré. Voilà pourquoi je glisse ici quelques remerciements.

En premier lieu, je tiens à remercier Hendrik Davi. J'ai apprécié l'autonomie que tu m'as laissée et la confiance que tu m'as accordée (merci pour les stylos qui sont restés après chaque réunion ;-)). Merci aussi à Sylvie Oddou-Muratorio, ma co-directrice, qui a pris son rôle très à cœur et m'a beaucoup appris à mettre mes idées au clair.

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vous deux, je dois dire que le service client était au top !

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Je remercie aussi très chaleureusement les membres de l'important réseau RENECOFOR géré par l'ONF, ainsi que Manuel Nicolas, Sébastien Cecchini, Sébastien Macé et François Lebourgeois pour m'avoir partagé l'ensemble de vos données et des informations associées.

Merci à François Lefèvre pour m'avoir initié aux modèles mixtes et pour tes relectures, ainsi que François Courbet pour nos discussions sur les limites des modèles (hélas, il restera sûrement des fautes de français dans cette thèse).

Merci à Ivan et Bruno pour les discussions sciences durant les pauses. Merci aussi Caroline pour nos discussions sur le sapin, ainsi que Marie-Claude, sauveuse gestionnaire.

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Pour mes parents, qui m'ont toujours soutenu et qui m'ont initié à la beauté de la nature

Résumé

Les changements climatiques en cours induisent des dépérissements forestiers massifs, qui peuvent aller jusqu'à la mortalité des arbres. Un des processus majeurs de la dynamique forestière est la reproduction sexuée, qui permet la régénération des peuplements, détermine la composition des communautés forestières, et affecte la capacité des populations d'arbres à persister localement au fil des générations grâce à l'adaptation, ou à suivre leur optimum bioclimatique par migration. Mais il reste de nombreuses incertitudes sur l'effet du climat sur la reproduction des arbres, notamment sur le moment et la manière dont sont allouées les ressources au pollen et aux graines. L'objectif principal de cette thèse est de développer une approche basée sur la modélisation des ressources et de la phénologie pour comprendre et prédire l'effet du climat sur la reproduction des arbres forestiers. Dans une première partie, j'ai étudié par une approche statistique les déterminants des variations temporelles et spatiales de la fructification dans des peuplements de Hêtre et de Chênes. J'ai trouvé que la durée de saison de végétation foliaire peut expliquer une part significative de la biomasse de fructification. Dans une seconde partie, j'ai quantifié l'allocation des ressources entre les fonctions de croissance et de reproduction chez le Cèdre de l'Atlas, à l'aide d'un modèle Bayésien hiérarchique, et de données de croissance et reproduction mâle et femelle. En tenant compte explicitement des variations individuelles du niveau de ressources disponibles, ce modèle m'a permis d'identifier des compromis entre croissance et reproduction lors de l'initiation florale, ainsi qu'entre reproduction de l'année et reproduction future. Dans la dernière partie, j'ai développé un modèle mécaniste de reproduction au sein d'un modèle biophysique et écophysiologique déjà existant (CASTANEA). Ce nouveau modèle incorpore les processus d'allocation des ressources et de phénologie depuis l'initiation florale jusqu'à la maturation des graines et fruits, et simule les variations spatiales et temporelles de production de graines. Le modèle a d'abord été calibré et validé sur le Sapin pectiné sur le Mont-Ventoux, puis utilisé pour prédire comment le changement climatique peut impacter la reproduction des arbres. Ce modèle pourra ensuite être utilisé sur d'autres espèces et à large échelle pour étudier les mécanismes physiologiques majeurs impliqués dans les variations de productions de graines et fruits.

Mots-clés : modélisation mécaniste, écophysiologie végétale, allocation du carbone, reproduction

Abstract

Long term climatic trends and extreme climatic events result in massive forest decline and can even lead to mortality. One of the major process of forest dynamics is sexual reproduction, which allows forest regeneration, determines the composition of forest community, and also the ability of tree populations to adapt locally to changing environmental conditions or to track their bioclimatic optimum through migration. However, there are still many uncertainties on the effect of climate change on trees reproduction, especially on when and how resources are allocated to pollen and seeds. The main objective of this PhD thesis is to develop an approach based on resource and phenology modelling, in order to understand and predict climate effects on forest trees reproduction. First, I used a statistical approach to investigate the drivers of temporal and spatial variation of fruit production in beech and oak stands. I found that the length of growing season is a limiting factor of fruit biomass production. In a second part, I quantified the allocation of resources between vegetative versus reproductive functions in the Atlantic cedar, using a hierarchical Bayesian model and observations of growth, male and female reproduction over several years. By explicitly accounting for inter-individual variation in the level of resources, this model allowed me to identify trade-offs between growth and reproduction during floral initiation, and between current and future reproduction. In the third part, I developed a process-based model of reproduction and included it in an existing biophysical and ecophysiological model of forest functioning (CASTANEA). The new reproduction model incorporates resource allocation and reproductive phenology from flower initiation to maturation, and simulates spatial and temporal patterns of seed production. The model was calibrated and validated on silver fir on Mont-Ventoux and used to investigate how climate change will impact fruit production. In the future, this model could be used at a larger scale to investigate the ecophysiological mechanisms involved in masting.

Keywords : mechanistic modelling, plant ecophysiology, carbon allocation, masting, reproduction

Table des matières

Avant-propos **i**

Remerciements **ii**

Résumé **vii**

Abstract **viii**

I Introduction générale **1**

1 Enjeux sociétaux et scientifiques associés à la réponse des forêts aux changements globaux 2

1.1 Enjeux sociétaux 2

1.2 Enjeux scientifiques 3

1 Effets du changement climatique sur la distribution des espèces forestières 3

2 Effet du changement climatique sur le fonctionnement et la dynamique des écosystèmes forestiers 7

3 Réponses possibles des espèces forestières au changement climatique 9

2 Le climat et la reproduction sexuée chez les arbres 10

2.1 Les effets du changement climatique sur la reproduction : des conclusions divergentes 10

2.2 Un autre aspect de la relation entre climat et reproduction : le *masting* 12

1 Le *masting* comme stratégie évolutive : les différentes hypothèses ultimes 12

2 Les mécanismes physiologiques responsables des variations spatiales et temporelles de la reproduction : des hypothèses « proximales » . 14

2.3 Variations inter-individuelles de la production de graines 17

3 Les mécanismes physiologiques de la reproduction 17

3.1 L'induction et l'initiation florale 18

3.2 L'anthèse et la pollinisation 20

3.3 La maturation des fruits 21
4 La modélisation de la reproduction 22
4.1 Les Resource Budget Models : des modèles pour étudier le *masting* 22
4.2 La reproduction, boîte noire, des modèles écophysiologiques forestiers 26
5 Questions de recherches et objectifs 31

II Espèces étudiées et données utilisées 33
1 Écologie générale et cycle de reproduction 35
1.1 Le Cèdre de l'Atlas 35
1 Écologie 35
2 Cycle de reproduction 35
1.2 Le Sapin pectiné 37
1 Écologie 37
2 Cycle de reproduction 38
1.3 Le Hêtre commun 39
1 Écologie 39
2 Cycle de reproduction 40
1.4 Les Chênes tempérés 41
2 Sites d'étude et récolte des données 41
2.1 Données à l'échelle locale 41
1 Le Mont-Ventoux 41
2 La Forêt domaniale de Sault 45
2.2 Données à l'échelle nationale 45
1 Le réseau de l'Office National des Forêts - RENECOFOR 45
2.3 Données climatiques 49

III Effets de la phénologie foliaire, comme proxy de la ressource, sur la reproduction 50
1 Contexte 51
2 Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in temperate oaks (*Quercus robur* and *Quercus petraea*) 52
3 Synthèse et Discussion 83

IV Utilisation d'un modèle bayésien hiérarchique pour estimer la ressource et son allocation entre croissance et reproduction 85
1 Contexte 86
2 A hierarchical Bayesian resource model to investigate trade-offs between growth and reproduction in a long-lived plant 87
3 Synthèse et Discussion 128

V Allocation des ressources lors de la reproduction à l'aide d'un modèle écophysiologique **131**
1 Contexte 132
2 Resource allocation to reproduction in forest trees : an ecophysiological model to predict cones production for silver fir (*Abies alba*) 132
3 Synthèse et Discussion 189

VI Discussion générale : De la compréhension des mécanismes à fine échelle vers la prédiction des patrons de reproduction à large échelle **191**
1 Prendre en compte les ressources pour étudier la reproduction des arbres forestiers 192
2 Vers une meilleure compréhension des mécanismes impliqués dans le *masting* 193
3 Des données aux modèles 197
4 Perspectives 199
5 Des modèles mécanistes intégrant la reproduction pour comprendre et prédire l'aire de répartition des espèces 202

Bibliographie **206**

Annexes **237**
1 Cartes issues des modèles de niches corrélatifs pour le climat actuel et futur sur deux espèces forestières européennes 239
1.1 Zone d'étude et données d'occurrences 239
1.2 Données climatiques utilisées 239
1.3 Modèles de niches corrélatifs : méthodes et résultats . . 240
2 Utilisation de modèle de niche corrélatifs pour prédire les effets du changement climatique sur la biodiversité 243
3 Impact de la défoliation des arbres sur la croissance et la reproduction 268
4 Contributions scientifiques de la thèse 292

Chapitre I

Introduction générale

1 Enjeux sociétaux et scientifiques associés à la réponse des forêts aux changements globaux

1.1 Enjeux sociétaux

« Quand on pense à la restauration des forêts ça capte du carbone de manière super simple, juste planter des arbres, et en plus ça a plein d'autres côtés positifs », Jean-François Bastin (1)

« Investir dans la reforestation partout », Emmanuel Macron (2)

Les forêts présentent de grands enjeux écologiques, économiques et sociétaux. En plus de leur importance dans les cycles biogéochimiques, les forêts abritent une grande biodiversité spécifique (Crowther et al., 2015). Enfin, elles ont un rôle économique et sociétal fondamental, notamment à travers la production de bois, la production d'énergie et le tourisme. En France, les forêts représentent environ 29.7% de la surface du territoire (Figure I.1).
Menacées par les changements climatiques et globaux, les forêts sont aussi au coeur des stratégies d'adaptation et d'atténuation de ces changements. Les dépérissements et mortalités massives observés actuellement diminuent la productivité des forêts (21-50% de perte économique attendue pour les forêts européennes d'ici à 2071-2100, Hanewinkel et al. 2012), et modifient la structure et le fonctionnement des écosystèmes forestiers dans leur ensemble (Anderegg et al., 2013). A l'échelle mondiale, de nouvelles politiques se développent pour assurer le maintien des forêts, notamment par la plantation et la replantation de territoires pour limiter les effets néfastes des changements globaux. Avec environ 315 Gt (3) de carbone, les arbres constituent la majeure partie de la biomasse terrestre totale (Bar-On et al., 2018). Les 3 milliard de milliards d'arbres présents sur Terre, ont un rôle important notamment en termes de stockage de carbone (Crowther et al., 2015). La plantation de près de 0.9 milliards d'hectares pourrait ainsi absorber de 1/3 jusqu'à 2/3 des émissions de carbones d'origine anthropogénique (Bastin et al., 2019; Krause et al., 2019). Mais la vitesse de stockage et la quantité de carbone stocké sont différentes suivant le type de forêt et les pratiques anthropiques. Par exemple, pour les forêts tempérées et tropicales, le puits de carbone reste stable sur la période 1990-2007, contrairement aux forêts boréales qui présentent une diminution du stockage notamment due aux feux et à la déforestation (Pan et al., 2011). En Europe, la biomasse des forêts est très variable suivant les latitudes, qui représentent entre 0.35 et 0.55 Gt de matière sèche par an (Figure I.1, Verkerk et al. 2019), mais son évolution

(1). La reforestation, la meilleure arme contre le changement climatique ?, *Vews-RTBF*, le 4 Juillet 2019. Entretien suite à l'étude de Bastin et al. (2019)

(2). Amazonie : au G7, Macron appelle à une "mobilisation de toutes les puissances", *Le Monde*, le 24 Août 2019

(3). 1Gt pour 10^{12}kg

avec les changements globaux demeure encore incertaine.

1.2 Enjeux scientifiques

L'impact des changements climatiques et globaux sur les écosystèmes est devenu un axe de recherche majeur en écologie. En parallèle de l'augmentation des températures et du CO_2, les observations et les modèles mettent en évidence une augmentation de la fréquence et de l'intensité des événements extrêmes, comme les sécheresses, incendies et gelées tardives, et des changements biotiques soudains (comme l'émergence de parasites, ou d'espèces invasives). Ces modifications abiotiques et biotiques peuvent avoir des effets majeurs sur la distribution des espèces forestières, sur le fonctionnement et la dynamique des écosystèmes forestiers, et plus généralement sur la composition future des communautés forestières et les services écosystémiques qu'elles rendent (Anderegg et al., 2013; Choat et al., 2018). Mais aussi, l'augmentation des concentrations en CO_2 peut avoir des effets bénéfiques pour les forêts, par exemple à travers un effet fertilisant avec un prélèvement de carbone dans l'atmosphère plus élevé ou bien encore une augmentation de l'efficacité de l'utilisation de l'eau (Keenan et al., 2013, 2014; Choat et al., 2018) et la hausse des températures peut induire un allongement de la durée de la saison de végétation.

1 Effets du changement climatique sur la distribution des espèces forestières

L'effet du changement climatique sur les aires de répartition des espèces a largement été abordé à l'aide des modèles de niches bioclimatiques (Encadré 1). Ces modèles prédisent la probabilité de présence actuelle d'une espèce en fonction des caractéristiques climatiques ou plus rarement pédoclimatiques, puis projettent sa probabilité de présence dans le futur. Une première étape de ces modèles consiste à caractériser la niche de l'espèce actuelle, puis une seconde étape peut être de projeter la niche future de l'espèce (Annexe 2). Ces approches prédisent que l'ensemble des espèces vivantes seront impactées par les changements climatiques, et ce quel que soit le groupe taxonomique considéré (Thomas et al., 2004; Thuiller et al., 2011). Il a par exemple été prédit une rétraction majeure de l'aire pour les espèces présentes en régions montagneuses, méditerranéennes et euro-sibériennes (Thuiller et al., 2005). Chez les arbres forestiers, les changements d'aire de distribution prédits diffèrent selon les espèces. Certaines espèces d'arbres auront tendance à agrandir leur aire de répartition comme le Sapin pectiné (*Abies alba*) et le Hêtre commun (*Fagus sylvatica*), alors que celles de l'Epicéa commun (*Picea abies*) et du Pin sylvestre (*Pinus sylvestris*) (Figure I.2) pourraient être fortement réduites par le changement climatique, quel que soit le scénario climatique futur considéré (Dyderski et al., 2018).

Cependant, les prédictions de répartition des espèces d'arbres obtenus à partir des modèles de niche corrélatifs sont à prendre avec précaution, notamment à

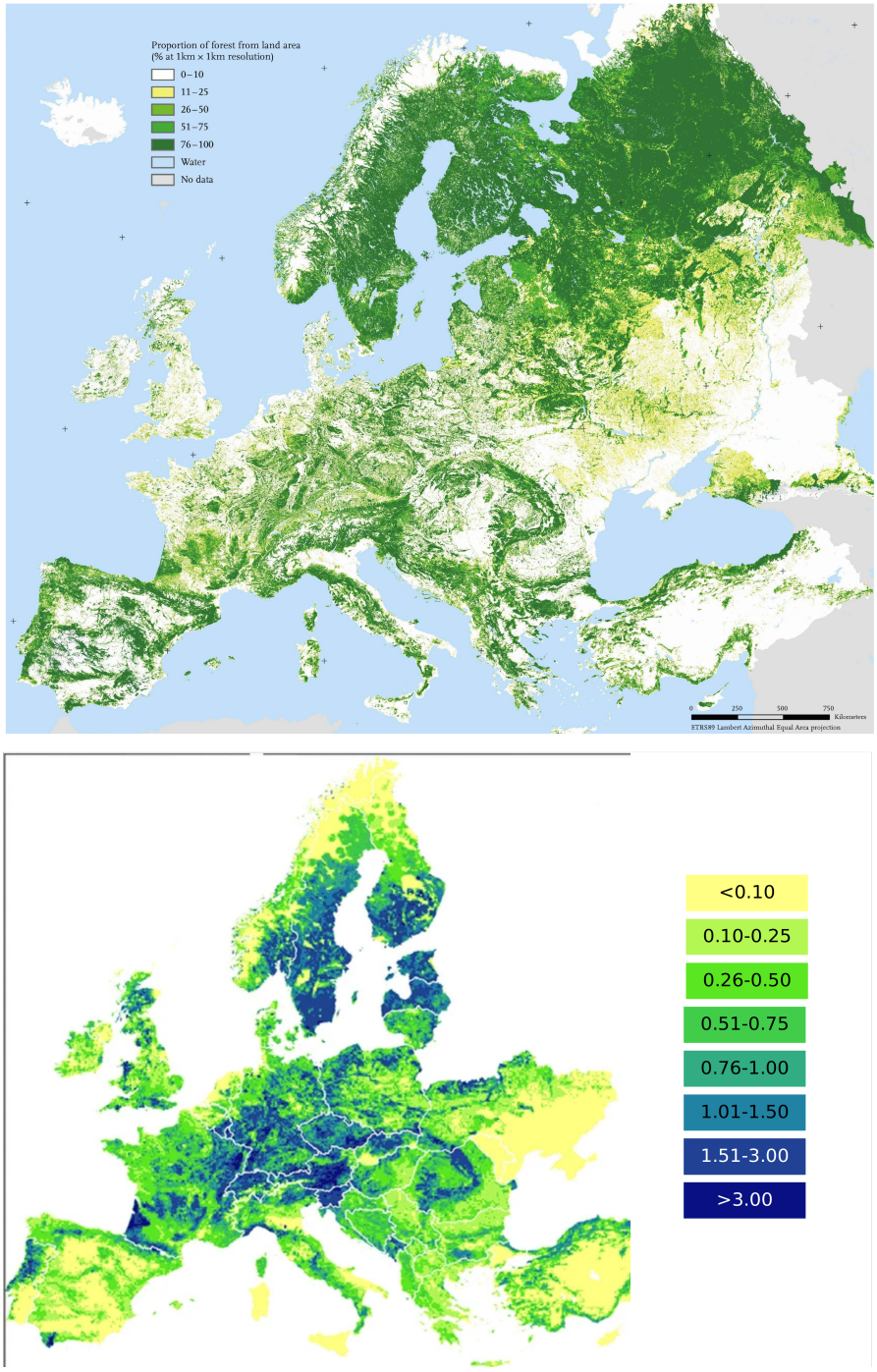

Figure I.1: Figure Haut : Répartition des forêts à l'échelle de l'Europe (d'après l'Institut européen de la Forêt, `https://www.efi.int/knowledge/maps/forest`*). Figure Bas : Estimation de la distribution spatiale de la biomasse des forêts (en t.ha^{-1}.an^{-1} à l'échelle 10*10km, d'après Verkerk et al. 2019).*

Encadré 1 :
La niche écologique des espèces : un concept écologique majeur pour étudier la biodiversité

Le concept de niche a d'abord été employé par Grinnell (1917), qui la définit comme l'ensemble des sites où l'espèce peut vivre. Ce concept a ensuite été repris par Elton (1927), pour qui la niche correspond au rôle fonctionnel d'une espèce et ses interactions biotiques. La définition de la niche que l'on retrouve souvent est celle de Hutchinson (1957), qui distingue la niche fondamentale de la niche réalisée. La niche fondamentale se définit comme un hypervolume à n-dimensions de variables pédoclimatiques dans lequel une espèce peut survivre et se reproduire. La niche réalisée peut différer de cette niche fondamentale du fait des interactions entre espèces, facilitation, compétition ou prédation. En 1977, Grubb redéveloppe à son tour le concept de niche, en le décomposant en quatre composantes principales : niche d'habitat, niche de forme de vie, niche phénologique et niche de régénération. Il précise qu'une espèce ne peut pas persister si les conditions sont favorables uniquement pour la croissance et la survie et non pour la reproduction, incluant la production de graines, la dispersion, la germination et la croissance des jeunes semis. La reproduction est donc une composante principale de la niche (Bykova et al. (2012) parlent de niche reproductive), qui influence la répartition des espèces, notamment par le biais de la température qui impacte des processus de développement des organes reproducteurs mâles et femelles, et la maturation des graines et des fruits. Des études ont même démontré que le succès reproductif est un facteur limitant essentiel, voir plus important que la survie, de l'extension de la répartition des espèces d'arbres (Morin et al., 2007; Duputié et al., 2015).

cause de la structuration spatiale des données climatiques qui peut fortement influencer la qualité des modèles (Bahn & McGill, 2007; Beale et al., 2008). Par exemple, Morin & Thuiller (2009) ont montré que les prédictions futures pour les aires de répartitions arbres sont beaucoup moins pessimistes avec des modèles mécanistes qu'avec des modèles de niche corrélatifs. En effet, la modélisation de certains processus clés, comme la phénologie, peut permettre de mieux prédire les aires de répartition, car les variations phénologiques de débourrement peuvent par exemple fortement influencer le potentiel adaptatif des espèces d'arbres forestiers (Duputié et al., 2015).

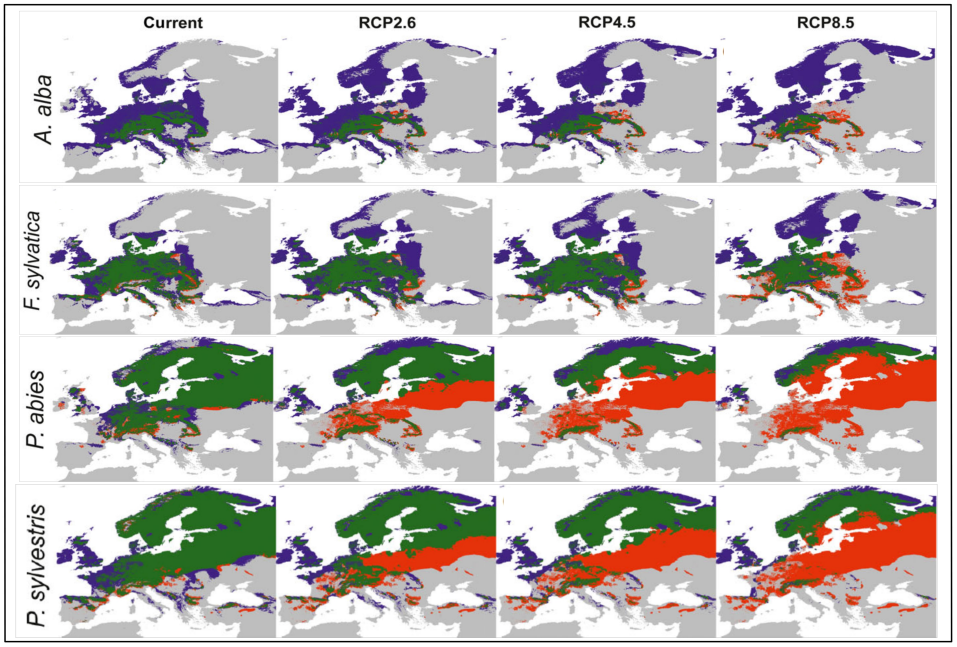

Figure I.2: Prédictions des aires de répartition d'Abies alba, Fagus sylvatica, Picea abies et Pinus sylvestris avec le climat actuel et trois scénarios climatiques futurs (optimiste, RCP2.6, modéré, RCP4.5, et pessimiste, RCP8.5). Les zones bleues correspondent à des prédictions d'expansion de l'aire de répartition de l'espèce, les zones rouges de contraction et les zones vertes de maintien de l'aire de répartition. Figure tirée de Dyderski et al. (2018).

2 *Effet du changement climatique sur le fonctionnement et la dynamique des écosystèmes forestiers*

Les changements progressifs ou brutaux du climat se traduisent d'ores et déjà par des réductions fortes de croissance (Vitasse et al., 2019a) et des signes de dépérissements de peuplements forestiers (Allen et al., 2010), susceptibles d'entraîner la mortalité massive des arbres.

Si l'on s'intéresse aux mécanismes physiologiques, la rupture du continuum hydraulique (*« hydraulic failure »*) et l'épuisement des ressources en carbone (*« carbon starvation »*) sont considérés comme deux processus pouvant entraîner la mort de l'arbre en condition de sécheresse (McDowell et al., 2011; Adams et al., 2017). Les interactions entre flux d'eau et flux de carbone sont en effet à prendre en compte, car les arbres exposés aux sécheresses sont soumis à un compromis majeur entre la limitation des pertes en eau et l'absorption du CO_2 pour assurer la photosynthèse (McDowell et al., 2011). La perte de conductance hydraulique est considérée comme le processus majeur, presque toujours impliqué dans les mortalités liées à la sécheresse (Choat et al., 2018). Enfin, les facteurs biotiques (comme par exemple les ravageurs), sont tout aussi importants et peuvent contribuer à la mortalité des arbres (McDowell et al., 2011; Anderegg et al., 2015).

Un autre facteur important également sensible aux variations climatiques est la phénologie, définie comme l'apparition d'événements périodiques (Schwartz, 2013) et peut ainsi être un très bon indicateur du changement climatique (Cleland et al., 2007; Fu et al., 2015). La phénologie foliaire (de la formation des bourgeons végétatifs à leur ouverture et l'étalement des nouvelles feuilles puis leur sénescence) et la phénologie reproductive (de la formation des bourgeons reproducteurs à la maturation des fruits) sont des processus importants. Ils peuvent avoir un effet direct sur la productivité de la forêt, par exemple sur les cycles biogéochimiques, mais aussi sur le succès reproducteur de l'espèce, par exemple avec la mise en place des fleurs et fruits (Chuine, 2010). Chez les espèces décidues, la phénologie foliaire détermine la période d'activité photosynthétique, qui influence à son tour la productivité des écosystèmes forestiers (Richardson et al., 2010; Keenan et al., 2014), et peut aussi impacter la présence de l'espèce (Chuine, 2010). L'augmentation des températures liée au changement climatique influence la durée de saison de végétation des arbres (*i.e.* période entre débourrement et sénescence, Chen et al. 2019). Menzel (2006) rapportent une avancée moyenne des saisons printanières et estivales de 2.5 jours par décennie, sur la période 1970 à 2000 et à l'échelle de l'Europe. A l'aide des expériences de réchauffement, cette avancée peut aller jusqu'à 4 jours pour la feuillaison et 8.5 jours pour la floraison (Wolkovich et al., 2012). Un décalage de la date de débourrement, peut aussi avancer la date d'entrée en sénéscence sans réduire ou augmenter la durée de saison de végétation. Par exemple, chez des espèces

décidues européennes (Hêtre et Chêne), un débourrement foliaire plus précoce, dû à l'augmentation des températures hivernales et printanières, s'accompagne aussi d'une entrée de l'arbre en sénescence plus précoce et d'un débourrement foliaire l'année suivante plus précoce aussi (Fu et al., 2014). De plus, l'insuffisance d'accumulation des températures froides (températures de *« chilling »*) pendant la période hivernale peut aussi retarder la levée de dormance et affecter la phénologie foliaire ainsi que la floraison. Des aléas climatiques peuvent avoir des conséquences néfastes sur la phénologie florale, en décalant par exemple les dates d'émission de pollen, ou bien en affectant directement la quantité et la qualité des fruits, par exemple en stoppant leur maturation (Petri & Leite, 2004; Chuine, 2010). Lors d'hivers trop doux, les températures trop élevées peuvent provoquer chez certaines espèces des anomalies sur les fleurs, comme des pistils trop courts ou la destruction des ébauches florales, engendrant par la suite une mauvaise fécondation (Sedgley & Griffin, 1989). De plus, la quantité de nutriments disponibles et le taux de CO_2 peut influencer la date de sénescence. Les faibles températures automnales (gelées automnales) permettent à la plante d'entrer en sénescence, mais si la plante a accumulé une quantité importante de nutriments, cela augmente sa résistance face aux gelées automnales et décale ainsi la date de sénescence (Sakai & Larcher 1987, cité in Piao et al. 2019).

Chez certaines espèces, l'effet de la photopériode pourrait atténuer les risques induits par une trop grande précocité du débourrement, et une exposition aux gelées printanières. En effet, le couplage entre l'accumulation de températures froides et de températures chaudes (températures de *« forcing »*) assure la levée de la dormance et le débourrement, qui peut être en plus modulée par la photopériode chez certaines espèces d'arbres décidus (Vitasse & Basler, 2013). Ainsi, lors de printemps chauds, l'avancée de la date de débourrement est limitée par la nécessité d'avoir une durée du jour suffisamment courte pour accumuler les températures chaudes. *A contrario*, lors de printemps froids, un débourrement trop tardif peut être évité par une durée de jour plus longue permettant qu'un besoin de températures chaudes plus faible induisent le débourrement (Fu et al., 2019). Cet effet de la photopériode semble aussi être différent suivant la localisation des populations : le débourrement pour les populations en marges « froides » de leur distribution (*« leading edge »*, limite de haute latitude, Gaston 2003) est principalement contraint par les températures et non la photopériode (Strømme et al., 2019).

Cependant, même si les mécanismes liés à la mortalité et la phénologie des arbres sont assez bien connus, il reste de nombreuses incertitudes notamment concernant l'effet du changement climatique sur l'altération du cycle de reproduction (LaDeau & Clark, 2001; Pearse et al., 2016). Le cycle de reproduction, qui peut être traduit en quantité et qualité de graines et pollen, est une phase

majeure pour le maintien (*i.e.* adaptation) et la migration (*i.e.* dispersion) des espèces d'arbres forestiers. De plus, la dynamique forestière locale et la colonisation de nouveaux milieux dépendent de la régénération naturelle et donc de la production de graines (Mencuccini et al., 1995). Les effets du changement climatique sont déjà observables sur les capacités de régénération, notamment sur la durée de vie des graines et leur germination (Walck et al., 2011).

3 Réponses possibles des espèces forestières au changement climatique

Face aux changements climatiques les populations d'arbres forestières peuvent (i) migrer pour suivre leur optimum bioclimatique, (ii) s'adapter sur place aux changements de leur environnement soit sur le court terme par la plasticité phénotypique, soit au fil des générations par l'adaptation génétique (Corlett & Westcott, 2013). La rapidité actuelle des changements climatiques (Loarie et al., 2009) suggèrent que les capacités de dispersion combinées au long cycle de vie des espèces forestières ne permettront pas aux espèces de suivre suffisamment vite le déplacement de leur aire bioclimatiques (Nathan et al., 2011). Il a été montré que la plasticité phénotypique peut être un facteur important pour l'adaptation des arbres au changement climatique du fait de la forte résilience de ces derniers (Vitasse et al., 2010). A large échelle, la plasticité liée à des traits phénologiques peut aussi contraindre les aires de répartitions futures ainsi que la niche des espèces (Duputié et al., 2015). Les capacités d'adaptation génétique des arbres forestiers sont généralement considérées comme élevées (Savolainen et al., 2007; Alberto et al., 2013), du fait de leurs grandes tailles de population, de leur diversité génétique élevée, et des forts flux de gènes (notamment par pollen) entre populations. Néanmoins, le long cycle de vie des arbres forestiers est aussi un obstacle majeur à une réponse rapide à la sélection.

En plus des mécanismes biologiques d'adaptation au sens large, les pratiques d'aménagement et de gestion forestière peuvent aussi contribuer à adapter les forêts au changement climatique (gestion pour l'adaptation). Ces pratiques de gestion peuvent être classées en fonction de leur impact sur les peuplements forestiers, depuis des options à fort impact, par exemple, le remplacement des espèces existantes par de nouvelle espèces plus adaptées, jusqu'à des options à faible impact (Lefèvre et al., 2014). Ces dernières consistent typiquement à accélérer le rythme naturel de l'adaptation via la plasticité ou la réponse à la sélection naturelle, en jouant sur les paramètres de ces processus (ex. augmenter les flux de gènes, raccourcir la durée de vie des peuplements etc.). Ces mesures à faible impact sont d'autant plus intéressantes qu'actuellement 80% de la forêt française est gérée par régénération naturelle (Michalak & Ministerial Conference on the Protection of Forests in Europe, 2011) et une mise en place de dynamiques massives de plantation peut être compliquée (actuellement moins de 15% de plantation en France Michalak & Ministerial Conference on the

Protection of Forests in Europe 2011). Le succès de ces pratiques de gestion pour l'adaptation repose fortement sur la phase de régénération et donc sur les processus de reproduction. Parmi les mesures d'adaptation des forêts au climat envisagées par les gestionnaires, la migration assistée repose sur le transport de graines issues de peuplements pré-adaptés à des conditions plus chaudes. Cette stratégie de conservation mise en place peut permettre de limiter les menaces liées au changement climatique sur la biodiversité (Richardson et al., 2009). Par exemple, en France et suite à la COP21 de 2015 (Conférences de Nations unies sur les changements climatiques), le projet Giono [(4)] porté par l'Office National des Forêts consiste à sélectionner des graines issues de populations de Hêtre et de Chêne du Sud de la France qui sont déjà soumises aux effets du changement climatique et adaptées à des conditions de sécheresses. Cela permet d'enrichir les peuplements des régions plus au nord de la France, et de participer à la conservation des populations transférées. Ces pratiques soulèvent un certain nombre de questions, sur la survie à court-terme des graines issues de peuplements plus au Sud, sur les distances optimales de transfert de graines, sur l'équilibre entre productivité à court-terme et adaptation au long terme des peuplements forestiers. Mais elles reposent en tout cas sur le succès de la reproduction dans les peuplements situés en marge de leur aire. Les impacts sévères du changement climatiques sur les forêts sont d'ores et déjà observés et prédits, tant en terme de mortalité massives ou de décalage de phénologie. Mais l'impact du changement climatique sur la reproduction reste largement sous-étudié et incertain.

2 Le climat et la reproduction sexuée chez les arbres

2.1 Les effets du changement climatique sur la reproduction : des conclusions divergentes

D'un point de vue théorique, on s'attend à ce que les variations climatiques en cours et prédites affectent la physiologie de la reproduction (Hedhly et al., 2009; Zinn et al., 2010). Tout d'abord, l'augmentation des températures, ainsi que de la fréquence des événements extrêmes altèrent les patrons de phénologie de la reproduction (Sherry et al., 2007). Deux stratégies de floraison en réponse au changement climatique ont été mises en évidence expérimentalement chez des herbacées : certaines espèces fleurissent avant le pic de chaleur, alors que d'autres espèces présentent un pic de floraison après le pic de chaleur. L'allongement de la période de reproduction peut rendre les arbres plus vulnérables, en augmentant leur fenêtre temporelle d'exposition aux stress comme les sécheresses. Des approches de modélisation ont aussi montré que la limitation de la distribution des espèces d'arbres en marges sud s'explique largement par les contraintes climatiques, telles que les sécheresses et gelées, par les dégâts

(4). <plus d'informations au lien ici>

qu'elles provoquent sur les fleurs et les fruits, et par la baisse de succès reproducteur qui en résulte (Morin & Chuine, 2005; Morin et al., 2007). Une date de débourrement foliaire plus tardive en marge de distribution comparée au centre, diminue le succès de maturation des fruits et *in fine* le succès reproducteur (Duputié et al., 2015). Pour les marges « froides » de distribution des espèces (*« leading edge »*, limite de haute latitude, Gaston 2003), les faibles températures diminuent la vitesse d'accroissement des cellules, ce qui retarde le développement et le débourrement des feuilles et fleurs et retarde ainsi la date de maturation des fruits (Duputié et al., 2015). Pour les marges « chaudes » (*« rear edge »*, limite de basse altitude, Gaston 2003), une avancée de la date de débourrement expose les feuilles et fleurs de l'arbre aux gelées printanières, ainsi que les fruits (Duputié et al., 2015). D'autres phases phénologiques, en plus de la phase de maturation des fruits, comme la phase d'initiation et de mise en place des fleurs (Delpierre et al., 2016b) et la phase de germination des graines (Walck et al., 2011) sont aussi affectées par les changements environnementaux.

De plus, les multiples conséquences du changement climatique sur la physiologie des arbres peuvent aussi avoir des répercussions sur la production de graines et de pollen. Un nombre croissant d'études s'intéressent aux variations de la production de graines en relation avec les variations environnementales liées au changement climatique, avec des conclusions contrastées (Tableau I.1). L'augmentation des températures, par exemple au printemps lors de la floraison, a été associée à une augmentation de la production de graines chez les Chênes tempérés en France (Caignard et al., 2017). En revanche, des effets négatifs sur la reproduction ont été rapportés dans des populations de marge sud, si l'augmentation des températures a lieu pendant la période de croissance et d'initiation des bourgeons (Redmond et al., 2012). De plus, l'étude de Pérez-Ramos et al. (2010) sur le Chêne vert, a montré un taux d'avortement et une production de graines stériles plus élevés avec l'intensification des sécheresses, même s'il n'y a pas d'effets sur le nombre final de graines et de fleurs. Enfin, d'autres études se sont intéressées aux effets climatiques qui peuvent influencer la quantité et la qualité de la reproduction, comme par exemple le pollen et son pouvoir germinatif, la qualité du pollen pouvant être un facteur limitant la qualité des graines produites (Bykova et al., 2018).

Il semblerait que les variations de précipitations ont un effet direct, notamment avec les risques de sécheresses lors de la pollinisation et fructification, mais aussi indirect en favorisant l'accès aux ressources en eau du sol (Allen et al., 2014). En outre, l'augmentation du taux de CO_2 atmosphérique devrait favoriser une augmentation de la production de graines. Des Pins (*Pinus taeda*) soumis à un taux de CO_2 d'environ 35% supérieur à la moyenne sont matures plus précocement, produisent jusqu'à trois fois plus de cônes (LaDeau & Clark, 2001)

et produisent aussi plus de pollen (LaDeau & Clark, 2006). L'augmentation du taux de CO_2 ne semble pas affecter la qualité des graines produites, ni la viabilité des graines, que cela soit pour le genre *Quercus* (Stiling et al., 2004) ou pour le genre *Pinus* (Way et al., 2010). Pour l'espèce *Fagus sylvatica*, il semblerait aussi que l'augmentation de CO_2 réduit la compétition entre le puits [(5)] de croissance et de reproduction (Han et al., 2011).

2.2 Un autre aspect de la relation entre climat et reproduction : le *masting*

Chez de nombreuses espèces pérennes, une variabilité entre années de la production de graines associée à une synchronisation entre individus est observée à l'échelle de la population, avec des années de forte production suivies d'années sans production de graines (Kelly & Sork, 2002; Pearse et al., 2016). Ce phénomène est appelé en anglais *masting* ou *mast seeding* (Kelly, 1994; Kelly & Sork, 2002; Koenig et al., 2003). La fréquence des épisodes de forte production de fruits est souvent irrégulière chez les arbres forestiers, contrairement aux arbres fruitiers où la forte production de fruits a lieu une année sur deux (Monselise & Goldschmidt, 1982; Sedgley & Griffin, 1989). L'alternance que l'on retrouve chez les arbres fruitiers est assez bien connue, et les arboriculteurs réduisent par exemple la quantité de bourgeons présents sur l'individu pour réduire la compétition future entre fruits (Sedgley & Griffin, 1989). Différentes hypothèses sont évoquées pour expliquer ces phénomènes de *masting* et leur variation entre espèces, notamment des hypothèses évolutives, qui s'intéressent aux causes ultimes du *masting*, et des hypothèses physiologiques, qui s'intéressent aux causes proximales du *masting*. Beaucoup de ces hypothèses, à des degrés divers, reposent sur l'étroite dépendance de la reproduction des plantes au climat.

1 Le masting comme stratégie évolutive : les différentes hypothèses ultimes

Le *masting* peut être l'expression d'une stratégie évolutive conséquence de la sélection naturelle. Une première hypothèse, dite « de satiété des prédateurs » [(6)], repose sur l'impact réciproque des variations de production de graines sur les tailles de populations de prédateurs de ces graines : les années de fortes productions de graines conduisent à la satiété des prédateurs, ce qui permet le recrutement de semis issus des graines épargnées, alors que les années de faibles production de graines permettent de diminuer la taille des populations de prédateurs (Silvertown, 1980; Clark et al., 2019). En lien avec l'interaction

(5). défini ici comme une structure qui consomme des ressources carbonées (Wardlaw, 1990)

(6). On parle aussi parfois « d'économie d'échelle », c'est-à-dire qu'une production massive de fleurs ou de graines est plus efficace (en terme de valeur sélective) qu'une production constante, car il y a potentiellement plus de pollen disponible ou de fruits (Pearse et al., 2016).

Étude	Espèces	Mécanismes	Réponse moyenne
Allen et al. 2014	*Nothofagus spp.*	Augmentation des précipitation estivales augmente la disponibilité des nutriments dans le sol	Augmentation du nombre de cônes
Bisi et al. 2016	*Pinus cembra, Larix decidua, Picea abies, Pinus mugo, Abies alba, Picea abies, Pinus sylvestris*	-	Pas de variation du nombre de cônes
Buechling et al. 2016	*Picea engelmannii*	Températures élevées et fortes sécheresses	Augmentation du nombre de cônes
Bykova et al. 2018	*Quercus ilex*	Augmentation des sécheresses	Augmentation de l'avortement du pollen mâle
Caignard et al. 2017	*Quercus petraea, Quercus robur*	Augmentation des températures printanières	Augmentation du nombre de fruits
Flores-Rentería et al. 2018	*Pinus edulis*	Augmentation des températures	Diminution de la germination du pollen
Hacket-Pain et al. 2019	*Picea abies*	-	Pas de variation du nombre de cônes
Kelly et al. 2013	15 espèces (famille d'arbre *Elaocarpaceae, Nothofagaceae*)	Différentiel de température pendant la saison de croissance (T_{n-1} - T_{n-2})	Pas de variation
LaDeau & Clark 2001	*Pinus taeda*	Augmentation de la concentration en CO_2	Augmentation du nombre de fruits
LaDeau & Clark 2006	*Pinus taeda*	Augmentation de la concentration en CO_2	Augmentation de la production de pollen
Mutke et al. 2005	*Pinus pinea*	Diminution des précipitations et risque de stress hydrique impactant la pollinisation et l'initiation des bourgeons	Diminution du nombre de cônes
Pearse et al. 2017	> 360 plantes	Facteurs multiples (stress environnementaux et variabilité environnementale)	Diminution
Pérez-Ramos et al. 2010	*Quercus ilex*	-	Pas de variations du nombre de fruits et de fleurs mâles
Overgaard et al. 2007	*Fagus sylvatica*	Augmentation des températures en été (juillet/septembre)	Augmentation du nombre de fruits
Redmond et al. 2012	*Pinus edulis*	Augmentation de la température pendant saison de croissance (de mars à octobre)	Diminution du nombre de cônes

Table I.1: Recensement des études portant sur l'effet du changement climatique sur la production de fruits/cônes moyenne et pollen des arbres forestiers à l'aide d'observations et d'expérimentations.

entre espèces, une plus large production de graine permet de disperser une plus grande quantité de graines aux alentours (Kelly & Sork, 2002) et a donc des effets sur les capacités de régénération et de migration des espèces forestières (Mencuccini et al., 1995), dispersion assurée notamment par les vertébrés (eg. mammifères, Bogdziewicz et al. 2016).

Une autre hypothèse basée sur les variations des conditions environnementales suppose qu'il existe des mécanismes qui permettent aux plantes de synchroniser leurs productions de graines à partir de signaux climatiques (Piovesan & Adams, 2001). Par exemple, pour une espèce de forêt boréale, *Picea glauca*, les larges variations climatiques (e.g. oscillation australe El Nino et oscillation atlantique multi-décennale) sont corrélées avec les périodes de sécheresses et de feux, et *in fine* avec les épisodes de *masting* (Ascoli et al., 2019). Cela signifie qu'après des épisodes de sécheresses et de feux, la plante produira beaucoup de graines contribuant ainsi à la régénération de la forêt avec d'autres espèces pyrophytes, des espèces co-existantes avec *Picea glauca* et qui ont besoin du feu pour se reproduire (Ascoli et al., 2019). Ces variations climatiques à large échelle et moyenne fréquence sont perçues par les plantes, permettant ainsi "d'anticiper" les périodes peu propices à son développement et sa reproduction et d'accumuler assez de ressources pour se reproduire après ces périodes pour des espèces tempérées (Fernández-Martínez et al., 2017a; Ascoli et al., 2017b) et boréales (Ascoli et al., 2019). Cette hypothèse, encore récente, permet de faire converger les hypothèses ultimes, par exemple liées à l'efficacité pollinique, l'abondance des prédateurs/disperseurs et perturbations climatiques, et les hypothèses proximales, comme nous le verrons par la suite, notamment sur les effets directs du climat sur la reproduction et indirects par l'impact du climat sur les ressources disponibles.

2 *Les mécanismes physiologiques responsables des variations spatiales et temporelles de la reproduction : des hypothèses « proximales »*

Actuellement, quatre hypothèses physiologiques majeures sont avancées pour expliquer les variations inter-annuelles de productions de graines en lien avec l'allocation des ressources et la phénologie (aussi appelées causes proximales, Pearse et al. 2016; Vacchiano et al. 2018). Trois d'entre elles reposent sur l'idée que d'importantes fructifications requièrent beaucoup de ressources qui sont présentes en quantités limitées, et que l'allocation de ces ressources à la reproduction dépend de celles allouées aux autres fonctions [(7)].

1. La première hypothèse, nommée « transfert de ressources » (*« resource*

(7). Il s'agit ici d'hypothèses d'allocation de ressources générales, et une modification de l'environnement ou l'apport d'hormones, peut par exemple modifier leur allocation entre la croissance, la survie ou bien la reproduction (Bonnet-Masimbert & Webber, 1995; Lauder et al., 2019; Bogdziewicz et al., 2019a)

switching »), est basée sur une compétition entre puits pour l'allocation des ressources (*« trade-off »*), par exemple entre les fonctions de croissance et reproduction. La phase reproductive peut affecter négativement la croissance des individus, mais aussi leur survie et leurs défenses (Obeso, 2002; Pearse et al., 2016; Bogdziewicz et al., 2019a).

2. La seconde hypothèse nommée « appariement de ressources » (*« resource matching »*) considère que l'arbre produit des graines quand l'ensemble des conditions environnementales sont favorables. Un climat propice favorise à la fois la croissance et la reproduction de l'arbre (Pearse et al., 2016; Bogdziewicz et al., 2019a).
3. La troisième hypothèse nommée « stockage de ressources » (*« resource storage »*) stipule que l'arbre doit accumuler des ressources jusqu'à un certain seuil pour pouvoir se reproduire. Ainsi, les années de fortes productions de graines sont suivies de faibles fructification les années suivantes (Satake & Iwasa, 2000; Pearse et al., 2016; Bogdziewicz et al., 2019a).
4. Enfin, une hypothèse plus récente, appelée « veto » implique un événement limitant l'investissement dans la reproduction au delà d'un seuil. Par exemple, il peut s'agir d'une gelée tardive ou bien d'un stress hydrique qui limite la quantité de fruits et impacte l'allocation des ressources (Tanentzap & Monks, 2018). Dans le cas de gelées tardives, l'individu qui fleurit trop tôt peut voir sa fécondité limitée par la disponibilité du pollen induisant une limitation pollinique (échec du taux de succès de la fécondation) ou bien subir un arrêt de la maturation de fruits, sans lien avec une stratégie d'allocation.

Ces différentes hypothèses ne sont pas mutuellement exclusives, les patrons temporels de production de graines peuvent résulter d'une combinaison entre l'accumulation de ressources (hypothèse 3) et des veto environnementaux (hypothèse 4) (Bogdziewicz et al., 2019b).

Néanmoins, les controverses persistent sur les facteurs déclencheurs du *masting* : *Est-ce que cette production synchrone est fonctionnellement liée au climat, par un impact direct des conditions climatiques sur les ressources disponibles pour la plante, comme le proposent les quatre hypothèses précédentes ? Ou le masting est-il « simplement » déclenché par un signal climatique, sans lien avec les ressources et permettant des variations interannuelles fortes sélectionnées d'un point de vue évolutif (cf ci-dessus) ?*

D'autres processus impliquent aussi un effet direct du climat sur le masting sans lien avec les ressources (Kelly et al., 2013; Pearse et al., 2014, 2016; Fernández-Martínez et al., 2017a). Par exemple, les variations inter-annuelles de reproduction sont principalement corrélées aux variations de température. Ceci a été montré à une échelle locale (hypothèse de la synchronisation de la phénologie, Koenig et al. 2015) comme à l'échelle de l'aire de distribution de l'espèce

(Drobyshev et al., 2014; Fernández-Martínez et al., 2017a; Vacchiano et al., 2017). De nombreuses études démontrent actuellement que certains signaux climatiques sont de très bons prédicteurs du *masting*, comme le différentiel entre les température entre l'année $n-2$ et l'année $n-1$ avant le *masting* (aussi appelé Δ_T, Kelly et al. 2013; Moreira et al. 2015; Vacchiano et al. 2017; Lebourgeois et al. 2018). Ce signal climatique qui a lieu deux ans auparavant reste encore difficile à interpréter d'un point de vue fonctionnel ou évolutif. Dans leur article, Kelly et al. (2013) mentionnent :

> *« seedfall for temperature-driven masting plants is proportional to the change in mean summer temperature over the preceding 2 years. »*

Une interprétation plausible a été évoquée dans l'article de Pearse et al. (2014), qui suggère que ce « signal climatique » résume des effets climatiques favorables de l'année précédant la fructification ($n-1$, effet direct) et des sous-effets liés à la limitation des ressources issues des années précédant la fructification (effet indirect). Ainsi, ce signal climatique aurait globalement un bon pouvoir prédicteur, mais les mécanismes sous-jacents peuvent différer entre espèces.

Par exemple, pour le Hêtre commun (*Fagus sylvatica*), les variations de production de graines seraient principalement dues à un compromis entre croissance et reproduction, plus qu'à un effet climatique (Vacchiano et al., 2017). Un été sec a un effet positif sur la production de graines l'année suivante, mais aussi un effet négatif sur la croissance (Hacket-Pain et al., 2015; Hacket-Pain et al., 2018). Cette forte allocation à la reproduction suite à un été sec peut être une stratégie de « fuite », telle que l'individu alloue principalement ses ressources à sa reproduction au détriment de sa survie et de sa croissance, et peut augmenter ses risques de mortalité à cause des effets de sécheresses (Lauder et al., 2019) (voir aussi Annexe 3). Toujours chez le Hêtre commun, d'autres études ont démontré qu'un différentiel climatique entre deux étés successifs est aussi un bon prédicteur de la reproduction, et qu'il existe une corrélation négative entre croissance et reproduction pour cette même espèce (Drobyshev et al., 2014; Lebourgeois et al., 2018). Pour les espèces de Chênes (*Quercus spp.*), il a été démontré que les compromis entre croissance et reproduction peuvent être dus à des réponses différentes de la croissance et de la reproduction au climat printanier. En effet, les précipitations printanières ont un effet positif sur la croissance, mais un effet négatif sur la reproduction en limitant les concentrations de pollen de l'air et donc *in fine* la production de graines (Knops et al., 2007). Il peut donc être difficile d'étudier de potentiel compromis entre traits liés à la croissance et à la reproduction. En effet, comme le suggèrent les études de Knops et al. (2007) et Hacket-Pain et al. (2018), les corrélations négatives observées ne sont pas forcément dues à des compromis entre traits d'histoire de vie (voir Chapitre IV) mais peuvent être induites par les variations climatiques, quand croissance et reproduction répondent à des signaux climatiques différents et ne

sont pas dépendantes du niveau de ressources.

2.3 Variations inter-individuelles de la production de graines

La production de graine varie non seulement dans le temps, mais aussi entre individus. Ces variations inter-individuelles peuvent résulter à la fois de différences environnementales et de facteurs endogènes. Chez différentes espèces, certains arbres produisent toujours de fortes quantités de graines, et d'autres non (Krouchi et al., 2004; Davi et al., 2016). Par exemple, une petite portion d'individus produit en général beaucoup de graines, ainsi dénommés « super producteurs » (*« super-producers »*), et ont tendance à toujours produire plus de graines que les autres individus présents dans la population (Minor & Kobe, 2017; Hacket-Pain et al., 2019). Ces différences peuvent être dues à la taille de l'individu, le niveau de compétition, à sa croissance (Minor & Kobe, 2017; Hacket-Pain et al., 2019) ou son état sanitaire. Elles peuvent aussi être dues aux variations spatiales de conditions abiotiques comme la réserve en eau du sol, la fertilité (Davi et al., 2016; Moracho et al., 2017; Hacket-Pain et al., 2019). En effet, pour certaines espèces décidues, les individus sur un sol plus fertile et humide produisent plus de fruits (Pérez-Ramos et al., 2014) en plus de l'influence de stress hydrique (Pérez-Ramos et al., 2010). Enfin, des effets génétiques pourraient être impliqués, qui seraient liés principalement à des effets de taille des individus (Seifert & Müller-Starck, 2009). Cependant les études sur la variabilité génétique de traits liée au *masting* restent limitées (exception Caignard et al. 2019).

3 Les mécanismes physiologiques de la reproduction

Pour mieux comprendre les relations entre climat et reproduction, il est nécessaire de tenir compte des différents mécanismes physiologiques impliqués dans la reproduction. Pour assurer leur reproduction, les arbres ont besoin d'atteindre une maturité sexuelle qui dépend de leur taille et de leur largeur de houppier (Chalupka & Cecich, 1997). En plus de la taille, l'architecture du houppier est aussi un caractère déterminant la floraison. Mais la relation entre taille et maturité n'est pas toujours valide, et il semblerait qu'il y ait un âge physiologique pour entrer en reproduction, dépendant des caractéristiques génétiques (où certains individus sont plus précoces) et environnementales (Junttila, 1980; Chalupka & Cecich, 1997; Taugourdeau, 2011). De plus, ces facteurs exogènes n'ont pas tous la même implication et ne sont pas tous connus (Taugourdeau, 2011). En général, une fois que l'individu peut se reproduire, il est possible de distinguer trois phases principales, que sont l'initiation, correspondant à la mise en place des

bourgeons floraux, l'anthèse, correspondant à la maturation des fleurs et enfin la maturation des fruits. Une fois les graines produites, constituant les fruits, ces dernières seront dispersées sur des sites plus ou moins favorables et germeront éventuellement.

La croissance de l'arbre, chaque année, utilise des ressources carbonées (C), de l'azote (N) et du phosphore (P) issues des ressources accumulées l'année précédente et en cours (Millard & Grelet, 2010). Le niveau des ressources accumulées une année impacte potentiellement la reproduction l'année suivante. Les réserves en azote sont importantes pour la floraison printanière des arbres fruitiers, et elles sont aussi impliquées dans le *masting* (Sala et al., 2012; Miyazaki et al., 2014). L'azote et le phosphore proviennent de la minéralisation de la matière organique et la décomposition de la litière (ex. champignons mycorhyziens), alors que le carbone est principalement issu de la photosynthèse. Les arbres accumulent de larges quantités de réserves carbonées dans leurs tissus souvent sous forme de de NSC (*Non Structural Carbohydrates*) incluant glucose, fructose, saccharose et amidon, mais parfois aussi sous forme de lipides (Dietze et al., 2014), même si la proportion de NSC reste minoritaire par rapport au carbone utilisé pour les structures. L'azote est lui stocké pendant l'hiver dans l'écorce et le bois, les racines et le tronc pour les espèces décidues et dans les aiguilles pour les conifères (Allen et al., 2017). Enfin, l'enchaînement des phases de la reproduction (de l'initiation à la maturation) sont aussi fortement conditionnées par la phénologie qui peut être variable suivant les espèces (ex. cycle de reproduction sur 2 ans ou plus, émission du pollen au printemps ou en automne).

3.1 L'induction et l'initiation florale

Cette phase pendant laquelle est initiée le nombre potentiel de fleurs détermine la quantité maximale de fleurs produites une année donnée. Tout d'abord, il y a l'induction florale qui correspond à la différenciation des méristèmes. Suite à cela, l'initiation florale correspond aux changements irréversibles que subissent les bourgeons végétatifs, qui évoluent ensuite en bourgeons reproducteurs (bourgeons floraux). Les primordia, qui sont les organes préformés, sont constitués dans le bourgeon pendant une période spécifique, avant de croître (Barthelemy & Caraglio, 2007). Un bourgeon végétatif hivernal contient plusieurs feuilles embryonnaires et primordia de feuille (ébauche d'organe qui donnera une feuille). Par exemple, chez le peuplier, les premières ébauches embryonnaires peuvent initier le bourgeon végétatif avant la dormance, les bourgeons floraux eux peuvent commencer leur initiation dès le printemps après le débourrement (Brunner & Nilsson, 2004). La photopériode ainsi que les températures seraient impliquées dans l'initiation chez le peuplier (Brunner & Nilsson, 2004), ainsi que chez

l'Épicéa (Owens, 1995). Mais d'autres facteurs exogènes, comme le déficit en irrigation pendant le développement de bourgeons semble affecter la qualité des bourgeons l'année suivante (Gordon et al., 2006). Les racines semblent aussi impliquées dans l'induction florale par le biais de hormones (ex. GA, cytokinines) (Bonnet-Masimbert & Webber, 1995).

Pour de nombreuses espèces d'arbres des forêts tempérées, les primordia floraux (ébauches d'organes reproducteurs) se forment à partir du printemps et jusqu'à l'été, et peuvent constituer le bourgeon dormant jusqu'au printemps suivant. Souvent, un été sec stimule la production de primordia floraux (Poole, 1948; Manson, 1974). Il semblerait que le ratio C/N augmente pendant les sécheresses estivales et soit un des facteurs déterminant le nombre de primordia initiés (Poole, 1948). Par exemple, pour le genre *Fagus*, la succession de printemps secs et chauds consécutifs sur deux ans est impliquée dans les variations de fructification (cite Bourne, in Poole 1948, 1949). De plus, il est mentionné dans l'article de Allen et al. (2014),

> *« Enhanced nitrogen uptake with greater resource priming precipitation potentially leads to increased internal storage which is subsequently remobilized for primordial development in the following growing season, particularly in relatively warm summers. »*

Les conditions climatiques peuvent aussi directement impacter l'induction florale. D'importantes précipitations peuvent rendre l'azote plus accessible, et ainsi augmenter la quantité totale de bourgeons floraux formées. L'approvisionnement en ressources, à travers l'assimilation et la remobilisation des stocks, contrôle l'abondance des bourgeons végétatifs, leur phénologie et facilite l'initiation florale (Owens, 1995). Ainsi, il semblerait que l'azote soit un élément majeur de la reproduction car il stimule l'induction florale quand les ressources azotées disponibles sont élevées (Miyazaki et al., 2014; Abe et al., 2016). Des expériences ont montré une augmentation de la production de fleurs, et *in fine* de la quantité de graines, quand le milieu est enrichi en azote (exemple avec *Nothofagus spp.*, Davis et al. 2004, *Quercus spp.*, Bogdziewicz et al. 2017a). Mais, chez les plantes pérennes, il est difficile de détecter le moment de l'induction florale à cause de la dormance, qui induit une pause dans le développement des bourgeons. Ainsi les mécanismes physiologiques impliqués lors de l'induction florale des plantes pérennes restent encore largement inconnus. A une échelle plus fine, le déterminisme de l'induction florale implique des réseaux de régulation de gènes, impliqués eux-mêmes dans la transition entre par exemple la croissance végétative et la reproduction (Miyazaki et al., 2014; Satake et al., 2019). La variation saisonnière de l'expression d'un gène FT (FLOWERING LOCUS T), affecte les changements morphogénétiques qui ont lieu pendant la phase végétative des bourgeons et l'initiation des organes floraux (Miyazaki & Satake, 2017). Ainsi pour *Fagus crenata*, ce gène est sur-exprimé notamment en

fin de printemps/début été, et permet de déterminer la période d'initiation. Un niveau d'expression élevé de ces gènes prédispose à une fructification abondante l'année suivante (Miyazaki & Satake, 2017).

Même si la mise en place des bourgeons floraux semble dépendre de l'azote, leur développement nécessite ensuite aussi plus de ressources que les bourgeons foliaires, et affecte aussi l'allocation des carbohydrates disponibles (Bonhomme et al., 1999; Han & Kabeya, 2017). De plus, il semblerait qu'il y ait un compromis entre la quantité de graines qui arrive à maturation et le nombre de bourgeons initiés, comme il est démontré avec les expériences d'extractions de fruits (Fox, 1995; Santos-del-Blanco & Climent, 2014). Lorsqu'il y a une quantité importante de fruits matures, cela réduit le nombre de bourgeon initiés (et donc la fructification de l'année suivante) et peut réduire les réserves carbonées disponibles (*i.e.* NSC, Crone et al. 2009).

3.2 L'anthèse et la pollinisation

L'anthèse correspond à la maturation des bourgeons reproducteurs en fleurs. Ramené à un même poids, les structures reproductives femelles nécessitent plus de carbohydrates que les structures reproductives mâles. Par ailleurs, il a été montré que la photosynthèse effectuée par les structures reproductives femelles contribue en partie à leurs propres besoins (Allen et al., 2017). Mais cette photosynthèse des fruits reste mineure en comparaison du carbone total assimilé par l'arbre (exemple chez *Pseudotusga menziessi*, McDowell et al. 2000). Pour les arbres forestiers, la floraison et l'expansion des feuilles vont donc puiser dans les réserves carbonées plus anciennes, stockées au niveau des branches ou bien du tronc. Une insuffisance de ces ressources peut en partie expliquer les avortements précoces. En revanche, la croissance des structures reproductives femelles et les nouveaux bourgeons hivernaux semblent plus dépendantes des photo-assimilats de l'année (McDowell et al., 2000; Hoch et al., 2013; Han & Kabeya, 2017).

Le taux d'avortement floral peut être très variable entre années (Stephenson, 1981) et peut aussi être responsable du taux de variation de production de fruits finaux. Nous pouvons en effet distinguer deux mécanismes induisant de fortes variations inter-annuelles de la reproduction : elles sont dues soit à des variations dans le nombre de bourgeons floraux initiés, soit à des variations dans le niveau d'avortement des fleurs. Une forte production de graines peut ainsi être le résultat de la survie d'un grand nombre de fleurs matures qui vont ensuite donner les graines (aussi nommée *mast-fruiting*), ou bien d'un fort investissement floral (aussi nommée *mast-flowering*) (Pearse et al., 2016; Bogdziewicz et al., 2017b). Par exemple, chez le Chêne, il semble qu'il y ait une production constante de fleurs, mais avec des années avec plus ou moins d'avortements. Chez le

Hêtre, au contraire, la production de fleurs est variable, avec des années de plus ou moins forte production de bourgeons floraux. *A contrario*, les années de faible production de graines sont le résultat (i) d'un avortement de fleurs plus important et/ou (ii) d'un nombre de bourgeons, donc de fleurs initiées plus faible ou (iii) les deux à la fois. Au total, les fleurs représentent une petite partie des ressources investies. Ce faible coût de la floraison par rapport à l'investissement total dans la biomasse de la reproduction, permettrait une grande variabilité du nombre d'avortements des fleurs entre années, ce qui pourrait être bénéfique sur le long terme pour certaines espèces qui ont tendance à produire beaucoup de fleurs (Allen et al., 2017). Certains auteurs décrivent cela comme une stratégie de minimisation des risques (*« bet hedging »*). Pour maximiser le succès reproductif sur le long terme et en dépit d'événements catastrophiques imprévisibles, les individus vont produire des fleurs en excès tous les ans (Slatkin, 1974; Montesinos et al., 2012), quitte ensuite à avoir un fort taux d'avortement. De plus, il faut qu'il y ait une allocation synchrone des ressources pour la fonction femelle et mâle pour augmenter l'efficacité pollinique (Rapp et al., 2013). En théorie, l'allocation entre la fonction mâle et femelle peut varier suivant le niveau de ressources (Korpelainen, 1998). Cependant, pour les espèces d'arbres monoïques qui font du *masting*, il a été montré qu'il n'y a pas de compromis entre fonction mâle et femelle, mais qu'il s'agit plutôt d'une efficacité pollinique plus importante lors des années de *masting*, où les individus allouent plus de ressources pour la reproduction femelle (Knops & Koenig, 2012; Rapp et al., 2013; Moreira et al., 2014). De plus, l'allocation à la reproduction mâle peut être variable dans le temps comme par exemple des individus âgés qui ont tendance à être plus mâle que femelles (Ne'eman et al., 2011), ou bien produire du pollen à un âge avancé (LaDeau & Clark, 2006). Pour un individu, augmenter sa production de pollen peut ainsi permettre une meilleure dispersion du pollen dans l'environnement et augmenter les flux de gènes entre les différentes populations (Kremer et al., 2012).

3.3 La maturation des fruits

La maturation correspond au processus de développement menant à des fruits constitués de structures reproductrices annexes et de graines (Allen et al., 2017). Chez les arbres tempérés, la maturation des fruits a lieu en même temps que la phase de croissance secondaire et avant que l'arbre ne rentre en dormance. Au début de la maturation, les réserves accumulées pendant l'année peuvent être utilisées, avant que les feuilles ne soient fonctionnellement autonomes et deviennent une source, permettant ainsi de re-remplir les réserves 2 à 6 semaines après l'expansion des feuilles (Hoch et al., 2013; Klein et al., 2016). Différents éléments minéraux influencent la maturation, tel que les concentrations en zinc et phosphore foliaire (Fernández-Martínez et al., 2017b), mais celle-ci s'achève

principalement grâce aux ressources carbonées (Hoch et al., 2013; Han & Kabeya, 2017). En effet, après l'expansion foliaire, la maturation des fruits est assurée notamment par les assimilats produits par la photosynthèse de l'année (Hoch et al., 2013). Les fruits sont donc un puits de carbone et ils ne produisent pas où très peu de photo-assimilats (Hoch et al., 2013; Ichie et al., 2013) et peuvent être en compétition avec d'autres organes ou fonction comme par exemple la phase d'initiation ou bien encore la croissance (Sanchez-Humanes et al., 2011). A noter aussi, que parfois la germination du grain de pollen mâle peut avoir lieu de quelques semaines à quelques mois après la pollinisation, mais que le fruit peut quand même grossir sans que ce dernier soit fécond (Singh & Owens, 1981, 1982; Williams, 2009).
Enfin, il s'en suivra une phase de dispersion et une germination potentielle qui pourra impacter aussi les capacités de régénération (Walck et al., 2011), mais non étudiées dans cette thèse.

4 La modélisation de la reproduction

Face à la complexité des processus et les incertitudes sur le devenir de la reproduction, l'utilisation et le développement de modèles peuvent être des outils majeurs pour lier les différents processus, ainsi que de potentielles interactions entre eux. La modélisation est une approche de plus en plus utilisée pour comprendre et prédire les conséquences des changements globaux (Mouquet et al., 2015). Un modèle permet de tester différentes hypothèses, mais peut aussi être un outil d'aide à la décision par exemple en testant l'effet de différents scénarios de gestion sur la biodiversité. Il faut néanmoins être conscient qu'aucun modèle ne peut être une représentation parfaite de la réalité. Levins (1966) montre notamment que les propriétés de précision, de généralité et de réalisme ne peuvent pas être simultanément optimisées par un même modèle. Dans le domaine de l'écologie et de l'évolution, les modèles corrélatifs, les modèles mécanistes basés sur les processus et les modèles théoriques sont des types de modèles favorisant respectivement plutôt les propriétés de précision, de réalisme et de généralité. Dans cette thèse, je me focalise sur les modèles mécanistes, et en particulier sur les modèles mécanistes basés sur l'allocation des ressources spécifiquement dédiés à la simulation du *masting* (*ressource budget model*, RBMs) et sur modèles mécanistes écophysiologiques qui visent à simuler le fonctionnement général de la plante (et pas seulement sa reproduction).

4.1 Les Resource Budget Models : des modèles pour étudier le *masting*

Objectif général : Les « ressource budget models », RBMs ont été spécifiquement développés dès la fin des années 1990 pour étudier les causes proximales

du *masting* (Isagi et al., 1997). Ces modèles s'inspirent des travaux théoriques en écologie générale de Robert M. May dans les années 70 (May, 1974, 1976) qui montrent qu'à l'aide d'équations différentielles simples avec des rétroactions densité-dépendantes, il est possible de simuler des dynamiques non linéaires complexes avec des fluctuations chaotiques. Les RBMs font l'hypothèse qu'un arbre a besoin de plus de ressources pour fleurir et produire des graines qu'il n'en acquiert en une seule année, et qu'il ne fleurit que s'il a atteint un certain seuil de ressources stockées (Satake & Iwasa, 2002a). Cette hypothèse centrale à ces modèles peut générer un comportement alternatif (*i.e.* année de forte production suivi d'une production nulle, « *alternate bearing* ») ou bien des patrons chaotiques, c'est à dire non prédictibles (Satake & Iwasa, 2000; Crone & Rapp, 2014). En d'autres termes, de petites différences dans les conditions initiales rendent toute prédiction impossible. Ces modèles plutôt théoriques à l'origine ont progressivement intégré d'autres mécanismes ainsi que des données, ce qui a fait d'eux des modèles de plus en plus mécanistes. Dans le Tableau I.2 il est présenté des exemples d'études basées sur les RBMs, qui intègrent des données d'observations et/ou mesures.

Mécanismes modélisés : Il y a trois postulats à la base aux RBMs : 1) la plante a besoin de plusieurs années pour accumuler des ressources jusqu'à dépasser un seuil et ensuite se reproduire 2) les patrons de *masting* sont régulés par un ratio entre ressources allouées à la floraison et ressources allouées à la fructification et 3) une large production de graines réduit la quantité de ressources et la reproduction future (Crone & Rapp, 2014; Pearse et al., 2016; Vacchiano et al., 2018).
Ces modèles sont employés pour comprendre quels sont les facteurs impliqués dans la synchronie de la fructification entre individus et la dynamique non linéaire des fructifications (Isagi et al., 1997; Satake & Iwasa, 2000). Chaque année, l'arbre accumule des photo-assimilats, dont une partie va à la respiration, et au renouvellement des organes aériens et souterrains (ex. feuilles, racines). Une fois qu'il y a assez de réserves et photo-assimilats accumulées (*i.e.* dépassement d'un seuil de reproduction), la floraison et la fructification sont possibles, avec un coût prélevé sur les réserves. L'ajout de la pollinisation est un mécanisme majeur inclut dans l'ensemble des RBMs (Tableau I.2) qui permet de réduire le comportement chaotique des fructifications et assure une synchronie à l'échelle de la population (Satake & Iwasa, 2000, 2002a,b). Les principales évolutions des RBMs ont consisté à détailler le coefficient d'appauvrissement, *i.e.* le coût de la fructification, en le décomposant en plusieurs paramètres pour représenter au mieux l'allocation des ressources entre les fruits et les fleurs femelles et mâles, et aussi revoir les fonctions liées à la pollinisation pour permettre des fructifications massives même s'il y a peu de pollen (Venner et al., 2016; Schermer et al., 2018). D'autres mécanismes ont été inclus comme une différenciation des ressources

Étude	**Espèces**	**Mécanismes**
Abe et al. 2016	*Fagus crenata*	Allocation azote et carbone, signal climatique et limitation pollinique
Bogdziewicz et al. 2018	*Quercus alba*, *Quercus rubra*	Limitation pollinique et veto environnemental
Bogdziewicz et al. 2019b	*Pinus albicaulis*, *Quercus humilis*, *Quercus ilex*, *Sorbus aucuparia*	Limitation pollinique et veto environnemental
Masaka & Maguchi 2001	*Betula platyphylla*	Limitation pollinique
Monks et al. 2016	*Chionochloa (Poaceae)*	Modèle mécaniste basée sur les ressources : stockage des ressources et induction climatique
Ranta et al. 2005	*Betula pendula*, *Betula pubescens*	Variables climatiques (précipitations estivales et température printanière) et limitation pollinique
Satake & Bjørnstad 2008	*Sorbus aucuparia*	Gradient de productivité et adaptation locale
Schermer et al. 2018	*Quercus petraea*, *Quercus robur*	Limitation pollinique
Schermer et al. 2019	*Quercus petraea*, *Quercus robur*, *Quercus ilex*	Limitation pollinique, veto environnemental et phénologie du pollen
Venner et al. 2016	*Quercus petraea*	Limitation pollinique et coût floraison
Ye & Sakai 2016	*Citrus unshiu*	Inclusion d'un nouveau puits : croissance végétative

Table I.2: Exemples d'études basées sur les « ressource budget model » (RBMs) et les différents mécanismes testés dans ces modèles pour simuler le masting.

allouées (par exemple en carbone et azote, Abe et al. 2016), l'induction de la floraison (Monks et al., 2016), un trade-off entre allocation des ressources pour la partie reproductive et la partie végétative (Ye & Sakai, 2016), mais aussi des veto environnementaux (Bogdziewicz et al., 2018) et la phénologie de la floraison (Schermer et al., 2019).

Principaux résultats : Des études basées sur les RBMs ont démontré que la quantité des ressources et la dynamique du pollen, en termes de production et de phénologie, sont des facteurs clés pour expliquer le *masting* pour le genre *Quercus* (Schermer et al., 2018, 2019). Cependant, une étude de Bogdziewicz et al. (2019b) suggère que le veto environnemental est beaucoup plus fréquent pour les espèces de Chênes que la limitation pollinique, et expliquerait la synchronie de la production de fruits. Une étude antérieure avait aussi démontré que les vetos environnementaux, *i.e.* aléas climatiques extrêmes, prédisent les patrons de *masting* et ce même sans limitation pollinique (Bogdziewicz et al., 2018). Ainsi, il semblerait qu'une combinaison de signaux climatiques et de limitation pollinique permettent de reproduire au mieux la variabilité et la synchronie entre individus (Abe et al., 2016), en plus des ressources.

Des études se sont intéressées à d'autres processus d'allocation. Par exemple Liu et al. (2017) ont trouvé que, pour des espèces qui peuvent se reproduire de manière asexuée et sexuée, les années où les ressources restantes sont faibles, la plante se reproduit de manière asexuée et de manière sexuée quand les ressources sont élevées. En tenant compte d'un puits de croissance végétative, il est aussi possible de simuler des patrons de *masting* (Ye & Sakai, 2016). Enfin, Satake & Bjørnstad (2008) ont démontré en travaillant sur un gradient de population au Nord de l'Europe, qu'il est possible de simuler des variations de productions de graines. Ces variations peuvent être dues à de l'adaptation génétique (où les populations à l'Ouest ont un seuil de reproduction plus faible que les populations à l'Est) et à un gradient de productivité différent (où les populations à l'Ouest ont une productivité plus forte que les populations à l'Est). Même si la productivité est élevée pour certaines populations, il se peut que le seuil de reproduction pour assurer la fructification soit lui aussi plus élevé.

Actuellement, quelques études se basent sur les RBMs, mais elles restent limitées à quelques espèces (principalement des Fagacées) et un nombre limité de processus à chaque fois. Enfin, même s'il est possible d'intégrer quelques mécanismes majeurs dans ces modèles pour mieux comprendre le *masting* (ex. signal climatique, migration), il n'est pas possible d'intégrer l'ensemble des caractéristiques de l'individu, des sites et divers processus impactant l'allocation. De plus, ces modèles restent assez théoriques et n'incluent pas la dynamique des ressources et la phénologie. Par exemple, les effets du climat sur les variations

des traits ou la phénologie, peuvent avoir des répercussions sur la dynamique des ressources (Schermer et al., 2019).

4.2 La reproduction, boîte noire, des modèles écophysiologiques forestiers

De nombreux modèles écophysiologiques, aussi appelé modèles basés sur les processus (*« process based model »*), ont été développés pour simuler le fonctionnement de l'écosystème forestier et la dynamique de la végétation, à diverses échelles spatiales (de la placette à l'aire de distribution) et temporelles (de l'heure à l'année). Les modèles strictement biophysiques et écophysiologiques simulent les cycles biogéochimiques entre la canopée, l'atmosphère et le sol en modélisant les processus physiques et physiologiques, tels que le transfert radiatif, l'évapotranspiration, la photosynthèse, la respiration ou l'allocation de carbone. On peut distinguer des modèles globaux, appelés modèle de végétation dynamique global (DGVM, pour *Dynamic Global Vegetation Model*, Prentice et al. 2007, dans lesquels la végétation est représentée par des types fonctionnels de plantes (PFT, *Plant Functional Type*)), et des modèles à l'échelle de placette (*Stand model*, Makela et al. 2000, dans lesquels la végétation est représentée par un arbre moyen, des cohortes ou une population d'arbres). Au cours de ces dernières années, des processus de dynamique forestière issus des *gap models* (Bugmann, 2001) ont beaucoup évolué pour inclure des processus écophysiologiques, en plus des processus de dynamique des populations (croissance, mortalité et régénération) (Pitelka et al., 2001). Le point commun à ces différents types de modèles est le nombre relativement élevé de paramètres physiques et physiologiques décrivant les caractéristiques de l'espèce ou du site étudié (Dormann et al., 2012; Evans et al., 2016).

Les modèles présentés dans cette section sont principalement des modèles basés sur des processus écophysiologiques (aussi nommé *« ecophysiological process-based model »* [(8)], Encadré 2). La plupart de ces modèles utilisent des coefficients d'allocation pour déterminer quelle quantité de ressources (très souvent, seulement les ressources carbonées) est allouée aux différents organes constituant un arbre (Lacointe, 2000; Le Roux et al., 2001; Davi et al., 2009). Ce processus d'allocation dépend généralement aussi de la phénologie des organes, qui définit l'ordre dans lequel le carbone est alloué à ces organes (De Kauwe et al., 2014; Delpierre et al., 2016b; Guillemot et al., 2017).

Cependant, le puits que peut constituer la reproduction est rarement considéré dans ces modèles (Vacchiano et al., 2018; Merganičová et al., 2019). Par exemple, souvent il est supposé qu'une fraction constante des ressources est

(8). terme employé dans le chapitre V et la discussion

allouée à la reproduction. Sinon les modèles intègrent directement des données empiriques comme puits (Vacchiano et al. 2018; Merganičová et al. 2019, voir Tableau I.3). D'autres modèles supposent que la reproduction n'a pas lieu quand il y a assez de ressources (*Net Primary Productivity*, NPP) ou bien assez de réserves accumulées (ex PDG model, Oddou-Muratorio & Davi 2014).

Améliorer la modélisation de l'allocation du carbone est une nécessité (Buckley & Roberts, 2006; Merganičová et al., 2019), en particulier pour la croissance afin de réduire les écarts observés entre la croissance simulée et la croissance mesurée (Babst et al., 2013; Guillemot, 2015). La validation de ces modèles par des données de croissance suggère que les processus d'allocation sont encore mal modélisés et qu'ils peuvent présenter de nombreuses incertitudes sur leurs prédictions futures, comme par exemple les variations de croissance (Guillemot, 2015) ou bien encore la productivité (Collalti et al., 2016). Le manque de précision des simulations peut être dû par exemple à l'incertitude liée au temps de résidence du carbone dans les écosystèmes (par exemple Friend et al. 2014), et l'allocation de ce carbone à différents organes (Lacointe, 2000; Le Roux et al., 2001).

Encadré 2 :
Présentation générale du modèle écophysiologique CASTANEA

Ce modèle simule les stocks (carbone et eau) et les échanges (matière – énergie) entre la forêt et l'atmosphère. Les simulations du fonctionnement et de la croissance des peuplements forestiers sont représentées à l'échelle de l'arbre moyen. Un arbre, dans ce modèle, est constitué de cinq compartiments : fines et grosses racines, tronc, branches et réserves. Les données d'entrée du modèle sont des variables météorologiques à l'échelle journalière et les caractéristiques du sol. L'ensemble de ces processus sont représentés dans la Figure I.3. Ce modèle comporte un grand nombre de paramètres physiques et physiologiques décrivant (i) les caractéristiques de l'espèce, (ii) les caractéristiques du site étudié, (iii) les constantes des équations décrivant les processus (Dufrêne et al., 2005). Le modèle simule différentes variables de sortie : la photosynthèse de la canopée, les coûts de respiration liés à l'entretien et à la croissance de l'arbre, la transpiration et l'évaporation, en plus du bilan hydrique du sol. Actuellement, le carbone est alloué d'abord aux fonctions de croissance des feuilles et de respiration, puis le carbone restant est alloué aux compartiments de biomasse aérienne, de racines et réserves. Les coefficients d'allocation du carbone aux compartiments sont spatialement et temporellement variables. Il existe actuellement deux versions de ce modèle. Une version est développée au laboratoire de ESE (version FORTRAN) et une autre version est développée à l'INRA URFM (version CAPSIS, `<http://capsis.cirad.fr/capsis/help_en/castaneaonly>`). Contrairement à la version FORTRAN, la version présente sur la plateforme de modélisation CAPSIS (Dufour-Kowalski et al., 2012), correspond à une librairie qui peut être connectée avec d'autres modèles présents également sur cette même plate-forme.

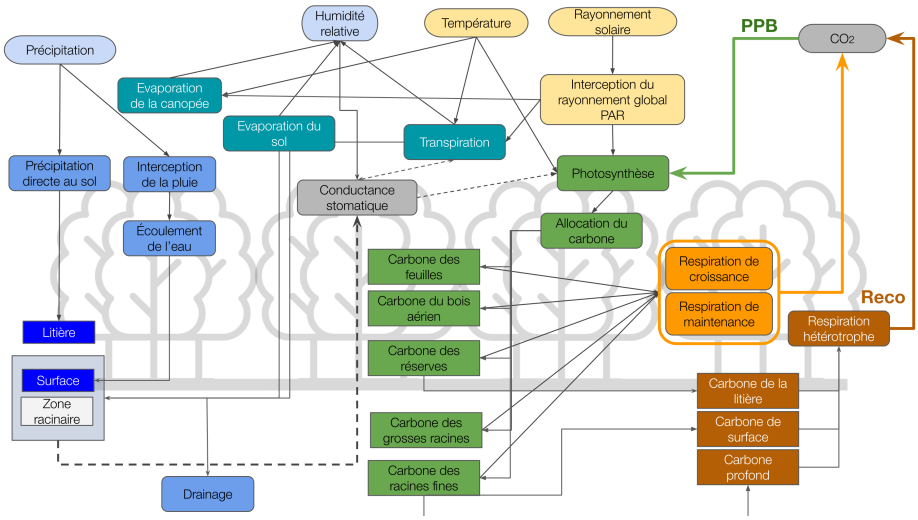

FIGURE I.3: Schéma général du modèle CASTANEA (version CAPSIS). Les ellipses représentent les variables d'entrées. Les rectangles représentent les stocks et les rectangles arrondis représentent les processus simulés.

Études	Modèles	Modélisation de la reproduction
Modèles globaux		
Oleson et al. 2013	CLM	Valide que pour les céréales. Compartiment pour la reproduction, basé sur les ressources carbonées et azotées, basé sur des coefficients d'allocation (coefficient reproduction = 1 - coefficient racine – coefficient tige – coefficient feuille).
Medvigy et al. 2009; De Kauwe et al. 2014	ED	Compromis dans l'allocation des réserves entre croissance et reproduction (70% pour la croissance et 30% pour la reproduction).
Best et al. 2011	JULES	Basé sur le modèle TRIFFID DGVM (Cox, 2001) qui inclut de la dynamique de population. Chaque « cellule » simulées inclut une fraction de graines à 0.01 pour l'ensemble des PFTs, réduisant la quantité de NPP disponible pour le PFT majeur.
Bondeau et al. 2007; Hickler et al. 2004; Krinner et al. 2005; Sitch et al. 2003; Smith et al. 2001; Zaehle & Friend 2010	LPJ, ORCHIDEE	10% de la NPP produite allouée à la reproduction.
Snell 2014; Snell & Cowling 2015	LPJ-DISP	Connexion avec un *gap model*. Inclut en plus l'âge de maturation, une proportion de carbone allouée à la reproduction et un nombre de graines. Coefficient défini pour des années de *masting* et de non *masting* pour l'espèce du genre *Fagus*.

Sato et al. 2007	SEIB-DGVM	Si la biomasse de bois dépasse 10kg de matière sèche (correspond à un proxy taille minimale pour la reproduction), 10% des ressources disponibles (défini ici comme la biomasse disponible) sont allouées à la reproduction.
Kleidon & Mooney 2000	KM2000	Compartiment pour la reproduction. Reproduction possible quand la quantité de photo-assimilats excède la quantité de photo-assimilats initiale (en gC).
Chuine & Beaubien 2001	PHENOFIT	Inclusion de la phénologie de la reproduction (fleurs et maturation des fruits).
Bachelet et al. 2001; Foley et al. 1996; Nielson 1995; Woodward et al. 1998; Brovkin et al. 1997; Law et al. 2012; Shevliakova et al. 2009; Friend et al. 1993	MC1, IBIS, MAPSS, SDGVM, VECODE, CABLE, LMV3, HYBRID	Pas de reproduction et/ou non mentionnée
Modèles arbre et placettes		
Bossel 1996; Hoffmann 1995	TREEDYN, FAGUS	Allocation du carbone et de l'azote, avec compartiment pour la reproduction. La quantité et la croissance des fruits dépend du surplus en assimilats de l'année, et de l'approvisionnement en azote.
Gracia 2003	GOTILWA	Surplus des réserves alloués aux organes reproducteurs.
Simioni et al. 2016	NoTG	Fraction de carbone allouée à la reproduction (fixe à 0.05).
Ogée et al. 2003; Moreaux 2012; Aber & Federer 1992; White et al. 2000; Landsberg & Waring 1997; Milne & Van Oijen 2005; Chertov et al. 1999; McMurtrie & Landsberg 1992; Misson 2004	MuSICA, GO+ (ancien modèle GRAECO et connexion avec MAESTRA), PnET, modèles BGC, 3-PG, EuroBiota, EFIMOD, GDAY, MAIDEN	Pas de reproduction et/ou non mentionnée.

Table I.3: Exemple de modèles écophysiologiques basés sur les processus (« ecophysiological process-based model ») et leur implémentation de la reproduction.

5 Questions de recherches et objectifs

En résumé, la reproduction des arbres est une composante majeure de la dynamique des populations d'arbres forestiers, qui détermine la composition spécifique, la productivité et les divers services écosystémiques rendus par les forêts (Fernández-Martínez et al., 2017b; Vacchiano et al., 2018; Clark et al., 2019). Les effets du changement climatique sur la reproduction sont difficiles à prédire, car les déterminants physiologiques de la reproduction sont multiples et peuvent être affectés de manière différentes par ces changements. Le développement de modèles mécanistes permettrait de mieux comprendre et prédire les variations de reproduction en réponse aux changements climatiques en cours et futurs. Dans ce contexte, l'objectif principal de ma thèse est de comprendre et prédire l'effet du climat sur les variations spatiales et temporelles de production de graines chez les arbres forestiers. L'originalité de mon approche est de prendre en compte l'acquisition et l'allocation des ressources aux différentes fonctions (croissance et reproduction) au cours du cycle de reproduction. Dans les deux premières parties, j'ai utilisé des approches statistiques, basées sur des jeux de données, qui m'ont permis de mettre en évidence le rôle de la durée de la saison de végétation comme un proxy des ressources, et l'existence de compromis d'allocation entre croissance et reproduction. Dans la troisième partie j'ai développé un modèle basé sur les processus qui tient compte de la variation des traits de l'espèce au cours du temps, de la phénologie et de l'allocation du carbone. Plus précisément, j'ai abordé les trois questions suivantes :

Question de recherche 1 : Est-ce qu'il existe un lien entre la durée de la saison de végétation foliaire et la reproduction chez les espèces décidues ? Ce lien peut-il expliquer les variations inter-annuelles de production de graines ?

Dans cette première partie, je me suis intéressé aux déterminants des variations temporelles et spatiales de la biomasse des fruits, à l'aide d'analyses statistiques fréquentistes. J'ai utilisé des jeux de données longitudinales (10 annéees) sur 50 populations suivies de Hêtre et de Chênes. J'ai testé l'hypothèse selon laquelle la durée de la saison de végétation affecte la quantité de graines produites, via son effet sur les ressources.

Question de recherche 2 : Quels facteurs endogènes déterminent les variations inter-individuelles de production de graines ?

Dans cette seconde partie, j'ai travaillé sur des données à échelle individuelle pour un conifère, le Cèdre de l'Atlas (*Cedrus atlantica*), avec deux modalités extrêmes ; une population à faible densité et une population à forte densité, partageant les mêmes conditions climatiques et de même âge. A l'aide d'un

modèle bayésien hiérarchique, j'ai étudié des mécanismes impliqués dans la reproduction en tenant compte des ressources. J'ai abordé les questions suivantes : a) Est-ce qu'il existe des compromis entre croissance et reproduction chez les arbres ? b) Est-ce que la prise en compte des ressources et de la phénologie des puits de reproduction (*i.e.* initiation et maturation) permet de détecter des corrélations significatives avec la croissance ? c) Est-ce que l'allocation à la reproduction sexuée et la densité de population peuvent masquer ces corrélations ?

Question de recherche 3 : Est-ce que l'accumulation des réserves carbonée est impliquée dans les variations de production de graines ? Comment le changement climatique peut impacter les productions de graines et de fruits pour des populations en marge sud de leur aire de répartition ?

Dans une troisième partie, j'ai développé un nouveau modèle de reproduction à partir d'un modèle existant, basé sur les processus écophysiologiques (CASTANEA). Ce nouveau modèle de reproduction tient compte d'une allocation différente entre la phase d'initiation et phase de maturation de graines. Ce modèle permet de mieux modéliser les variations de productions de graines spatiales et temporelles. Je l'ai développé et utilisé sur l'espèce de Sapin pectiné, *Abies alba*, sur le Mont-Ventoux.

Chapitre II

Espèces étudiées et données utilisées

Dans le cadre de ma thèse, j'ai étudié le cycle de reproduction de plusieurs espèces d'arbres forestiers, Gymnospermes ou Angiospermes, choisies à la fois pour leur importance économique et écologique, et pour la disponibilité de jeux de données de reproduction. J'ai principalement travaillé sur le Hêtre commun, *Fagus sylvatica*, dans les chapitres III et V, le Sapin pectiné, *Abies alba* dans le chapitre V et le Cèdre de l'Atlas, *Cedrus atlantica* dans le chapitre IV. En outre, je me suis également intéressé à deux espèces de Chêne de climat tempéré, *Quercus robur* et *Quercus petreae* dans le chapitre III.

Les deux espèces de Gymnospermes retenues sont des conifères sempervirents, c'est-à-dire qu'ils conservent les aiguilles de l'année pendant la période hivernale, contrairement au Hêtre et aux Chênes, des espèces feuillues décidues, qui perdent leurs feuilles à l'automne. Le Hêtre, le Sapin et le Cèdre sont trois espèces modèles étudiées à l'URFM depuis de nombreuses années. Le Chêne est une espèce emblématique en Europe, dont la comparaison avec le Hêtre est intéressante, car elles sont présentes en mélange et potentiellement en concurrences. Hêtre, Sapin et Chêne sont des espèces suivies dans le cadre de divers réseaux à l'échelle de la France ou de l'Europe.

La biologie de la reproduction des espèces que j'ai étudié présentes plusieurs points communs. Ces espèces sont toutes monoïques, c'est-à-dire qu'un même individu porte les fleurs mâles et les fleurs femelles. Elles se caractérisent aussi par des variations inter-annuelles de productions de semences, *i.e. masting*, mais aussi des variations inter-individuelles avec des individus plus fructifères que d'autres, notamment dû par exemple à des effets de taille (Davi et al., 2016; Hacket-Pain et al., 2019). Ces espèces sont anémophiles : la pollinisation est principalement réalisée par le vent, ce qui la rend dépendante des conditions environnementales. L'anémophilie implique de fortes productions de pollen, aussi connue sous le nom de pluies de soufre, qui peut aussi être synonyme de pertes énormes de pollen (Petit & Hampe, 2006). La distance de dissémination dépend de nombreux facteurs : taille, morphologie, vitesse de sédimentation du pollen, caractéristiques du vent, conditions météorologiques et topographie. Un grain de pollen est capable de voyager sur de longues distances, mais au détriment de son pouvoir fécondant. La fécondation se fait la majorité du temps donc sur de courtes distances, et reste efficace quand elle a lieu sur une courte période. Une fois le grain de pollen réceptionné par la fleur femelle, vient la phase de germination : le grain de pollen hydraté germe au contact du nucelle, tissu formant l'intérieur de l'ovule. Dans les sections suivantes, je décris brièvement l'écologie de ces espèces ainsi que leur cycle de reproduction puis les sites et données utilisés.

1 Écologie générale et cycle de reproduction

1.1 Le Cèdre de l'Atlas

1 Écologie

Cette espèce, *Cedrus atlantica* (Manetti ex Endl.) Carrière, est une espèce endémique de l'Afrique du Nord, avec des populations encore présentes au Maroc et Nord de l'Algérie (Wazen et al., 2018). Dans ces régions, le Cèdre est présent de 1200 à 2800 m d'altitude et supporte tous types de sol, excepté les sols trop compacts et présentant un excès d'eau pendant l'hiver. Cette espèce, emblématique de la région Méditerranéenne, a été largement introduite en Europe (Figure II.1). En France, plus de 20000 ha de Cèdre de l'Atlas ont été plantés ou semés (Courbet et al., 2007). Les populations de Cèdres sont, dans leur aire d'origine, beaucoup plus soumises aux sécheresses ce qui impacte négativement leur croissance et le risque de mortalité y est plus élevé (Bentouati, 2008; Linares et al., 2013). Ces augmentations de mortalité se traduisent par une modification des communautés, les Chênes verts et les genévriers remplaçant progressivement les populations de Cèdre (Linares et al., 2011). A noter que cette espèce est aussi sensibles aux ravageurs de graines et peut limiter sa production de graines viables (*Megastimus spp*, Boivin et al. 2015). Ainsi, le Cèdre est classé comme « espèce en danger » par l'IUCN (« endangered », IUCN 2019), notamment à cause de la diminution de la taille de ses populations dans son aire d'origine. Il est prédit dans son aire d'origine un mouvement des populations vers les plus hautes altitudes, induisant une fragmentation plus grande de son aire de distribution (Bouahmed et al., 2019).

2 Cycle de reproduction

Le Cèdre atteint sa maturité sexuelle entre 15 et 30 ans en moyenne, et jusqu'à 40 ans en population issues de la régénération naturelle. Le cycle reproducteur de cette espèce s'étale sur trois ans (Figure II.2). Les bourgeons floraux (ou futurs cônelets) se développent pendant l'été de l'année $n-2$: début juin pour les fleurs et les futurs strobiles mâles et fin août pour les fleurs et les futurs cônelets femelles. La pollinisation commence à partir du mois de septembre, lorsque les écailles des cônelets femelles sont ouvertes, permettant ainsi la réception du pollen. Ensuite, les chatons mâles finissent par faner et les cônes femelles par refermer leurs écailles en octobre-novembre. La fécondation a lieu au printemps de l'année $n-1$, soit 8-9 mois plus tard. Les cônes femelles continuent leur développement jusqu'à l'automne-hiver de l'année n, en se sclérifiant, avant leur désarticulation. L'ouverture des cônes femelles est alors provoquée par une déshydratation (facteur exogène) et non la croissance du cône (Toth, 1978). Les graines relâchées par les cônes sont ensuite dispersées par le vent et restent au

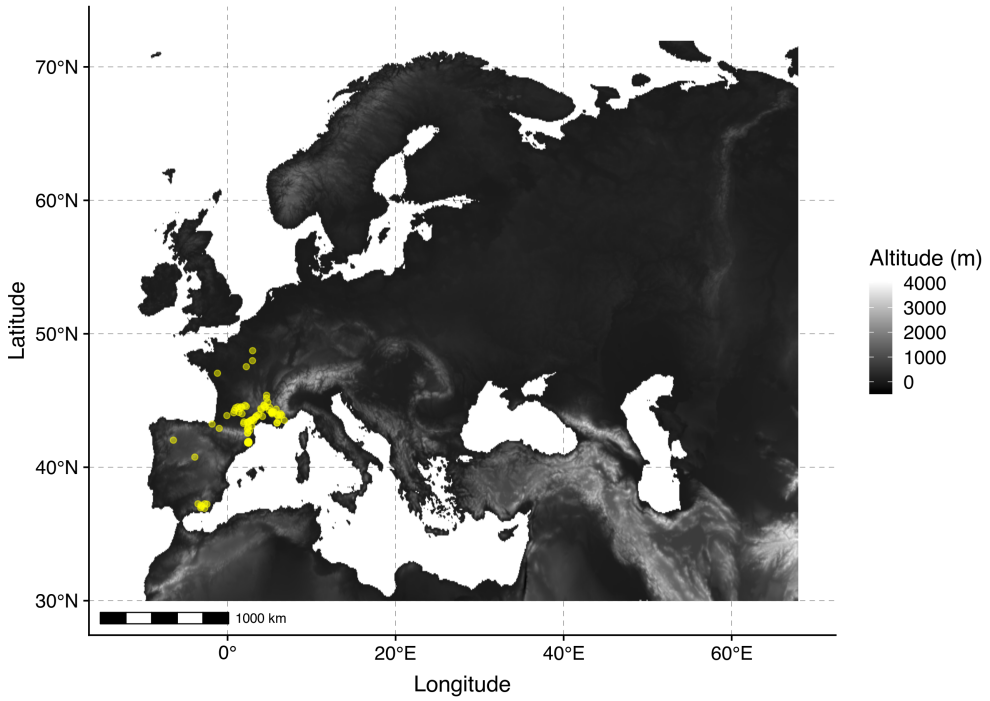

Figure II.1: Occurrences du Cèdre de l'Atlas en Europe (en jaune). Données issues d'inventaires forestiers (Mauri et al., 2017).

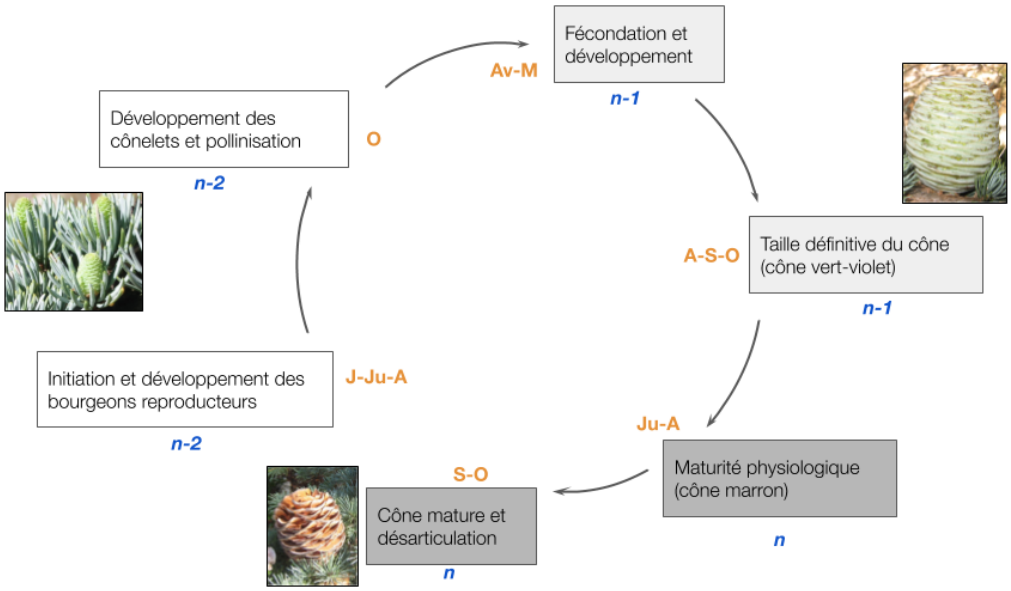

FIGURE II.2: Cycle de reproduction du Cèdre de l'Atlas. Photos de cônelets femelle, cône arrivé à sa taille finale et désarticulation d'un cône femelle mature. Cycle sur trois années ($n-2$, $n-1$ et n). Abréviations : J : juin, Ju :juillet, Av : avril, M : Mai, A : août, S : septembre et O : octobre. Crédits photos : A. Chalon, F. Jean.

sol jusqu'au printemps suivant ($n+1$, non représenté). Un individu peut donc porter plusieurs générations de cônes femelles sur la même branche.

1.2 Le Sapin pectiné

1 Écologie

L'aire de distribution du Sapin pectiné, *Abies alba* Mill. s'étend principalement en Europe centrale, des Pyrénées au Carpathes et du Sud de l'Italie au Nord de la Pologne (Figure II.3). On rencontre cette espèce principalement de 500 à 2000 mètres d'altitude, sur des sols profonds, riches en nutriments et bien drainés (pH acide à neutre). Cette espèce a besoin d'un minimum de précipitations (700-1800 mm par an). Elle est souvent présente en association avec l'Épicéa commun et le Pin sylvestre, et avec le Hêtre commun à plus basse altitude. Elle est sensible aux gelées tardives, aux insectes (ex. Coléoptère comme les scolytes et Homoptère comme les pucerons) et aux champignons. D'autres ravageurs interviennent aussi sur la production de graines (par exemple *Dioryctria abietella*). Les populations de cette espèce sont stables (IUCN, 2019), mais le devenir de cette espèce face au changement climatique est sujet à controverse.

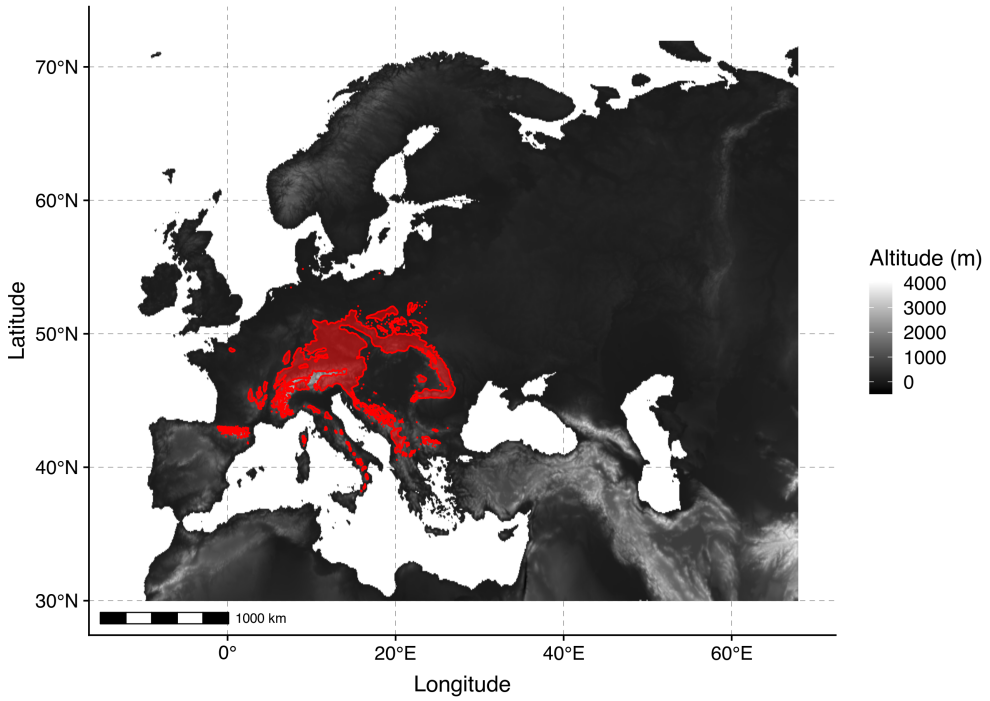

FIGURE II.3: Aire de répartition du Sapin pectiné. Données issues de Euforgen (2019) <http://www.euforgen.org/>.

Les études paléo-écologique suggèrent que cette espèce peut être abondante à des températures très élevées, contrairement aux études basés sur les modèles de niches corrélatifs qui tendent à prédire un forte diminution de la répartition de cette espèce (Vitasse et al., 2019b).

2 *Cycle de reproduction*

Ce gymnosperme atteint sa maturité sexuelle après 30 ans. Il y a un fort risque d'autofécondation, principalement chez les individus isolés (Restoux, 2009). Le cycle de reproduction du Sapin pectiné s'étale sur deux années. L'initiation des bourgeons a lieu à la fin du printemps/début de l'été, puis ils se développent jusqu'à une période de dormance hivernale. Au printemps de l'année suivante courant avril-mai, les bourgeons reproducteurs mâles et femelles continuent leur développement permettant *in fine* la pollinisation en mai (Figure II.4). Le pic d'émission du pollen est observé vers la fin mai (communication et observations

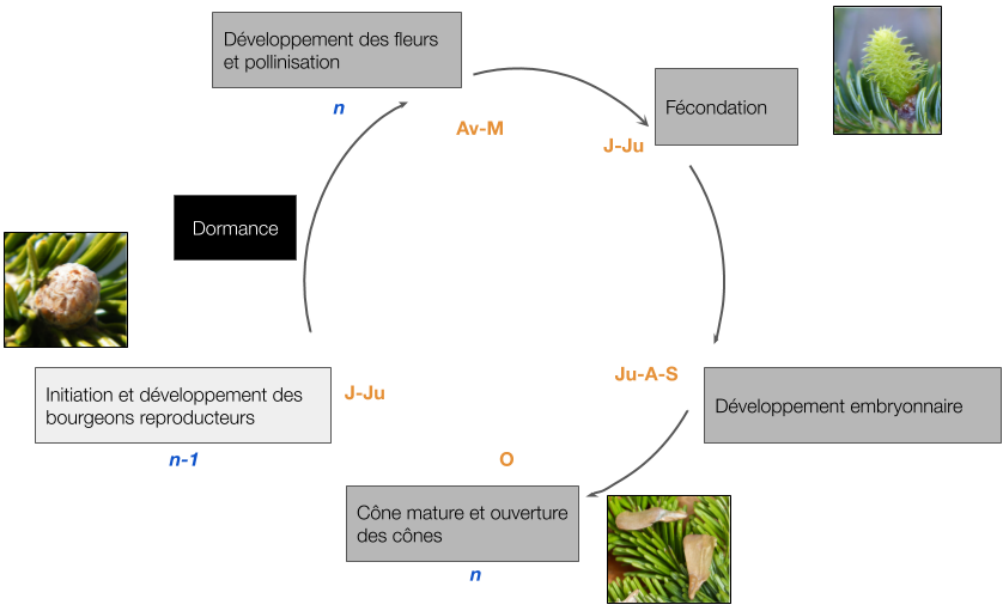

FIGURE II.4: Cycle de reproduction du Sapin pectiné. Photos d'un bourgeon femelle dormant, développement du cônelet femelle et graines de Sapin. Cycle sur deux années (n-1 et n). Abréviations : J : juin, Ju : juillet, Av : avril, M : mai, A : août, S : septembre et O : octobre. Crédit photos : F. Jean

personnelles au Mont-Ventoux). Même si les cônes de Sapin grossissent rapidement après la pollinisation, la germination du grain de pollen n'a lieu que de 5 à 8 semaines après sa réception. Après la fécondation au début de l'été, les graines se développent jusqu'à octobre pour obtenir un cône mature. La dissémination des graines peut commencer à partir de septembre suivant les situations.

1.3 Le Hêtre commun

1 Écologie

Le Hêtre commun, *Fagus sylvatica* L., est une espèce emblématique des forêts européennes. Son aire de distribution s'étend du Sud de l'Italie au Sud de la Scandinavie, et de l'Angleterre à la mer Noire (Figure II.5). Cette espèce peut être présente jusqu'à 2000 m d'altitude, notamment pour les populations situées en marge Sud de l'aire de distribution. Cette espèce a besoin de sols bien drainés comme les sols calcaires ou légèrement acides, mais elle tolère de nombreux substrats et une large gamme de pH. Le Hêtre tolère les hivers rigoureux, mais est sensible aux gelées tardives, aux champignons et aux ravageurs (ex. coléoptères). On retrouve aussi des infestations des faînes induites par des chenilles (ex. *Cydia fagiglandana*) qui altèrent la germination des graines. D'après l'IUCN (2019),

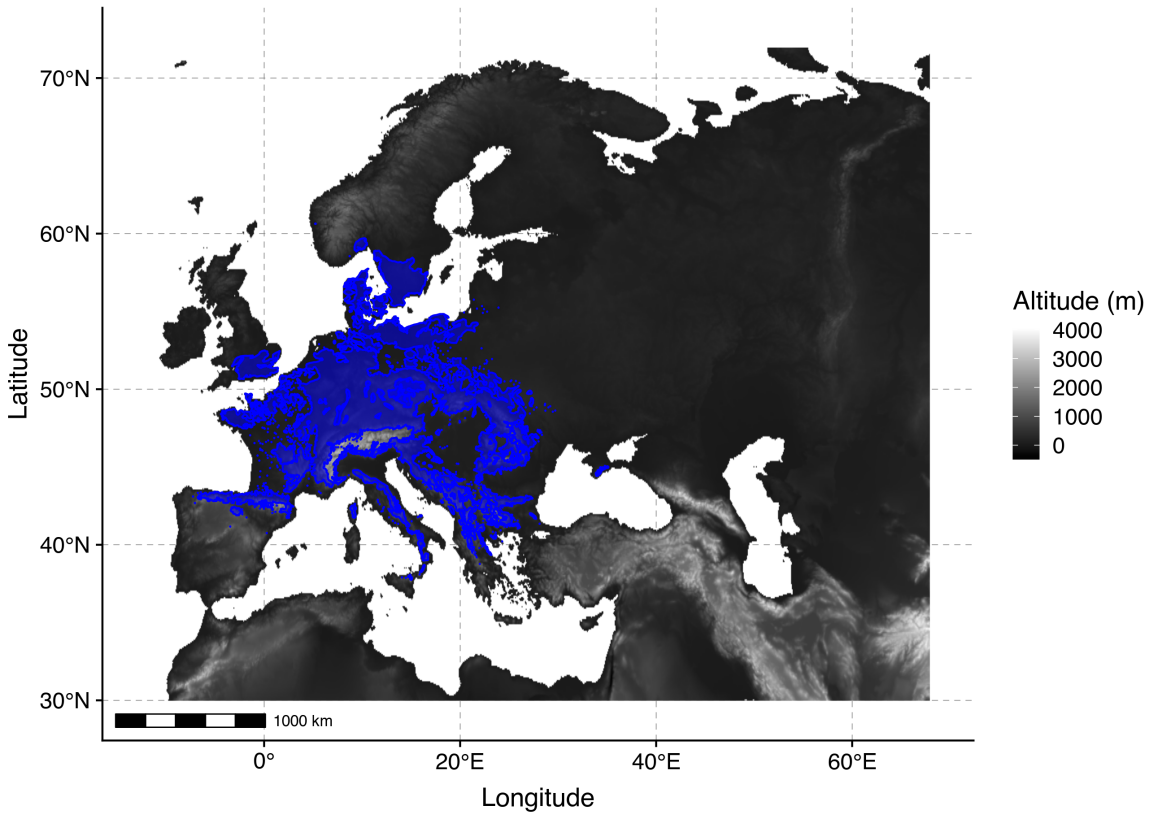

FIGURE II.5: Aire de répartition du Hêtre commun. Données issues de Euforgen (2019) <http://www.euforgen.org/>.

et du fait que cette espèce couvre une large partie de l'Europe, cette espèce est utilisée en recherche comme une espèce modèle pour comprendre la réponse de cette espèce au changement climatique. Face à ce phénomène, les modèles de niches bioclimatiques prédisent une diminution de l'aire de répartition en marge Sud, mais aussi une large expansion en marge Nord (Dyderski et al., 2018).

2 *Cycle de reproduction*

La maturité sexuelle du Hêtre peut être atteinte vers 40-50 ans, voire à partir de 80 ans dans le cas de peuplements denses. Son cycle reproducteur est très proche de celui du Sapin pectiné, c'est-à-dire sur deux ans entre l'initiation et la

fin de la maturation des fruits, mais avec des phases plus courtes (Figure II.6). La floraison a lieu aux alentours de début mai (fin mars pour hêtraies méridionales, début juin pour populations en altitude et sous climat froid). Il y a un décalage entre la floraison des fleurs mâles et femelles. Les stigmates des fleurs femelles d'un arbre donné sont réceptifs environ 4-5 jours avant que les anthères ne commencent à s'ouvrir et libérer du pollen chez les fleurs mâles de ce même individu (protogynie). Cependant, la protogynie est variable suivant les individus et elle est parfois absente. Il existe aussi des cas de protandrie (quand les femelles s'ouvrent après fleurs mâles). La protogynie est un phénomène lié aux conditions climatiques et permet de limiter l'autofécondation. Un temps froid et pluvieux stimule le développement des fleurs femelles, tandis que les fleurs mâles libèrent le pollen seulement après quelques jours de temps sec et doux. La floraison mâle dure environ 9 jours. Cependant, les fleurs femelles non pollinisées (de manière allogame ou autogame) peuvent rester réceptives pendant 10-15 jours. Le grain de pollen, réceptionné par le stigmate, germe environ trois semaines plus tard, vers fin mai-début juin, une fois que l'ovule est prêt à être fécondé. La phase de croissance des graines aura ensuite lieu de juin à début septembre, jusqu'à l'obtention d'un fruit totalement mature et avant la dissémination des graines qui a lieu majoritairement pendant le mois d'octobre (Bonnet-Masimbert & Webber, 1995; Lebret et al., 2001).

1.4 Les Chênes tempérés

Les aires de répartition des Chênes étudiés, *Quercus petraea* (Matt.) Liebl. et *Quercus robur* L., sont similaires à celle du Hêtre commun, avec cependant une aire de répartition plus étendue vers l'Est de l'Europe, la Turquie et le Royaume-Uni. Même si les déterminants impliqués dans la reproduction semblent différents, leurs cycles de reproduction pour les Chênes tempérés étudiés dans le chapitre III sont similaires à celui du Hêtre, étalé sur 2 ans entre l'initiation des bourgeons et la maturation des glands.

2 Sites d'étude et récolte des données

2.1 Données à l'échelle locale

1 Le Mont-Ventoux

Ce massif est situé dans le Sud-Est de la France, à peu près 110 km au Nord de Marseille (Figure II.9, A & B). Le Hêtre y est présent de 750 à 1700 m d'altitude en coexistence avec le Sapin. On y retrouve également différentes espèces de Sapin et des espèces de Pin (Pin sylvestre, Pin noir, Pin d'Alep, Pin à crochet) issues des reboisements artificiels de la fin du XIXième siècle. Depuis 2006, le Sapin et le Hêtre font l'objet d'un suivi dit « de long-terme » de la phénologie

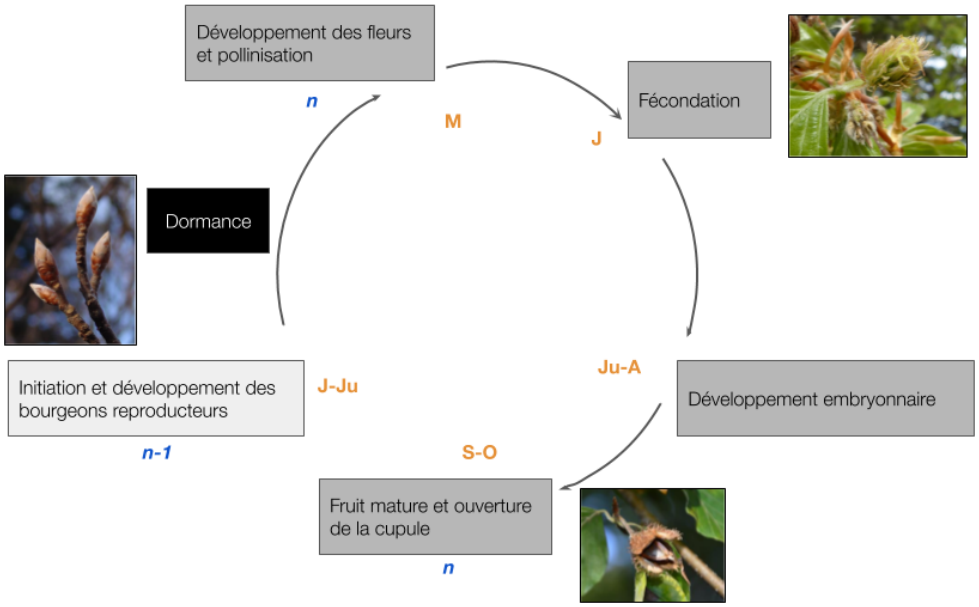

Figure II.6: Cycle de reproduction du Hêtre commun. Photos d'un bourgeon dormant, développement de la fleur femelle avec fleur mâle après pollinisation, ouverture de la cupule avec les graines à l'intérieure. Cycle sur deux années (n-1 et n). Abréviations : J, juin, Ju, juillet, M, mai, S, septembre et O, octobre. Crédit photos : O. Gilg, F. Jean et S. Cecchini.

(foliaire et reproductrice) le long d'un gradient altitudinal situé en versant Nord (5 placettes et un transect continu de 900 m à 1500 m d'altitude). Pendant ma thèse, j'ai participé à un suivi plus précis de la phénologie, notamment de la reproduction, par caméra, ce qui m'a permis d'estimer des dates de floraison, de maturation et d'initiation des bourgeons (données de 2015 à 2018 chez le Sapin pectiné) sur un site situé à 1400m. Diverses mesures avaient été effectuées pour caractériser l'environnement (ex. texture du sol, profondeur, teneur en cailloux, climat) et sur les arbres (ex. hauteur, diamètre, concentration en azote foliaire...) dans le cadre de projets et de thèses passés. J'ai ainsi pu compiler et utiliser ces données pour la calibration du modèle CASTANEA dans le cadre du chapitre III, pour le Hêtre et le Sapin pectiné.

J'ai aussi voulu tester d'autres approches d'observation destinées à affiner les connaissances de plusieurs phases du cycle de reproduction des espèces d'intérêt mais celles-ci n'ont pu être valorisée dans le cadre de ma thèse : mise en place d'un suivi pollinisation avec détermination du pollen (non présenté), suivi d'avortement des fleurs et fructification, détermination de biomasse reproductive. En 2017, nous avons installé plusieurs filets afin de quantifier le taux d'avortement pour le Hêtre, sur différentes placettes, avant le débourrement végétatif et jusqu'à la maturation des fruits. Deux filets ont été placés par population, et ce pour trois populations le long du gradient climatique au Mont-Ventoux. Les objectifs étaient de caractériser les avortements de fleurs chez le Hêtre au Mont-Ventoux entre différentes populations le long d'un gradient altitudinal. Pour chaque population nous avons installé deux filets (environ 2*5m), avec un petit bac récolteur à l'extrémité. Les fleurs mâles avortées ont été définies comme avortées si elles étaient d'aspect noir (suite à une gelée par exemple) avec des étamines non sorties. Les fleurs mâles saines avaient les étamines bien développées, de couleur jaune/blanc et d'aspect duveteuses. Pour les fleurs femelles/fruits avortées, si les fruits étaient présents avant la date de maturation, et de petite taille ils étaient considérés comme avortés. De ce que nous avons récolté, nous avons remarqué qu'il y avait plus de fleurs mâles récoltées aux deux extrêmes du gradient altitudinal, avec aussi plus de fleurs mâles avortées à haute altitude (Figure II.7). Mais il aurait pu être intéressant de placer plusieurs filets sur les parcelles pour limiter certains dégâts dus aux intempéries climatique (neige, vent) sur les filets et sur la production de biomasse (saturation des récolteurs) pour avoir des meilleures estimations à l'échelle de la placette.

En 2018, j'ai mis en place un suivi de la biomasse allouée à la reproduction. L'objectif principal était de savoir s'il était possible de tirer une relation entre trait foliaire, tel que la masse foliaire par unité de surface (LMA, pour *Leaf Mass per Area*), et la biomasse allouée à la reproduction. Un second objectif était de quantifier la reproduction mâle, en termes de biomasse, à l'échelle de

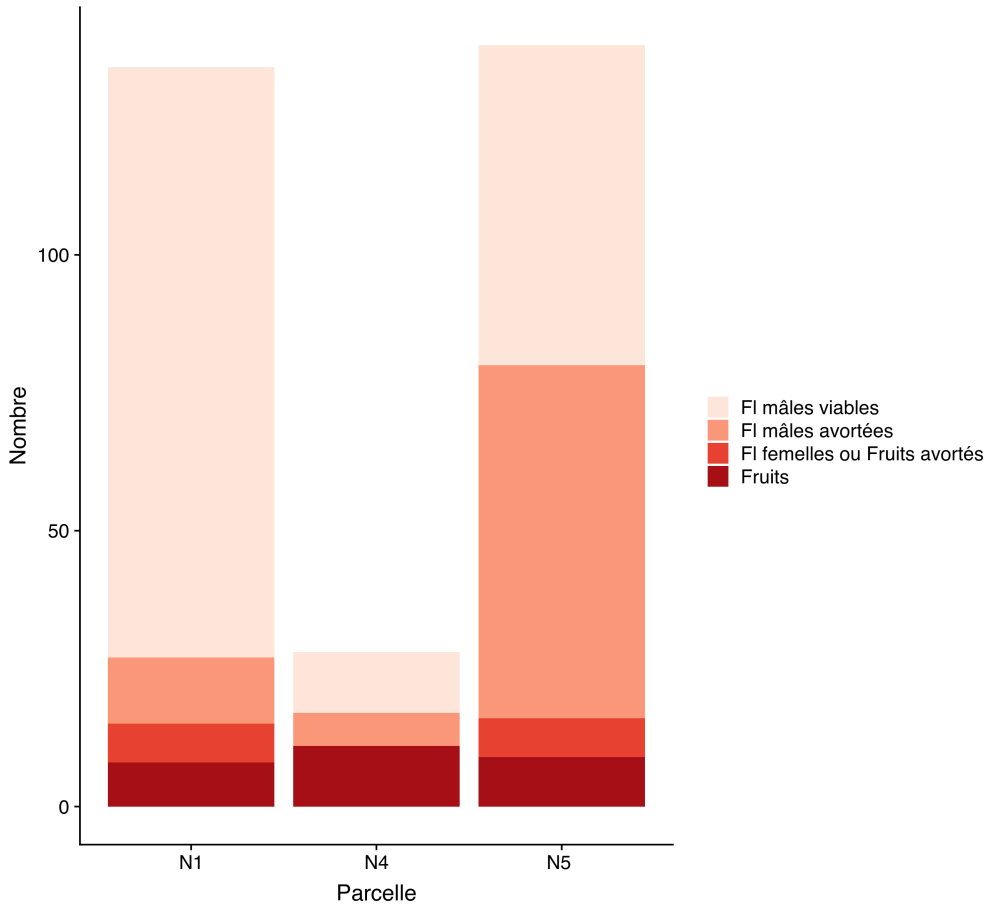

Figure II.7: Suivi de l'avortement de fleurs de Hêtres au Mont-Ventoux, où le nombre de fleurs a été dénombré dans des filets placés à différentes altitudes (N1 à 995m, N4 à 1350m et N5 à 1500m). Fl pour fleurs mâles ou fleurs femelles.

l'individu. Nous avons travaillé sur le Hêtre au Mont-Ventoux (population à 1400m d'altitude), sur 11 individus, au moment de la pollinisation. Nous avons, pour chaque individu, défini trois zones dans le houppier (partie basse, milieu et haute), et prélevé dans chaque zone 4 rameaux d'environ 50cm, faisant un total de 12 rameaux par individu. Les branches ont ensuite été effeuillées, et nous avons fait des mesures complémentaires (ex. unité de croissance des rameaux, mesures LMA). A la fin de l'été nous avons aussi fait un comptage de faînes, mais peu de faînes ont été produites. Nous avons observé que la biomasse mâle était assez faible en moyenne. La production de biomasse reproductive est variable entre les zones du houppier, avec plus de biomasse reproductive produite en haut du houppier (Figure II.8, B). Il semblerait aussi qu'il y ait un compromis entre le ratio de biomasse reproductive femelle (en terme de fleurs) et biomasse reproductive mâle (Figure II.8, A). Nous avons remarqué que cette année, peu de faînes étaient produites (Figure II.8, D). Même si cette expérimentation est assez fastidieuse, nous avons préféré ne pas inclure le faible coût en biomasse de la reproduction mâle dans le modèle CASTANEA (chapitre V).

2 La Forêt domaniale de Sault

Localisée sur la partie Est du Mont-Ventoux, ce site est situé à environ 1150 m d'altitude. L'INRA y a établi en 1964 une plantation de Cèdre à objectif sylvicole, avec une densité initiale de 2500 individus par hectare. La plantation a été divisée en 4 placettes, où il a été appliqué différents scénarios sylvicoles (placette témoin sans sylviculture, puis intensité faible, moyenne et élevée). J'ai utilisé des données de reproduction et de croissance issues de deux placettes densité contrastées (1200 tiges.ha^{-1} vs 250 tiges.ha^{-1}, Figure II.9, C & D), dont les peuplements partagent les mêmes conditions climatiques et ont le même âge. De 2002 à 2005, ces placettes ont fait l'objet d'un suivi de fructification, de la pollinisation (utilisation d'un indice pollinique pour qualifier la quantité de pollen présent à l'échelle de l'arbre), ainsi que de la croissance. J'ai utilisé ces données dans le cadre du chapitre IV.

2.2 Données à l'échelle nationale

1 Le réseau de l'Office National des Forêts - RENECOFOR

Il s'agit d'un réseau national de suivi long terme des écosystèmes forestiers, géré par l'Office National des Forêts (Ulrich, 1995). Les principales espèces forestières françaises y sont suivies, dont le Sapin pectiné, le Hêtre commun et deux espèces de Chênes tempérés (sessile et pédonculé) (Figure II.10). Pour le Hêtre il y a 20 placettes suivies, 30 pour l'ensemble des Chênes et 11 pour le Sapin pectiné. Plusieurs types d'observations ont été effectuées à travers la France, notamment pour caractériser le sol, le climat, la biodiversité végétale.

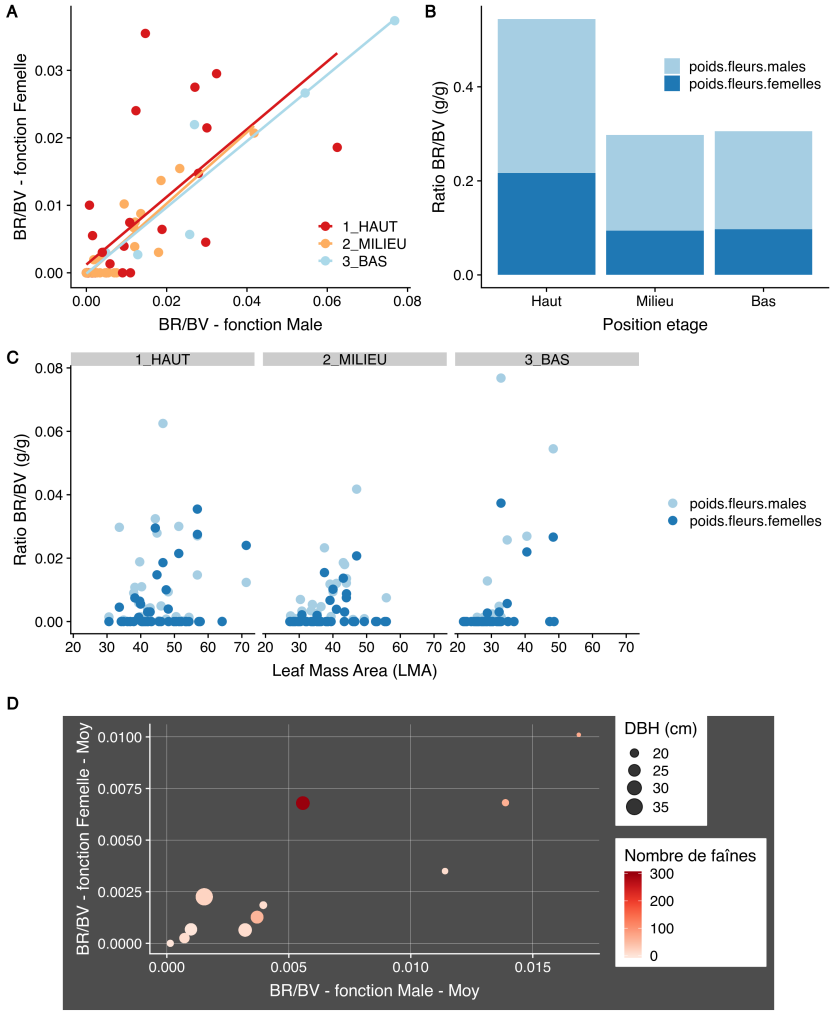

Figure II.8: Suivi de la biomasse reproductive du Hêtre au Mont-Ventoux. Abbreviation BR = Biomasse Reproductive en g, BV = Biomasse végétative en g (= masse de la branche + masse totale des feuilles), LMA = Leaf Mass per Area en g.m2, DBH = Diameter Breast Height en cm. A) Ratio entre la biomasse reproductive femelle et la biomasse végétative en fonction du ratio de la biomasse reproductive mâle et la biomasse végétative pour l'ensemble des branches prélevées. B) Ratio de la biomasse reproductive en fonction de la position de la branche dans le houppier. C) Ratio de la biomasse reproductive en fonction du LMA. D) Ratio moyen de la biomasse reproductive femelle et du ratio moyen de la biomasse reproductive mâle entre les différents individus. Moyenne établie sur l'ensemble des branches prélevées par individu, après le calcul du ratio BR/BV pour chaque branche. Taille de l'individu représentée par son diamètre moyen (DBH) et son intensité de fructification (en rouge pour une forte fructification).

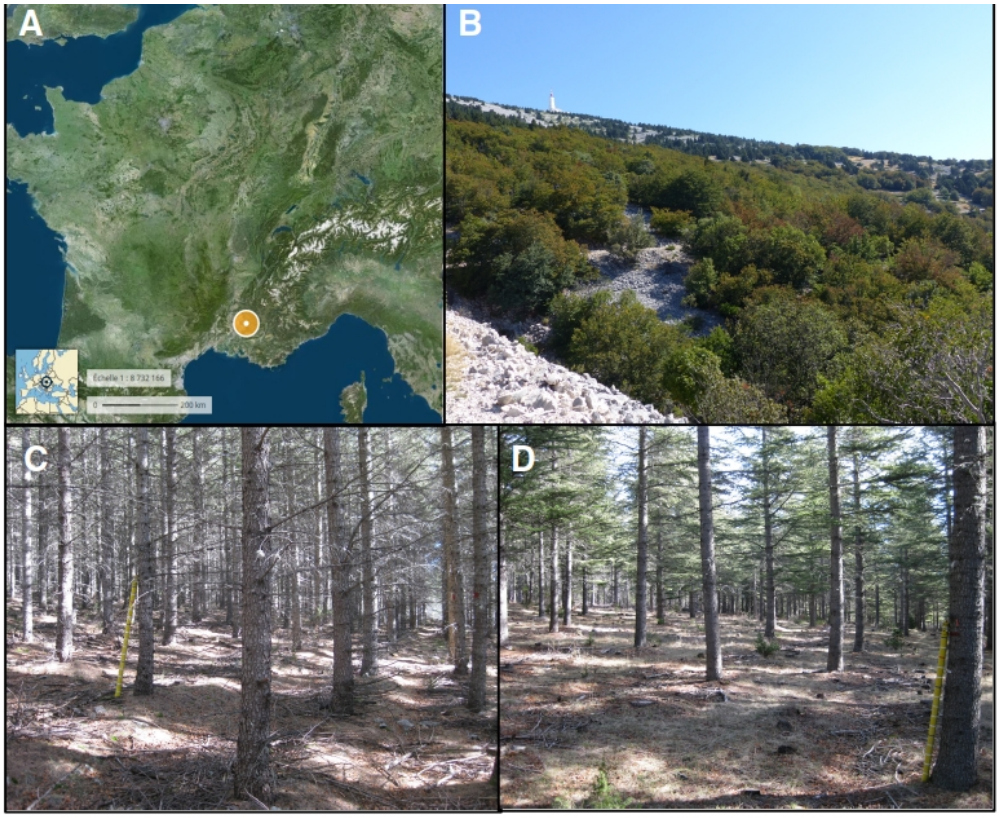

Figure II.9: Présentation du Site de suivi au Mont-Ventoux et la forêt domaniale de Sault. A) Localisation du Mont-Ventoux (carte issue de géoportail, consultée en décembre 2019 <https://www.geoportail.gouv.fr/>). B) Photographie du Mont-Ventoux (par F. Jean, en 2016). C et D) Suivi expérimental des placettes du Cèdre de l'Atlas dans la forêt domaniale de Sault, avec une plantation à 1200 tiges.ha^{-1} et 250 tiges.ha^{-1}, respectivement.

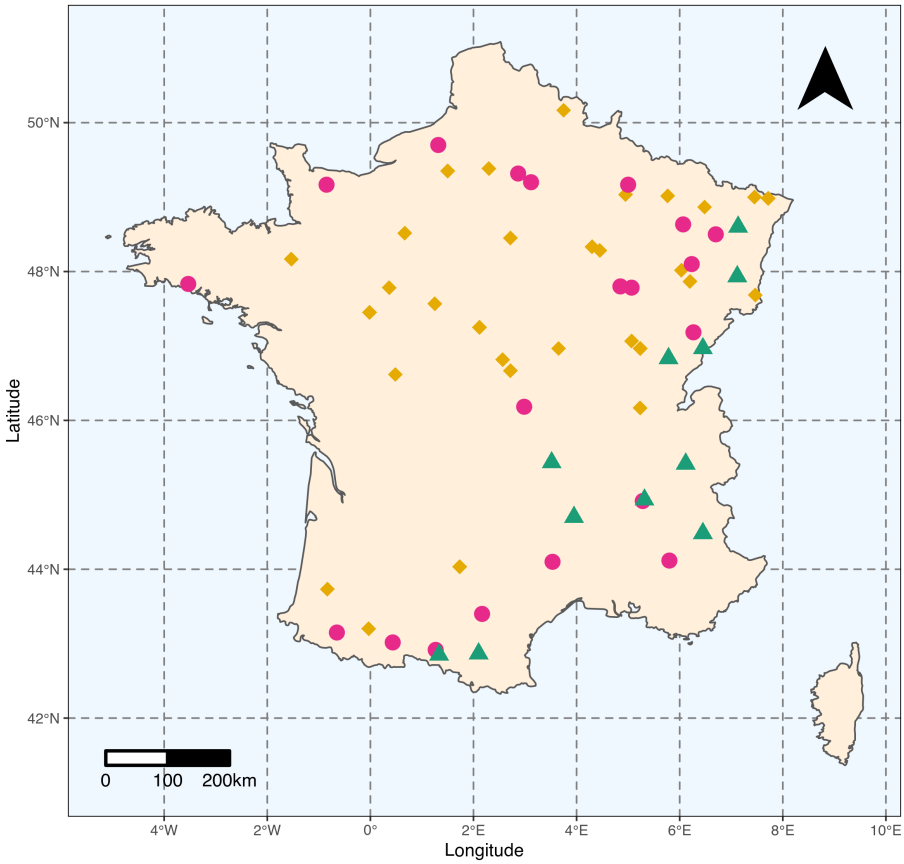

Figure II.10: Répartition des sites de suivis RENECOFOR. Les ronds roses correspondent aux sites suivis pour le Hêtre commun, les losanges jaunes pour les Chênes, et les triangles verts pour les sites suivis pour le Sapin pectiné.

Parallèlement à cela des mesures dendrométriques, mais aussi des observations de phénologie, de production de litières ont été effectuées à l'échelle de la population d'arbres ou des individus. Cependant ces placettes sont présentes dans des forêts de climat tempéré où les conditions de vie étaient jusqu'à présent moins contraignantes qu'en région méditerranéenne. On peut noter que les données du suivi de litière, notamment basées sur la biomasse de la fructification ont été valorisées par plusieurs études, en lien avec des données dendrométriques mises en regard de données climatiques (ex. température, précipitation, cf chapitre III). Dans le cadre de ma thèse j'ai utilisé les données de phénologie à l'échelle du peuplement (chapitre III & V), les données de litières (chapitre III), les données de croissance (chapitre V), les données de sols (chapitre V), ainsi que les données climatiques (chapitre V). Il y a aussi eu des analyses biochimiques qui ont servies à calculer des coûts de construction des organes tels que branches, feuilles et fruits (chapitre V).

2.3 Données climatiques

Pour les sites de Sault et du Mont-Ventoux (cf chapitre IV et chapitre V), nous avons utilisé des données climatiques locales issues d'enregistreurs type HOBO (Hobos ProV2 micro-logger) installés en 2007. Les conditions climatiques locales (précipitation, température, humidité relative, vitesse de vent et radiation globale) ont ensuite été estimées de 1960 à 2015 à partir des données météorologiques nationales de 1960 à 2015, et corrigé des effets altitudes à l'aide de régression statistiques sur les sites locaux (Quintana-Seguí et al., 2008). Pour les sites RENECOFOR, nous avons utilisé les données climatiques SAFRAN, données issues de ré-analyses atmosphériques et à haute résolution (échelle 8*8km). Pour chaque population, nous avons retenu la station la plus proche (cf chapitre III et chapitre V).

Chapitre III

Effets de la phénologie foliaire, comme proxy de la ressource, sur la reproduction

1 Contexte

La phénologie foliaire et la production de fruits sont sensibles aux changements climatiques. Des variations de phénologie foliaire influencent la saison de végétation, qui peut impacter à son tour l'activité photosynthétique, mais aussi le stockage de carbone, la respiration et la productivité de l'écosystème. En effet, les variations de saison de végétation influencent la période d'assimilation du carbone (Delpierre et al., 2009; Richardson et al., 2010) et peuvent potentiellement impacter la croissance des arbres (par exemple Myneni et al. 1997; Vitasse et al. 2009a; Delpierre et al. 2017). L'hypothèse est qu'une période d'assimilation du carbone plus longue peut augmenter la croissance de l'arbre. Mais cette relation n'est pas universelle, et il se peut qu'un décalage de la phénologie foliaire n'ait pas de conséquences sur la croissance (Čufar et al., 2015; Delpierre et al., 2016a). Cela peut s'observer notamment si la durée de la saison de végétation augmente pour compenser des événements extrêmes, comme des sécheresses ou gelées, sans effets direct sur la croissance (Kuster et al., 2014; Čehulić et al., 2019). On s'attend aussi à ce que la phénologie foliaire n'affecte pas la croissance, si la croissance n'est pas limitée par la source de carbone, mais par d'autres processus comme la phénologie du bois (Delpierre et al., 2016a; Friend et al., 2019). Peu d'études se sont intéressées aux conséquences des variations de phénologie foliaire sur la production de fruits. Tapper 1996 a identifié qu'une précocité de la date de débourrement diminue la probabilité de produire des fruits l'année suivant pour l'espèce *Fraxinus excelsior*. Pour l'espèce *Quercus crispula*, l'augmentation des températures augmente la saison de végétation et *in fine* augmente la production de fruits (Nakamura et al., 2010).

Dans notre étude nous avons étudié le lien potentiel entre la durée de la saison de végétation et la fructification, en terme de biomasse fructifère, chez trois espèces d'arbres forestiers majeures : le Hêtre commun et les Chênes pédonculé et sessile. L'hypothèse que nous avons voulu tester est la suivante : Est-ce que la durée de la saison de végétation peut influencer la production de biomasse des fruits ? Les fruits de ces espèces se développent sur deux ans, avec l'initiation des bourgeons à l'année n et la production des fruits lors de l'année $n+1$. En tenant compte des autres mécanismes impliqués dans la reproduction, par exemple les températures estivales passés pour le Hêtre, et les températures printanières pour les Chênes, nous avons aussi inclut la durée de la saison de végétation foliaire de l'année précédant la fructification et celle de l'année de fructification. La saison de végétation de l'année précédant la fructification peut affecter la production de fruits de l'année, en ayant par exemple un impact sur la quantité de bourgeons floraux formés. La durée de la saison de végétation l'année de la fructification, peut affecter la production de fruits de l'année, si les carbohydrates néo-assimilés sont principalement utilisés pour la maturation des fruits (Hoch et al., 2013; Han & Kabeya, 2017). Une autre hypothèse est que,

comme la croissance (Čufar et al., 2015; Delpierre et al., 2017), la production de fruits n'est peut-être pas limitée par la disponibilité en carbone, ce qui conduirait dans ce cas à une absence de lien entre durée de la saison de végétation et la production de fruits. Dans cette étude, nous avons défini la saison de végétation comme la période comprise entre la date de débourrement et la date sénescence des feuilles. Nous avons utilisé le jeu de données RENECOFOR, constitué d'une série continue de 10 ans sur la production de fruits et la phénologie foliaire de trois espèces décidues, les Chêne tempérés (i.e., *Quercus robur* et *Quercus petraea*) et le Hêtre (*Fagus sylvatica*), avec un total de 50 populations à l'échelle de la France. La phénologie foliaire est observée depuis 1997 à l'échelle de la population, ainsi que la biomasse de fruits (en $kg.ha^{-1}$), estimée par la récolte de la litière. Comme les deux espèces de Chêne s'hybrident très largement, nous avons regroupé ensemble les données les concernant. Par contre, Hêtre et Chêne se distinguent notamment par l'anatomie de leur bois : le Chêne présente un bois à zone poreuse, contrairement au Hêtre qui a un bois à pores diffus. Cette différence anatomique influence notamment leur dépendance aux anciennes et nouvelles ressources carbohydratées. Elles sont aussi différentes concernant les stratégies de fructification : le nombre de fructifications du Chêne est principalement déterminée par les taux d'avortement, alors que celle du Hêtre dépend principalement du niveau de fleurs produites (Pearse et al., 2016; Bogdziewicz et al., 2017b).

Ce projet a été amorcée lors d'une réunion avec M. Bogdziewicz et T. Caignard lors du groupe de travail sur le *masting* organisée par G. Vacchiano. L'article a été soumis dans la revue *European Journal of Forest Research* en Mai 2019, et est en cours de ré-soumission dans la même revue.

2 Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in temperate oaks (*Quercus robur* and *Quercus petraea*)

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Mots-clés : Espèces décidues, Hêtre commun, saison de végétation, Chênes tempérés, fructification

Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in temperate oaks (*Quercus robur* and *Quercus petraea)*

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#Number of figures: 4

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#1 Supporting Information

Abstract

Phenology and fruit production are sensitive to climate. Variation of leaf phenology alters growing season length, which in turn affects forest ecosystem functioning and tree productivity. However, the influence of this process on tree reproduction is poorly explored. In this study, we investigated how growing season length influence fruit production in three major European deciduous trees, European beech (*Fagus sylvatica*) and two temperate oaks (*Quercus robur* and *Quercus petraea*). We used a long-term (10 years) monitoring dataset from 50 populations. In addition to the widely reported main effect of previous summer temperature on fruit production in European beech, we detected a non-linear relationship between current growing season length and fruit production. This suggests that fruit production initially increases in response to lengthening growing season, and decreases afterwards. In oaks, current growing season length and fruit production were positively correlated. Growing season length appears as a limiting factor for fruit production in these species, which suggests that carbon assimilated during fruit maturation may limit fruit production in beech and oaks. These results suggest contrasting effects of expected increase in growing season length on fruit production: negative in European beech, and positive in oaks.

Keywords: Deciduous trees, *Fagus sylvatica*, growing season length, masting, *Quercus sp.*

Introduction

Change in the timing of leaf phenology events has a major impact on ecosystem functioning by affecting primary productivity (Richardson et al. 2010; Dragoni et al. 2011), respiration (Piao et al. 2008; Barichivich et al. 2013) and carbon stocks (Churkina et al. 2005; Dragoni et al. 2011; Pan et al. 2011; Barichivich et al. 2013; Keenan et al. 2014). The timing of leaf phenology changed during the past decades with an advance in leaf unfolding and a delay in leaf senescence. This has resulted in an increase in growing season length (Menzel et al. 2006; Vitasse et al. 2009b), defined here as canopy duration (White and Nemani 2003). These changes, along with changes in temperature and CO_2, have increased the capacity of trees to take up carbon (Saxe et al. 2002; Barichivich et al. 2013). This increase in carbon assimilation may in turn increase primary productivity (Nemani et al. 2003; Delpierre et al. 2009; Richardson et al. 2010; Keenan et al. 2014; Forkel et al. 2016). However, if growing season length extends into autumn, it may extend the period during which respiration is higher than photosynthesis, that reducing net annual carbon uptake (Piao et al. 2008; Barichivich et al. 2013).

On a tree scale, variation in growing season length may also affect tree productivity, resulting in variability of tree growth or reproduction (White et al. 1999; Linderholm 2006; Nakamura et al. 2010). In trees, carbon resources accumulated during the period of photosynthesis activity are allocated between maintenance, growth and reproduction (Wardlaw 1990; Lauder et al. 2019). Some studies have shown that longer growing season length is associated with higher tree growth, although this relationship is not universally reported (Myneni et al. 1997; Kramer et al. 2000; Oleksyn et al. 2001; Bronson et al. 2009; Vitasse et al. 2009a; Čufar et al. 2015; Delpierre et al. 2017). For example, an advance of leaf unfolding did not increase tree growth in European beech (Čufar et al. 2015). A possible explanation is that during very long growing seasons, the higher productivity only compensates for extreme events that happen very early or very late during the season, resulting in no net effect on tree growth (Barber et al. 2000; Kuster et al. 2014; Čehulić et al. 2019). For example, an advance in leaf unfolding exposes trees to late-spring frost injury, while leaf activity in autumn may cease due to freezing temperature (Norby et al. 2003). Another potential explanation could be due to the fact that growth is not strongly limited by carbon input, but by other processes such as wood phenology or weather (Delpierre et al. 2016, Friend et al. 2019, Mund et al. 2020). Yet, the link between length of growing season and fruit production has rarely been investigated. Tapper (1996) found that an advance of leaf flushing date increased the probability of an individual to produce fruit in the following year in *Fraxinus excelsior.* In *Quercus crispula*, experimentally manipulated higher temperatures extended the growing season length, which in turn increased the production of fruits (Nakamura et al. 2010).

Annual variation in season length can be potentially important for reproduction in masting plants which are characterized by large and synchronized variations in fruit production between years (Kelly 1994). This variation and synchrony in reproduction in turn affects forest dynamics and species

interactions (Kelly and Sork 2002; Bogdziewicz et al. 2016; Vacchiano et al. 2018). The annual variation in fruit production represents a non-linear resource investment into reproduction (Satake and Iwasa 2000; Crone and Rapp 2014). According to the resource budget model of masting, plants need to accumulate a threshold amount of resources to initiate reproduction (Isagi et al. 1997; Satake and Iwasa 2000). If this threshold cannot be reached in the first year, then plants accumulate resources over several years, which translates into intermittent fruit production by individual plants (Satake and Iwasa 2000; Crone et al. 2009). Furthermore, variation in resource supply over the current and past years appear implicated in bud initiation, flower and fruit maturation (Allen et al. 2017; Han and Kabeya 2017). The carbon stored during the previous year is used to fuel the beginning of fruit development, and then the final stage of fruit maturation is supplied with carbon assimilated during the current year (Hoch et al. 2013; Han and Kabeya 2017). Furthermore, due to the high reproductive cost, there is a trade-off between previous and current fruit production, where a large fruit production limits next year production (Knops et al. 2007; Pearse et al. 2016, Fernández-Martínez et al. 2019). This trade-off appears to be caused by a large depletion in resources such as non-structural carbohydrates, nitrogen and phosphorus (Crone et al. 2009; Sala et al. 2012; Barringer et al. 2013; Crone and Rapp 2014; Pearse et al. 2016; Allen et al. 2017; Moreira et al. 2019). However, from another point of view, negative correlation between previous and current fruit production could be the consequence of the economies of scale that drive the selection of masting. For example, predator satiation, where plants use highly variable seed produce to reduce seed predator populations, may create this negative correlation even in the absence of resource limitation.

The aim of this study was to investigate how growing season length can influence reproduction, in terms of fruit biomass, of three major temperate deciduous trees; European beech (*Fagus sylvatica*) and temperate oaks (*Quercus petraea* and *Quercus robur*). These species differ in how weather affects their fruit production. For the *Quercus* species, warm spring temperatures favor flowering and pollination (Fernández-Martínez et al. 2017a; Lebourgeois et al. 2018; Bogdziewicz et al. 2019; Schermer et al. 2019), which in turn increase fruit production (Caignard et al. 2017). In contrast, for *Fagus* species, previous summers' temperatures are the main driver of fruit production However, the effects of extended growing season length on carbon allocation, in terms of absolute and relative carbon, including to growth and reproduction, are more controversial. For example, longer growing seasons can correlate positively with tree growth (Myneni et al. 1997; Kramer et al. 2000; Čufar et al. 2008; Vitasse et al. 2009a), but other studies have reported no effect (Čufar et al. 2015; Delpierre et al. 2017). (Vacchiano et al. 2017; Hacket-Pain et al. 2018; Lebourgeois et al. 2018; Bogdziewicz et al. 2019), corresponding to the season of floral transition (see Table 1). We accounted for previous summer conditions for European beech as a major determinant of fruit production and current spring temperature for temperate oaks. Temperate oaks and beech have a long dormancy period with a floral initiation that starts in a year *n-1*, which is then followed by fruit maturation in the year *n* (Owens 1995). Both, previous- and current-year assimilated resources are often used for fruit

115 production (Tapper 1996; Nakamura et al. 2010), thus they might have an impact on both
116 reproductive stages, i.e. floral initiation, flower buds with previous assimilated resources and fruit
117 maturation with current assimilated resources. Specifically, growing season length of the previous
118 year may influence fruit production of the current year by affecting the quantity of floral buds. In turn,
119 growing season length of the current year might affect fruit production, as carbohydrates are used for
120 fruit maturation (Hoch et al. 2013; Hoch 2015; Han and Kabeya 2017). An increase of growing season
121 length could increase fruit biomass production, such as seed and fruit mass. Therefore, we expected
122 that growing season length to be positively correlated to fruit biomass production, or not limited by
123 growing season length as found for example with tree growth (Vitasse et al. 2009a; Čufar et al. 2015;
124 Delpierre et al. 2017). Alternatively, we hypothesize that long growing seasons might be associated
125 with increases in environmental stresses that might reduce or did not impact fruit productivity.
126 Therefore, we also tested for relationships between growing season length and the frequency of
127 climatic events, including extreme high and low temperatures and dry events (Xie et al. 2015). Due to
128 the widely reported trade-off in reproductive allocation between current and previous year that
129 characterizes masting species (Knops et al. 2007; Pearse et al. 2016; Moreira et al. 2019), we also
130 accounted for previous year of fruit production in our analyses.
131

132 **Material and Methods**

133 **Study species**

134 European beech, *Fagus sylvatica,* and the temperate oaks, *Quercus petraea* and *Quercus*
135 *robur,* are major forest-forming species in Europe. Past studies examining the relationship between
136 the growing season length and growth in these species are inconclusive, with some reporting a
137 positive relationship (Vitasse et al. 2009a), while others found no relationship (Delpierre et al. 2017,
138 Čufar et al. 2015). These species differ in their leaf and wood formation phenology, and their wood
139 anatomy (Barbaroux and Breda 2002; Michelot et al. 2012; Vitasse and Basler 2013; Lebourgeois et
140 al. 2018) which in turn influence their resource allocation scheme. Oaks are ring porous species.
141 Thus, they use stored carbohydrates for earlywood vessel formation before leaf unfolding and leaf
142 expansion. In contrast, beech is a diffuse porous species. Thus, growth commences after leaf
143 unfolding and is mainly reliant on carbon assimilated in the current season (Barbaroux and Breda
144 2002; Michelot et al. 2012). While all these species exhibit the variable and synchronized fruit
145 production characterized as masting, they show contrasting masting mechanisms. Oak is a "fruit
146 maturation" masting species, in which annual variability in fruit production is primarily driven by
147 differences fruit abortion, while beech is a "flowering masting" species, where variability is largely
148 determined by variation in flower production (Pearse et al. 2016; Bogdziewicz et al. 2017c, b). For all
149 the studied species, flower initiation begins in spring of the year preceding fruit maturation. Flowering
150 and pollination take place in the following spring, followed by fecundation and fruit maturation until fruit
151 dispersion in autumn.

152

153 **Study sites and data collection**

154 We used data collected at 50 sites of the French Permanent Plot Network for the Monitoring
155 of Forest Ecosystems (RENECOFOR, Ulrich 1995). Sites are widely distributed across France
156 between latitude 50.1° and 42.9°N and longitude -3.53° and 7.71°E, covering various climatic and soil
157 conditions (Fig. 1). In total, 20 sites dominated by European beech species and 30 sites dominated by
158 two European oak species were monitored. Due to the high hybridization rate in oaks (Abadie et al.
159 2012), some sites have monitored mixed population of *Q. robur* and *Q. petraea*. Hence, we combined
160 and merged all oaks records collectively. The monitored plots have a size of approximately 2 ha, with
161 a central fenced zone of 0.5 ha. For every site, fruit production was monitored from 1993 to 2007 and
162 leaf phenology from 1997 to 2015. Because we were interested in the link between leaf phenology
163 and fruit production, we used data from 1997 to 2007 corresponding to the matching period of both
164 datasets. Litterfall was collected at the population scale with ten traps of 0.5 m^2, distributed over the
165 central fenced zone. Every season, the litter fallen into the traps was collected and sorted in different
166 category: leaves, branches and fruits (acorns and nuts). All compartments were dried and weighed,
167 and then divided by the total area of the trap. Fruit production is in $kg.ha^{-1}$. Leaf unfolding and leaf
168 coloring were monitored at the population scale based on a sample of 36 trees per site. Phenological
169 stages were monitored every week during spring for leaf unfolding (from March to June) and autumn
170 for leaf coloring (from September to November) (Lebourgeois et al. 2010). Leaf unfolding and leaf
171 coloring dates (both in Julian days) were defined when 90% of sampled trees had 20-50% of opening
172 buds and when 90% of sampled trees had 20-50% yellowing leaves, respectively. We defined the
173 growing season length as the number of days between leaf unfolding and leaf colouring. We extracted
174 the closest climatic data for each of the 50 sites by using French climate station data obtained from
175 SAFRAN atmospheric re-analysis (8-km gridded spatial resolution, Vidal et al. 2010). We extracted
176 daily temperature data and summarized it for summer and spring period from the closest station to
177 each of the RENECOFOR sites: in total we extracted climate variable from 50 stations. We also
178 extracted daily temperature for autumn, spring and summer and precipitation during summer to define
179 different climatic events happening during the growing season.

180

181 **Statistical analysis**

182 We first investigated how species differ in their growing season length and fruit production.
183 We used a *t*-test to identify differences in the mean between species and an *F*-test of equality of
184 variance to test if the two species have equal variance. Next, with the matching data (1997-2007), we
185 tested for the relationships between growing season length and fruit production using linear mixed
186 models (LMMs) implemented via *glmmTMB* package (Brooks et al. 2017). We built two separate
187 models, one for beech and one for oaks. In beech, we used mean maximum summer temperature
188 (June to July) from one and two years preceding fruit production as a covariate (Vacchiano et al.

2017, Lebourgeois et al. 2018). In oaks we used mean spring temperature (April to May) from the same year of fruit production (Lebourgeois et al. 2018; Bogdziewicz et al. 2019) as a covariate. We used log-transformed fruit production as a response variable. To allowed log-transformation of zeros in fruit production we added 1 to all observations. Linear and quadratic terms for both current and the previous year growing season length, and the previous year fruit production were scaled and included as fixed effects. Climate covariates for beech and oaks were also scaled in order to evaluate their respective weights. Quadratic terms were added by computing orthogonal polynomials with the function *poly()*. In the case the quadratic effect was not significant, it was dropped from the initial model. We then calculated the marginal R^2 (i.e. variance explained by fixed effects) and conditional R^2 (i.e. variance explained by both fixed and random effects) (Nakagawa and Schielzeth 2013). Year and site were included as random effects in these two models (i.e. one model per species).

We also tested whether the occurrence of climate events was related to growing season length, focusing on climate events that we hypothesized might affect tree phenology (Xie et al., 2015, 2018). We used GLMMs and a Poisson family. With all the datasets (i.e. 1997-2015) and for each growing season length, we counted the number of frost days during spring season (minimum temperature from April to June < 0°C) and autumn season (minimum temperature from September to October < 0°C). We also calculated the number of hot days during summer season (maximum temperature from June to August ≥ 30°C) and during autumn season (maximum temperature from September to October ≥ 30°C), and dry spells which corresponds to the number of events without rain during 7 consecutive days. We built models with the frequency of the five climate events occurring during growing season length as the response variable and the growing season length as the explanatory variable. Consequently, in total we had five models for oaks, and five models for beech. We scaled growing season length (i.e. the explanatory variable) and included it as fixed effect. Year and site were included as random effects in all the models. All statistics were done using the R software (R Core Team 2018). We used *visreg* package to plot model predictions (Breheny and Burchett 2017), and model diagnostics were run with the DHARMa package (Hartig 2019). Conditional and marginal R^2 were obtained with the package *sjstats* (Lüdecke 2019).

Results

Fruit production (mean ± standard deviation) was different between species and equaled 161.2 ± 303.7 kg/ha for beech and 246.5 ± 389.9 kg/ha for oaks (*t*-test, t = -3.22, df = 655, $P = 0.001$) with higher variations for oaks (*F*-test of equality of variances; $F_{263, 433} = 0.60$, $P < 0.001$) (Fig. 2). Also, the growing season length estimated for beech (mean = 173.9 ± 19.8 days) was significantly shorter than the growing season length estimated for oaks (mean=187.0 ± 18.5 days) (*t*-test, t = -9.19, df = 764, $P < 0.001$) whereas the variations were similar (*F*-test of equality of variances; $F_{290, 474} = 1.15$, $P = 0.17$) (Fig. 2).

In beech, inter-annual variation in fruit production was positively related to temperature in the previous summer (t = 4.6, $P < 0.001$), negatively to the summer temperature two years before (t = -5.93, $P < 0.001$), and negatively to previous year fruit production (t = -2.8, $P = 0.04$, Table 2, Fig. 3c). However, we found that significant additional variance in fruit biomass could be explained by a concave relationship between fruit production and current growing season length (degree 1: t = 0.38, $P = 0.70$, degree 2: t = -2.59, $P = 0.009$, Table 2, Fig. 3a). The quadratic terms of previous growing season length were dropped from the final model ($P = 0.22$). We did not detect a relationship between previous growing season length and fruit production ($P = 0.73$, Fig. 3b).

In oaks, we detected a positive correlation between spring temperature of the year and fruit production (t = 2.26, P = 0.02). Previous year fruit production was negatively correlated with current year fruit production (t = -2.52, $P = 0.011$, Table 2, Fig. 4c). Moreover, both current and previous growing season length were correlated with fruit production and explained additional variance. We found a positive relationship between current growing season length and fruit production (t = 2.32, $P = 0.02$, Table 2, Fig. 4a), and negative relationship between fruit production and previous growing season length (t =-2.96, $P = 0.003$, Fig. 4b). The quadratic terms of previous ($P = 0.5$) and current growing season length ($P = 0.4$) were not significant and were dropped from the final model.

We then investigated relationships between growing season length and relevant climate events. For growing seasons length, we found a positive relationship between number of frost days during autumn and growing season length for beech (t =11.08, $P < 0.0001$) and for oaks (t = 7.26, $P < 0.0001$). Furthermore, for oaks we found a positive relationship between frost days during spring and growing season length (t = 9.25, $P < 0.0001$) and number of hot days during autumn and growing season length (t = 3.88, $P = 0.0013$). We also found a relationship between dry spells and growing season only for oaks (t= 1.72, $P = 0.029$). For all species, we did not detect relationships between the number of summer hot days and growing season length (Table S1 in Supplementary Material).

Discussion

Variability in growing season length affects forest productivity as it determines the period of carbon assimilation (Richardson et al. 2010, 2013), and there is widespread evidence of enhanced carbon assimilation as a response extended growing season length (Nemani et al. 2003; Delpierre et al. 2009; Richardson et al. 2010; Keenan et al. 2014; Forkel et al. 2016). However, the effects of extended growing season length on carbon allocation, in terms of absolute and relative carbon, including to growth and reproduction, are more controversial. For example, longer growing seasons can correlate positively with tree growth (Myneni et al. 1997; Kramer et al. 2000; Čufar et al. 2008; Vitasse et al. 2009a), but other studies have reported no effect (Čufar et al. 2015; Delpierre et al. 2017). Few studies have investigated the effect of increased growing season length on allocation to reproduction, and indicated that longer growing seasons may be positively correlated with fruit

261 production (Tapper 1996; Nakamura et al. 2010). In our study, we show that once the well-
262 documented climate cues of fruit production in beech (*F. sylvatica*) and oak (*Q. robur* and *Q. petraea*)
263 were accounted for, growing season length was correlated with fruit biomass production. In beech,
264 fruit production was non-linearly related to growing season length, while in oak this relationship was
265 linear. We suggest several non-exclusive mechanisms that may help to explain the previously
266 unreported relationships between growing season length and fruit production. A first hypothesis is
267 related to a direct effect of growing season length. When growing season length increases it could
268 increase carbon assimilation and then resource availability. A second hypothesis is related to indirect
269 effect of growing season length on fruits, linked to the relationship between growing season length
270 and climate events such as spring frost, early freezing and hot days, which may influence annual fruit
271 production.
272
273 **European beech**
274 We suggest that the initial increase in fruit production with growing season length may be
275 related to increased resource assimilation, which in turn could increase total reproductive biomass. A
276 longer growing season length may influence total fruit biomass by either increasing the number of
277 fruits, increasing the mean mass of each fruit, or both. The maximum number of fruits is determined
278 by the number of flowers, which are initiated in the previous growing season in response to summer
279 temperature cues (Vacchiano et al. 2017), but Mund et al. (2020) showed that once mass flowering
280 was initiated in beech, the final fruit biomass was increased by dry conditions during flowering. In
281 oaks, the proportion of flowers that are aborted before maturation into fruits appears to be key control
282 on the size of the final fruit crop (Espelta et al. 2008, Pearse et al. 2016, Bogdziewicz et al. 2017c).
283 The maturation process is not well studied in beech, but a similar process might explain our results –
284 i.e. greater plant resources increase the fraction of flowers that mature in to fruits, thus increasing the
285 total fruit biomass produced in association with longer growing seasons. Additionally, the mean mass
286 of individual fruits may also be higher in association with longer growing seasons, if greater resource
287 availability results in larger seed size. Finally, we note that unfertilized beech flowers still develop into
288 non-viable fruits (Bogdziewicz et al. 2020). As these non-viable fruits have a pericarp but no
289 developed embryo, they have significantly lower average seed mass (Hacket-Pain, unpublished data).
290 Consequently, weather conditions during pollination in the early part of the growing season may
291 influence the proportion of fully-developed seeds, and thus the mean seed mass.
292 The decrease of beech fruit production associated with the longest growing seasons may be
293 related to compensatory effects of climate events (drought, heat, frosts) that occur more frequently in
294 long growing seasons, and act to reduce fruit biomass. For example, we show that the frequency of
295 climate events is positively correlated with the growing season length. Decrease of fruit biomass
296 production with very long growing seasons implies that in very long growing seasons, extreme events,
297 such as drougth (Adams et al. 2015), cancel any possible positive effects of growing seasons length

298 on carbon assimilation as we found for oaks, or could be due to the higher cost of respiration in
299 autumn (Piao et al. 2008; Barichivich et al. 2013).

300 In beech, the lack of correlation between the previous growing season length and the
301 following year fruit production suggests that flower initiation is not affected by the previous year leaf
302 phenology. In support, previous experimental studies found that stored carbon is used for flowers and
303 leaves expansion, and it is not a limiting factor for flower initiation (Hoch et al. 2013; Han and Kabeya
304 2017). This is also in accordance with studies that combined experimental and modeling approach
305 and showed that stored carbon resources are not implicated in oaks and beech reproduction
306 (Lebourgeois et al. 2018). Other elements, including nitrogen, zinc or phosphorus, may limit fruit
307 production more than carbon (Miyazaki et al. 2014; Abe et al. 2016; Fernández-Martínez et al. 2017b;
308 Bogdziewicz et al. 2017a). Indeed, nitrogen seems to be a major determinant implicated for bud
309 initiation in *Fagus* genus (Miyazaki et al. 2014; Han and Kabeya 2017).

310

311 **Temperate Oaks**

312 Growing season length correlated positively with fruit production in oaks. Similar to beech,
313 this result suggests that carbon availability during the fruit maturation may limit reproduction in that
314 species. In support, Camarero et al. (2010) showed that masting episodes were preceded by longer
315 growing seasons in *Quercus ilex*. Also, in a warming experiment, increased growing season length
316 was also associated with higher acorn production in *Quercus crispula* (Nakamura et al. 2010). In
317 Caignard et al. (2017), an increase in spring temperature was responsible for increased fruit
318 production. Then, the negative effect of the previous growing season length on current fruit production
319 most likely corresponds to the effect of previous growing season length on previous fruit production.
320 Indeed, previous year fruit production and previous year growing season length correlate positively in
321 our data (log transformation of previous fruit production with linear scale previous growing season
322 length; $t = 2.05$, $P = 0.04$).

323 However, in addition to growing season length, other factors such as pollen limitation and
324 water availability may also help to explain fruit production patterns in oak species. For example,
325 previous studies have shown that pollen limitation limits oak fruit production (Koenig et al. 2012,
326 Venner et al. 2016; Bogdziewicz et al. 2017c, b; Schermer et al. 2019). Moreover, other direct climatic
327 effects, such as drought, are also linked to episodic fruit production (Pérez-Ramos et al. 2010;
328 Lebourgeois et al. 2018). Schermer et al. (2019) demonstrated that pollen dynamics was the key
329 driver of fruit production in *Quercus petraea* and *Q. robur*, and Lebourgeois et al. (2018) showed that
330 spring temperature was important for oak fruit production for the same dataset, due to its positive
331 effects on pollination (Caignard et al. 2017; Schermer et al. 2020). Spring temperature during year of
332 fruit maturation is an important determinant of fruit production, but also a major determinant of leaf
333 season (Vitasse et al. 2009c).

For oaks, we also found longer growing seasons associated with an increased occurrence of early freezing in autumn and to high autumnal temperatures. Drought is also a determinant of leaf senescence (Xie et al. 2015). We also found that earlier-commencing growing seasons increase the occurrence of late frosts during spring, which can cause major foliar damages (Vitasse et al. 2014), could reduce photosynthetic activity (Zohner et al. 2019), and kill flowers and developing fruits (Inouye 2000). In our study, we considered growing season length as a proxy of photosynthetic activity that influences carbohydrate accumulation. However, in oaks the development of leaves from leaf unfolding to maturation can take up to 70 days (Morecroft et al. 2003). This implies that growing season length may not be a reliable proxy of the length of the carbon assimilation period. Future investigations should thus also include flux data to better estimate of carbon uptake and release.

Reproductive cost and differences in species strategies

The negative correlation in fruit production observed between current and previous year is generally interpreted as a trade-off between current and future reproduction (Knops et al. 2007; Crone et al. 2009; Sala et al. 2012; Santos-del-Blanco and Climent 2014; Moreira et al. 2019). A review by Pearse et al. (2016) showed that carbon-based resources have a short period of residence, and are unlikely to be directly linked to this trade-off, but can act as a mobile signal interacting with hormones. Therefore, carbon-based resources can affect fruit production without being stored. Furthermore, oak and beech differ in their reproductive strategies where growth and reproduction are negatively correlated for beech but are positively correlated for oaks (Lebourgeois et al. 2018), and in their masting habit, flower vs fruit maturation masting species, where oaks have a higher level of flowers abortion (Espelta et al. 2008; Pearse et al. 2016; Bogdziewicz et al. 2017c, b). We hypothesized that our species are dependent of carbohydrates assimilated during the growing season, but other factors limit both bud initiation and fruit maturation. For oaks, from all these flowers initiated, only a fraction of them will mature into fruits, which will depend of pollination success (Pearse et al. 2016; Bogdziewicz et al. 2017c, b; Schermer et al. 2019), weather conditions like drought or late frost limiting fruit maturation (Espelta et al. 2008; Pérez-Ramos et al. 2010) and macro-nutrients other than carbohydrates (Pearse et al. 2016, Fernández-Martínez et al. 2019). Indeed, our model that included spring temperature and growing season length explained little variance. For beech, major determinants of fruit production are previous summer conditions with a relatively small effect of growing season length. Growing season length is not the main driver of fruit production, but it could be a new mechanism involved in masting patterns.

Perspective and conclusion

In addition to previously known cues on fruit production for beech and oaks, we show that growing season length is also important in determining annual fruit production. While more research is required to fully understand the mechanism(s) responsible for the observed relationships with growing

season length, we speculate that this may be related to 1) resource assimilation and 2) indirect effects of growing season length on climate events that influence fruit production. Beech and oaks tend to produce different amounts of fruit biomass, which is higher for oaks, and they differ in their growing season length which is longer for oaks. We speculate that the difference we found in the relationship between growing season length and fruit production in oaks and beech is due to different strategies of carbohydrates allocation (ring porous vs diffuse porous species) and different phenology (Barbaroux and Breda 2002; Michelot et al. 2012). The positive effect of current growing season length on fruit production is in accordance with a reported relationship between high levels of gross primary productivity and increased fruit production (Fernández-Martínez et al. 2017b), although in a beech forest in Germany Mund et al (2020) reported no relationship between annual GPP and fruit production. Climate change and climate events, which impact leaf and flower phenology and photosynthetic activity (Adams et al. 2015; Zohner et al. 2019) may also impact fruit production. An increase of growing season length can increase the exposure to climatic events, and also impact positively fruit biomass production of oaks but, eventually, negatively for beech. This variation of growing season length impacts nutrients remobilization, which can make elements less available for reproduction and impact fruit production. While we worked at the population scale, future research may focus on individual plants, as they present considerable variation in fecundity (Davi et al. 2016; Hacket-Pain et al. 2019) as well as their leaf phenology which in turn can impact individual tree growth (Delpierre et al. 2017). Inter-annual and inter-individual variation of leaf phenology could improve our understanding of resource allocation and variability in plant reproductive patterns.

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Data availability

Data used are available upon request from M. Nicolas (manuel.nicolas@onf.fr) and S. Macé (sebastien.mace@onf.fr).

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411 **List of Tables and Figures**

412

413 **Table 1**: Summary of studies exploring factors determining fruit production in European tree species
414 based on the RENECOFOR network (which is also part of the ICP forest network, International Co-
415 operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests <http://icp-
416 forests.net/>).

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Study	Species	Factors explaining variation in fruit production
Bogdziewicz et al. 2019	*F. sylvatica, Q. petraea*	- In *F. sylvatica*, positive correlation with summer temperature in the year before fruit maturation - In *Q. petraea*, positive correlation with spring temperature in the year of flower pollination
Caignard et al. 2017	*Q. robur, Q. petraea*	- Positive relation with spring temperature (April/May). Positive relation between growth and reproduction
Fernández-Martínez et al. 2017a	*P. nigra, P. sylvestris, P. abies, P. pinaster, A. alba, P. menziesii, F. sylvatica, Q; robur, Q. petraea*	- Foliar zinc and phosphorus concentration positively correlated - High level of gross primary productivity increase fruit production
Fernández-Martínez et al. 2017b	*A. alba, F. sylvatica, P. abies, P. menziesii, Q. petraea, Q. robur*	- In *F. sylvatica* and *P. abies*, positively correlated with dry and cold autumns, with dry and warm spring and with dry summers - In *Q. robur* and *Q. petraea*, positive relationship with warn and wet autumns (and also with wet summers and cold winters for *Q. robur*) - In *P. menziesii*, positive correlation with cold and dry autumns, warm and wet winters and warm springs - In *A. alba*, positive correlation with dry and warm spring and negative correlation with warm and wet winters

Lebourgeois et al. 2018	*F. sylvatica, Q. robur, Q. petraea*	- In *F. sylvatica*, positive correlation with summer temperature signal (Differential of June/July temperature of year$_{-1}$ – year$_{-2}$). Trade-off between growth and reproduction -In *Quercus*, positive correlation with the period of pollen emission and spring temperature (April). Positive relation between growth and reproduction
Schermer et al. 2019	*Q. robur, Q. petraea*	- Positive correlation with amount of airborne pollen and its sensibility to spring weather
Schermer et al. 2020	*Q. robur, Q. petraea*	- Positive effects of spring temperature and rainfall. Pollen release sensitive to late frost.

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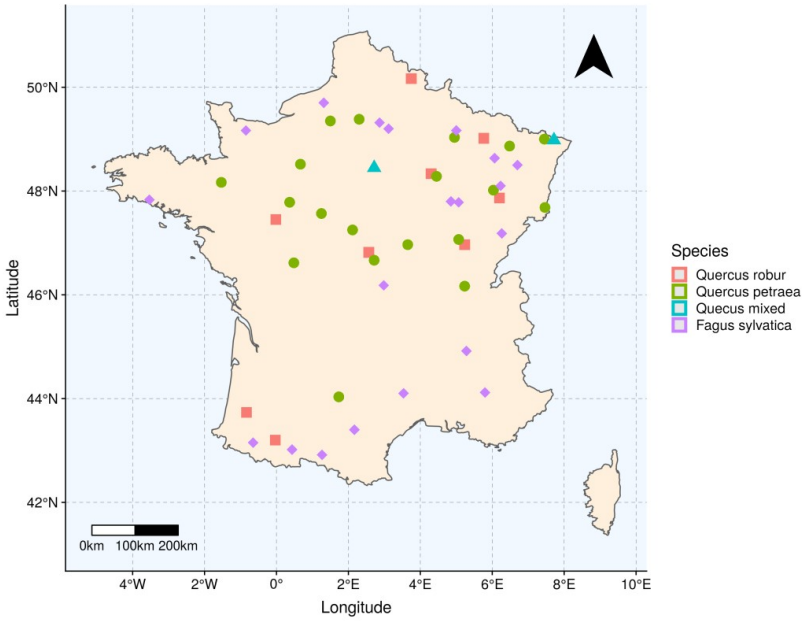
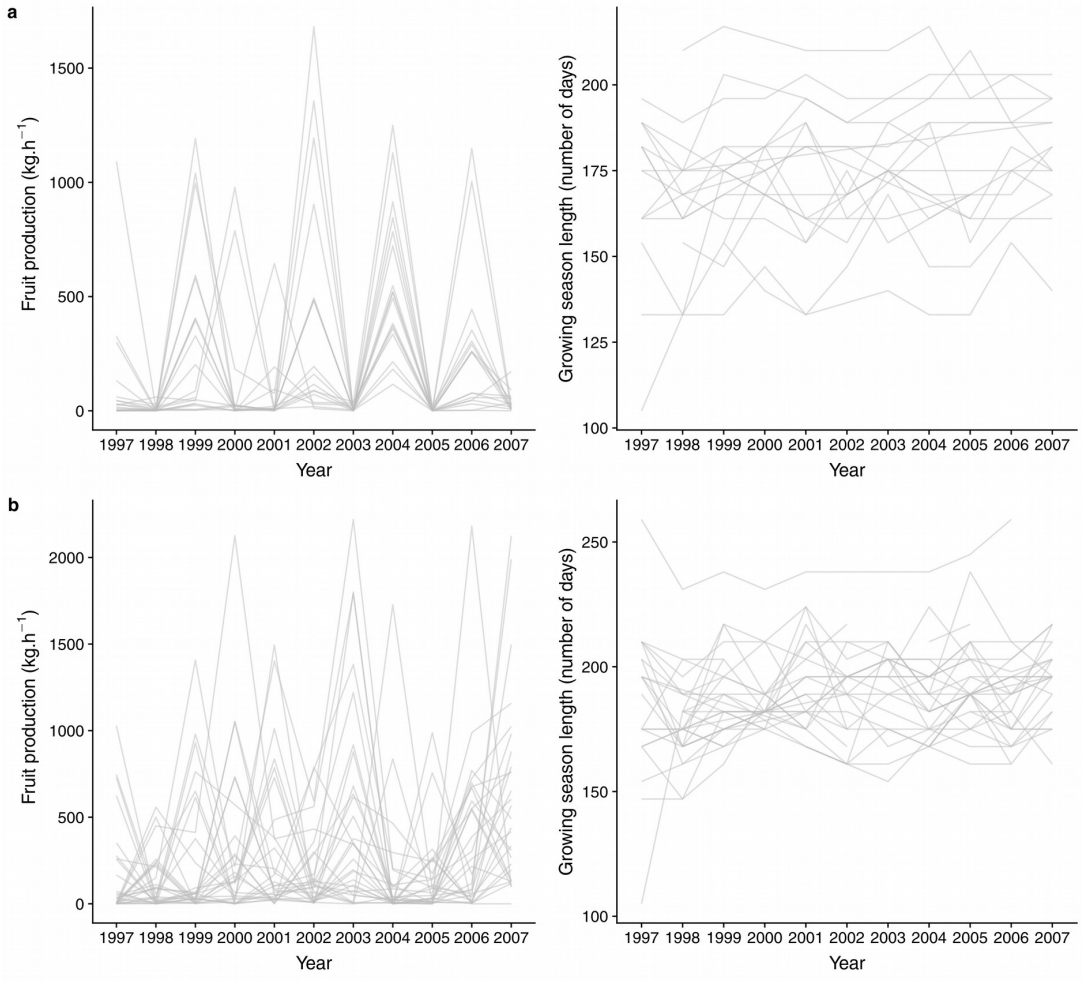
Table 2: Summary results of linear mixed models (LMMs) for beech and oaks (including *Q. robur* and *Q. petraea*). Level of significance are indicated with stars in the last column. GSL for growing season length of the current year (n) or previous year (n-1), including quadratic variable only for beech with current growing seasons length (dropped in oaks due to it non significance, and in previous growing seasons length for beech). F_{n-1} for previous year fruit production. $TmaxSummer_{n-1}$ for previous year maximal temperature (average June-July), and $TmaxSummer_{n-2}$ for two previous year maximal temperature (average June-July) were tested only for beech. $TmeanSpring_n$ for the mean temperature of the current year of fruit production (average April-May) only for oaks. The marginal R^2 of the model for beech was 0.45 and the conditional value was 0.65. For oaks, the marginal R^2 was 0.13 and the conditional value was 0.28.

Species	Variables	Estimate	Standard error	t-value	P value
Beech	Intercept	6.70	2.88	2.33	0.02
	GSL_n	0.96	2.55	0.38	0.7
	GSL^2_n	-4.26	1.65	-2.59	**0.009**
	F_{n-1}	-0.55	0.19	-2.88	**0.004**
	GSL_{n-1}	0.64	1.91	0.34	0.7
	$TmaxSummer_{n-1}$	12.88	2.78	4.62	**<0.00001**
	$TmaxSummer_{n-2}$	-16.76	2.82	-5.93	**<0.00001**
Oaks	Intercept	0.05	2.44	0.02	0.98
	GSL_n	4.44	1.90	2.32	**0.02**
	F_{n-1}	-0.41	0.16	-2.52	**0.011**
	GSL_{n-1}	-5.58	1.88	-2.96	**0.003**
	$TmeanSpring_n$	5.56	2.47	2.26	**0.02**

Figure 1: Sites location from the RENECOFOR network. Distribution of the studied European beech (*F. sylvatica*) and Temperate oaks (including *Q. robur*, *Q. petraea* and mixed) populations across France for a total of 50 sites.



440 **Figure 2**: Fruit biomass production (in kg.ha^{-1}) and growing season length (in number days) across
441 years for a) beech (*F. sylvatica*) and b) oaks (including *Q. robur*, *Q. petraea* and mixed). Grey lines
442 represent fruit production for each stand monitored.
443



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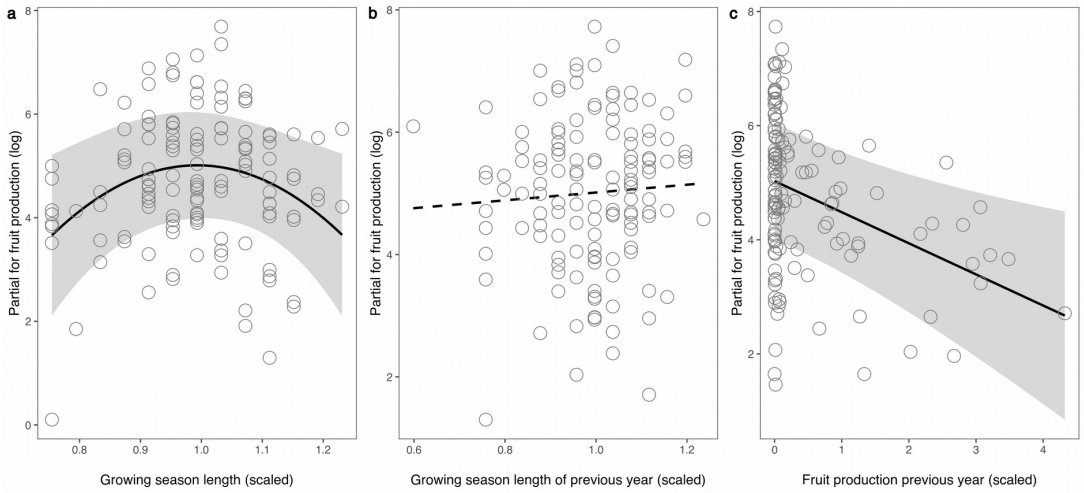
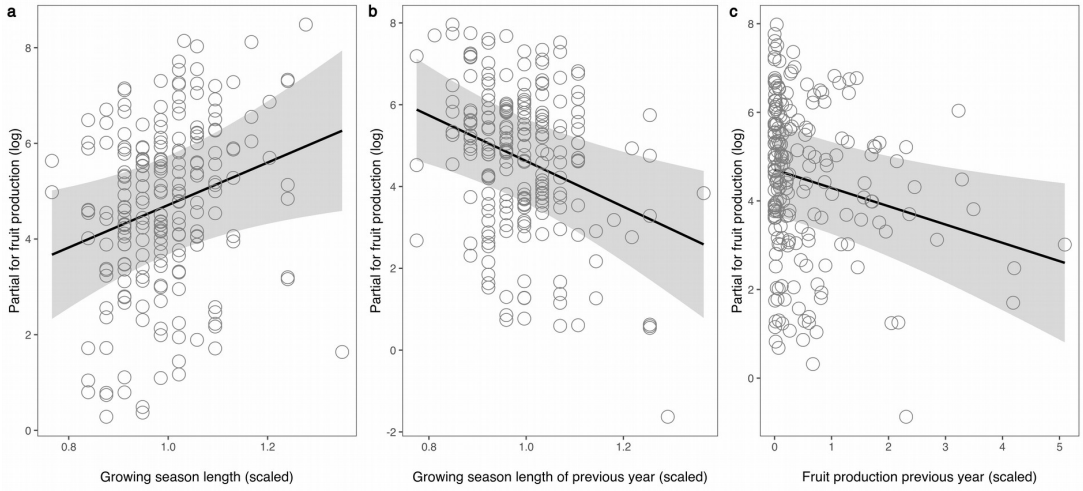
444 **Figure 3**: Relationship between fruit production of beech and growing season length (a), previous
445 growing season length (b) and previous fruit production (c). Trend lines are based on LMM while
446 shaded regions correspond to 95% confidence intervals. Axis-*y* are given at the scale of partial
447 residuals and axis-x are scaled variables. Dashed line for non-significant relationship are presented in
448 (b).
449



451 **Figure 4**: Relationship between fruit production of oaks and growing season length (a), previous year
452 growing season length (b) and previous year fruit production (c). Trend lines are based on LMM while
453 shaded regions correspond to 95% confidence intervals. Axis-*y* are given at the scale of partial
454 residuals and axis-x are scaled variable
455



Supplementary material

Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in temperate oaks (*Quercus robur* and *Quercus petraea*)

Valentin Journé, Thomas Caignard, Andrew Hacket-Pain & Michał Bogdziewicz

Table S1: Relationship between climatic events and growing seasons length. Summary results of generalized linear mixed models (GLMMs) for beech and oaks (including *Q. robur* and *Q. petraea*) with climatic events as response variable and growing seasons length as explanatory variable. A total of 10 GLMMs were used (i.e. 5 GLMMs for oaks and for beech). Level of significance are indicated with stars in the last column.

DS for dry spells (i.e. number of events when more than seven consecutive days without precipitation), FDspring for the number of frost days during spring season (minimal temperature from April to June < 0°C), FDautumn for the number of frost days during autumn season (minimal temperature from September to October < 0°C), HDsummer for the number of hot days during summer season (maximal temperature from June to August ≥ 30°C) and HDautumn for the number of hot days during autumn season (maximal temperature from September to October ≥ 30°C). Year and sites were included as random effects.

Species	Climate event (response variable)	Estimate	Standard error	t-value	P value
Beech	DS	1.39	1.04	1.33	0.18
	FDspring	0.94	3.36	0.28	0.77
	FDautumn	11.08	1.60	6.91	**<0.0001**
	HDsummer	0.10	0.51	0.20	0.83
	HDautumn	1.55	3.05	0.50	0.61
Oaks	**DS**	1.72	0.78	2.18	**0.029**
	FDspring	9.25	1.73	5.34	**<0.0001**
	FDautumn	7.26	0.93	7.75	**<0.0001**
	HDsummer	-0.021	0.28	-0.076	0.94
	HDautumn	3.88	1.21	3.21	**0.0013**

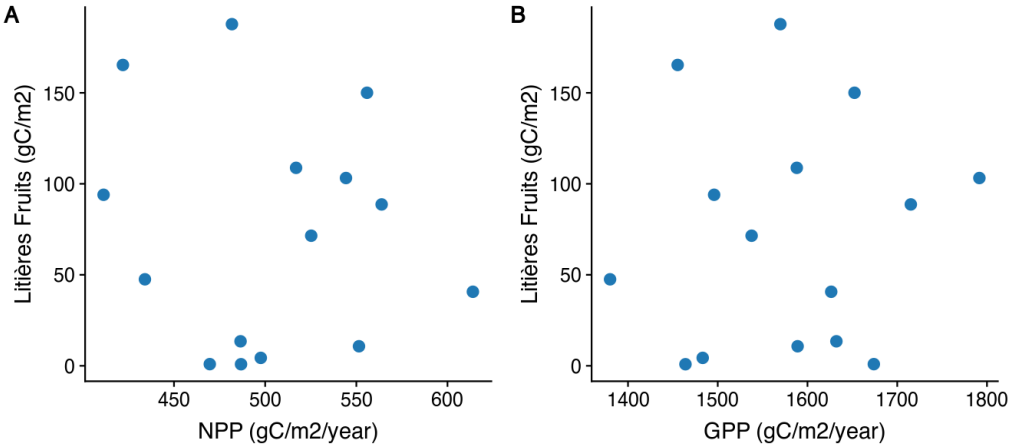


FIGURE III.1: Lien entre productivité et biomasse de fruits chez le Hêtre à Hainich (Allemagne). Graphique entre NPP annuelle et biomasse de fruits produits en A ; GPP annuelle et biomasse de fruits produits en B. Données issues de M. Mund, sur le site Hainich.

3 Synthèse et Discussion

Nous avons identifié un nouveau facteur permettant d'expliquer une part significative même si elle demeure faible, de la variation de la production de graines chez les décidus étudiés. Plus précisément, nous avons trouvé une relation non linéaire entre la durée de la saison de végétation de l'année et la production de fruits chez le Hêtre, et une relation linéaire entre la durée de la saison de végétation et le nombre de fructifications chez les Chênes. Pour le Hêtre, la biomasse de fruits augmente jusqu'à un certain seuil de durée de saison de végétation (environ 170 jours) puis diminue. Pour les Chênes la biomasse fructifère augmente linéairement avec durée la saison de végétation. Ainsi l'augmentation de la saison de végétation augmente toujours la biomasse fructifère pour les Chênes, mais peut la diminuer chez le Hêtre. Lors d'une saison de végétation longue, plus de carbone peut être assimilé avec plus de ressources disponibles pour la fructification. Mais lors d'une saison de végétation longue, il se peut aussi qu'il y ait plus d'aléas climatiques (jours de gelées, sécheresses) qui augmentent avec la saison de végétation, ce qui pourrait avoir des effets négatifs indirects sur la fructification du Hêtre. Cependant, la variance expliquée par nos modèles résulte principalement des effets aléatoires (sites et années) et reste assez faible.

Nous avons suggéré dans la discussion de l'article qu'il pourrait être intéressant de corréler les données de biomasse fructifère à d'autres proxy de l'assimilation de carbone et de la productivité, pour mieux comprendre les causes de l'effet de la durée de végétation. En effet, la durée de la saison de végétation,

n'est pas directement corrélée à la production primaire nette (White & Nemani, 2003). En utilisant des données flux sur le site de Hainich, en Allemagne, où il y a un site de tour à flux et un suivi de litière sur du Hêtre commun (récolte aussi la biomasse des fruits), nous ne trouvons pas de relations significatives entre la production de fruits et la productivité de la forêt (Figure III.1). Nous ne trouvons pas de lien significatif entre la NPP (*Net Primary Productivity*) annuelle et biomasse de fruits annuelle (P = 0.72), et pas de lien non plus entre la GPP (*Gross Primary Productivity*) annuelle et biomasse de fruits annuelle (P = 0.76). Comme montré dans Fernández-Martínez et al. 2017b, certains sites avec une GPP élevée produisent une biomasse de fruits plus importante. Mais comme dans les données du site de Hainich, la variation inter-annuelle de GPP ou NPP est forte et n'est globalement pas corrélée avec la biomasse fructifère. Comme pour la croissance, cela peut être dû au fait que les forêts tempérées ne sont pas limitées par le carbone (Mund et al., 2010; Delpierre et al., 2016a; Friend et al., 2019). Ainsi, le carbone assimilé pourrait avoir peu d'influence sur la croissance (Mund et al., 2010), et ainsi peu sur la reproduction. En effet, les années où la croissance du Hêtre est limitée, il s'agit souvent d'une année de forte fructification, ce qui suggère un changement d'allocation des ressources entre la croissance et la reproduction (Mund et al., 2010). Une allocation plus importante dans la reproduction diminuerait ainsi la quantité de ressources disponible pour la croissance. Enfin, l'effet de la phénologie foliaire que nous avons reporté peut aussi potentiellement être lié à un effet de la phénologie de la reproduction. La date de débourrement et de floraison sont très proches pour les trois espèces étudiées, et un décalage de la phénologie foliaire peut aussi décaler la floraison (Koenig et al., 2012; Schermer et al., 2019).

Chapitre IV

Utilisation d'un modèle bayésien hiérarchique pour estimer la ressource et son allocation entre croissance et reproduction

> Of course there are general laws in ecology. However, our science has rather few universal laws.
>
> Lawton, 1999

1 Contexte

La croissance et la reproduction des arbres, deux composantes de la valeur sélective, sont affectées par le changement climatique et la réponse à ces changements peut être différente suivant les populations étudiées. Par exemple, des populations en marge Nord ont tendance à croître et se reproduire plus que les populations en marge Sud (Jump et al., 2006; Overgaard et al., 2007; Lindner et al., 2010; Caignard et al., 2017). Un climat favorable peut promouvoir la croissance et la reproduction, contrairement à des zones moins favorables qui peuvent impacter négativement la croissance et la reproduction. A large échelle, ceci peut générer mécaniquement des corrélations entre croissance et reproduction, masquant d'éventuels compromis entre ces deux processus. Ainsi, le compromis concernant l'allocation des ressources entre croissance et reproduction, dépend de l'échelle d'observation (ex. la région, ou la population) (Sanchez-Humanes et al., 2011).

Le concept du compromis (*« trade-off »*), utilisé dans de nombreuses disciplines, se définit comme le coût d'un changement bénéfique pour un trait conduisant à un changement néfaste d'un autre trait (Stearns, 1989). Dans cette étude, nous avons étudié les compromis entre croissance et reproduction chez les arbres. Plusieurs études ont auparavant étudié ces compromis, mais n'ont pas trouvé de réponse univoque (Obeso, 2002; Thomas, 2011). Un compromis entre les deux fonctions devrait être trouvé si les deux puits sont en compétition pour l'utilisation des ressources (Koenig & Knops, 1998; Lebourgeois et al., 2018) ou si la croissance et la reproduction utilisent les ressources hiérarchiquement, par exemple d'abord pour la reproduction, ensuite pour la croissance (Suzuki, 2001). Mais le compromis peut être absent si ces deux puits n'utilisent pas les mêmes ressources (i.e. indépendance des puits) (Yasumura et al., 2006; Knops et al., 2007) ou si ces puits utilisent la même ressource, mais suivant une fraction constante pour la croissance et la reproduction (Pérez-Ramos et al., 2010; Lebourgeois et al., 2018). En plus des ressources, le climat peut avoir un effet direct sur la reproduction et la croissance. Par exemple, des précipitations printanières abondantes sont favorables à la croissance, mais négatives pour la reproduction, en limitant la dispersion du pollen. D'autre part, comme suggéré par Knops et al. 2007, le compromis majeur n'est pas entre croissance et reproduction, mais plutôt entre reproductions successives. Des expériences de suppression fruits ont par exemple montré, qu'une production moindre de fruits augmente la quantité de bourgeons floraux et produit plus de fruits l'année suivante (ex. Elmqvist et al. 1991; Santos-del-Blanco & Climent 2014).

L'objectif de cette partie est d'étudier les potentiels compromis entre croissance et reproduction, en tenant compte des ressources disponibles. Nous avons pour cela développé un modèle bayésien hiérarchique, qui définit un niveau des

ressources acquises et leur allocation entre croissance et reproduction. Le modèle intègre une allocation différentiée entre la reproduction mâle et la reproduction femelle, et tient compte de la variation inter-individuelle et inter-annuelle. Le modèle est divisé en deux parties, une partie processus avec les variables non observées comme la ressource, mais aussi les corrélations potentielles entre puits de croissance et de reproduction. La seconde partie est la partie "données", où l'on spécifie la distribution des données suivant les processus d'intérêts (Wikle, 2003). Au final, le modèle utilise des données de croissance et de reproduction, de taille des individus, ainsi que la température moyenne annuelle et les précipitations estivales. Nous avons utilisé ce modèle sur le Cèdre de l'Atlas (*Cedrus atlantica*), dont le cycle entre l'initiation et la maturation des cônes se fait sur deux ans. La production de cônes mâles et femelles et la croissance ont été suivies pendant 4 ans, dans une plantation sylvicole à Sault. Dans cette plantation expérimentale, trois parcelles sont soumises à différents traitements sylvicoles (coupe d'intensité faible à forte), avec une autre parcelle témoin (Guillemot et al., 2015). Dans notre étude, deux parcelles ont été étudiées, une à forte densité (1200 ind.ha^{-1}) et une faible densité (250 ind.ha^{-1}), de 2000 à 2004.

Ce projet a été amorcé après des analyses statistiques fréquentistes faites avec F. Lefèvre, H. Davi et S. Oddou-Muratorio. Une collaboration a été établie entre notre laboratoire et le laboratoire BioSP pour la construction du modèle bayésien et l'analyse des résultats. L'article a déjà été soumis une première fois en Mai 2019 et en préparation pour une re-soumission dans *Methods in Ecology and Evolution*.

2 A hierarchical Bayesian resource model to investigate trade-offs between growth and reproduction in a long-lived plant

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Mots-clés : Cèdre de l'Atlas, conifères, fructification, modèle mécaniste, allocation des ressources, compromis, croissance

A hierarchical Bayesian resource model to investigate trade-offs between growth and reproduction in a long-lived plant

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#Total word count main text: 5607 #Details word count: 206 (Summary), 1233 (Introduction), 1654 (Materials & Methods), 500 (Results), 1460 (Discussion), 80 (Acknowledgments), 474 (Legends)

#Number of figures (5, in colour) #Number of tables (1) # 1 Supporting Information

1 Summary

1. A trade-off between growth and fecundity, reflecting the inability of simultaneously investing in these two functions when resources are limited, is a common feature of life history theory. However, this trade-off is often difficult to demonstrate in natural populations of long-lived plants.

2. We developed a hierarchical Bayesian model to estimate the correlation among growth and several component of reproduction, using observations at individual level over several years. The model introduces unobserved latent variables for the individual resource level and the number of initialized reproductive buds. We applied it to a Mediterranean coniferous tree, Atlas Cedar (*Cedrus atlantica*) at two contrasted competitor densities.

3. We found that trees initializing many reproductive buds had a lower growth. Moreover, trees investing more resources to maturate female cones initiated less reproductive buds. There was no significant effect of competitor densities on these two trade-offs. By contrast, no trade off was detected between growth and cone survival.

4. We showed that individual trees displayed various strategies of resource allocation between growth and reproduction, independently of competitor density. However to highlight these potential trade-offs, it is necessary to integrate the dynamics of resources and the phenology of sinks from initiation to maturation of both male and female reproductive organs.

Keywords: *Cedrus atlantica*, coniferous, masting, mechanistic model, resource allocation, trade-off, tree growth

2 Introduction

Considering their paramount importance for terrestrial biodiversity and carbon sink, forests responses to climate variations need to better understood and predicted (Pan *et al.*, 2011). For instance, growth and reproduction, two of the main components of tree fitness, have been shown to be affected by climate change across species range. In cold and mild areas, such as boreal and temperate forests, global warming is extending the growing season, promoting tree growth (Briceño-Elizondo *et al.*, 2006; Lindner *et al.*, 2010) and reproduction (Overgaard *et al.*, 2007; Caignard *et al.*, 2017). By contrast, in warmer and drier areas, negative impacts of global warming on tree growth (Jump *et al.*, 2006; Allen *et al.*, 2010; Lindner *et al.*, 2010) and reproduction have been reported (Mutke *et al.*, 2005; Pérez-Ramos *et al.*, 2010). These large-scale trends suggest a positive environmental correlation between growth and reproduction. However, negative environmental correlations are also well-described for instance in seed orchards, where management practices such as stem girdling, which mechanically reduces growth, are used to induce flowering (Bonnet-Masimbert and Webber, 1995). This apparent contradiction stresses the need to consider the level of available resource allocated to each fitness component, and to take into account the scale of observation, e.g. population or individual, when investigating the coordinated response of life-history traits to climate variation.

Trade-off between life-history traits are expected to be ubiquitous throughout the living world. The concept of trade-off is used in many disciplines, and from it classical view in evolutionary ecology "trade-offs represent the costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another" (Stearns, 1989). In this sense, trade-off corresponds to a negative correlation between two traits related to fitness, which is observed in a set of individuals, or at different life-stages for a given individual. This correlation can be due to a combination of factors involving resource allocation scheme, the respective levels of environmental and genetic variation in life-history traits, and the spatio-temporal heterogeneity in the resource level (Partridge and Sibly, 1991). Trade-offs between traits can occur when the resources, i.e. energy and

nutrients, are limited because of the result of resource allocation to different sinks sharing a common pool of resources. Some of the trade-offs observed within a population may result from the variation in allocation strategies among individuals or among life-stages. This inter-individual variability of allocation strategies is expected to be driven by a combination of environmental and genetic factors (Garland and Carter, 1994). To disentangle these effects, the common approach consists in using experiments to measure both the environmental and genetic components of the correlation (Stearns, 1989). Finally, strong environmental correlations are expected in natural populations, because resources, such as soil quality and climatic conditions vary through time and space and affect individual resource allocation (Rausher, 1992). The theoretical model of van Noordwijk and de Jong (1986), demonstrated that the patterns of resource acquisition versus resource allocation can change the sign of the correlation between two life history traits: when resource acquisition is highly variable among individuals while the fraction allocated to each life history traits is similar, the between-trait correlation is positive. In the reverse case, when resource allocation is highly variable among individuals, but not resource acquisition, the correlation becomes negative. To better track trade-offs, one solution is to account for the variability of resources acquisition and allocation between individuals together with the measurement of life history traits. This approach requires combining ecophysiology with population ecology to identify potential trade-offs (Olijnyk and Nelson, 2013).

Trade-offs between reproduction versus growth-related life-history traits have received much attention (Bell, 1980; Lovett Doust, 1989), in particular in annual and perennial plants (Obeso, 2002; Thomas, 2011). Most studies investigated trade-offs through the phenotypic correlations between growth and reproduction at individual or population level, and reported either positive correlations, no relation or negative correlations (Sánchez-Humanes *et al.*, 2011; Thomas, 2011). Various hypotheses related to resource allocation have been advanced to explain such idiosyncratic patterns across study sites or species (Pulido *et al.*, 2014): resource allocation to growth and reproduction can be either (i) based on a hierarchy, where resource are first allocated to reproduction and

then to growth (Wardlaw, 1990; Suzuki, 2001) or (ii) linked to different resource pools, so that resource allocated to growth is independent from resource allocated to reproduction (Cremer, 1992; Yasumura *et al.*, 2006; Knops *et al.*, 2007; Żywiec and Zielonka, 2013) or (iii) based on a same pool, with a constant fraction of resource allocated to each sink (Despland and Houle, 1997; Pérez-Ramos *et al.*, 2010; Berdanier and Clark, 2016; Lebourgeois *et al.*, 2018) or finally (iv) based on a same pool with competition among resources allocated to each sink (Koenig and Knops, 1998; Martín *et al.*, 2015; Lebourgeois *et al.*, 2018). Only in cases (i) and (iv) is a trade-off expected to be observed, while cases (ii) and (iii) can lead to positive or non significant correlation. Besides resources allocation scheme, climatic conditions can have contrasted direct effects on reproduction and growth and generate negative correlation without real trade-off, for instance when favorable conditions for growth are unfavorable for reproduction. This is well illustrated by the *Quercus sp* study by Knops *et al.* (2007), where the meaningful trade-off does not occur between growth and reproduction of the same year, but between current and future reproduction. Indeed, due to the high reproductive costs in trees, an important seed production in a given year can decrease the level of resources to invest in future reproduction, explaining why less seeds are produced the year after (Sala *et al.*, 2012). This trade-off between current and future reproduction was confirmed by removal experiments, where removing fruits increase the number reproductive buds and increase fruit production in the next year (Elmqvist *et al.*, 1991; Fox and Stevens, 1991; Fox, 1995; Santos-del Blanco and Climent, 2014). However, removal experiment to quantify male reproduction cost is difficult to implement for monoecious species due to potential damage on vegetative structure (Santos-del Blanco and Climent, 2014).

Another important trade-off in monoecious plants can occur between male and female reproduction. Studies investigating the cost of reproduction usually neglect the male function and in particular the abortion of reproductive flowers. The major assumption supporting this simplification is that male function needs fewer resources than female function (Elmqvist *et al.*, 1991; Obeso, 2002), and is not limiting for reproduction. How-

ever, this hypothesis may no longer hold under changing climate. Moreover, resources allocation to male versus female reproduction determines the phenotypic gender (Lloyd, 1980), which is also important from the point of view of population genetics. In trees, studies relating phenotypic gender to male and female reproductive biomass are rare due to the difficulty to measure them. Two hypotheses have been formulated: male biomass can be relatively constant across years whereas reproductive female biomass follows available resource (Knops and Koenig, 2012), or both male and female biomass can co-vary through time (Houle, 2001). But studying reproduction only from female aspect, usually based on a final seed production, can confound the reproductive effort and lead to a wrong correlation among growth and reproductive traits (Knops *et al.*, 2007; Knops and Koenig, 2012).

The aim of this study is to investigate the trade-off between growth and male/female reproduction within a tree population. We first developed a hierarchical Bayesian model based on processes of resource acquisition and allocation, which simultaneously accounts (i) for the timing of growth and reproductive processes, and (ii) for the variation among individuals and years in the level of resource and in the phenotypic gender (both considered as latent variables). This approach allows the correlation between growth and reproduction to be directly estimated without biases related to resource level heterogeneity. It requires repeated measurements of growth and reproductive effort, as well as of climatic and plant size variables determining resource acquisition. Then, we applied this general model to the case of a Mediterranean coniferous species, *Cedrus atlantica*. This monoecious species is characterized by a long reproductive cycle, with female cones maturation spreading across two years. We measured male and female cone production and growth increment during four consecutive years in a mature even-aged silviculture experiment planted at two contrasted competitor densities. We address the main question: *Does the integration of resources help us to identify trade-off between growth and reproduction in trees?*. Then, we address three shorter questions: 1) Does density affect the level of resource and phenotypic gender ? 2) Are there significant correlations between growth,

early-stage reproduction (i.e. reproductive bud initiation) and late-stage reproduction (i.e. the number of mature female cones) ? 3) Does density and phenotypic gender affect these correlations ?

3 Material and Methods

3.1 Study species and site

Atlas cedar, *Cedrus atlantica* (Manetti ex Endl.) Carrière, is a coniferous species originating from the Mediterranean region. This monoecious species reaches it sexual maturity between 15 and 30 years old (Toth, 1978), and carry male and female organs on different branches of the same individual. Biases in phenotypic gender have been reported to be stable in time, with male or female individuals (Krouchi *et al.*, 2004). Male reproduction, from reproductive bud initiation to pollen maturation, is achieved within one year, whereas female reproduction, from cone initiation to maturation, spread over two years (Fig. 1). Reproductive buds are initiated in the summer period (June-July for male buds and late August for female buds) at year *n*, followed by pollination in September, when female cones open and receive pollen. Female cones close their scales in October-November, at the period when male cones fall down. A time lag between pollination and fecundation characterizes the coniferous species (Williams, 2009), with a duration of nine month for Atlas cedar. Pollen germinates in spring at year *n+1* , then ovules are fertilized and seeds begin to maturate (Boivin *et al.*, 2015). Female cones fall in autumn at year *n+1*. Hence, two generations of female cones can co-exist on a given individual and it is possible to distinguish green one-year cones from brownish two-years cones. *Cedrus atlantica* can be referred as a masting species, characterized by a seed production highly variable among years and synchronized among individuals (Krouchi *et al.*, 2004; Kelly and Sork, 2002).
The study site is a 35 years-old plantation located in Mont-Ventoux, a Mediterranean mountain (France), at 1170 meters of elevation (44°07' 05" N, 5°20' 38" E). All the trees were planted in similar pedo-climatic conditions. The initial tree density was 2700 stems ha^{-1}. Two thinning strategies were applied, leading to contrasted competitor den-

sities: high density (1200 stems ha^{-1}) versus low density (250 stems ha^{-1}) plot. More details on the general experiment are presented in Guillemot *et al.* (2015).

3.2 Observations of growth and reproduction

We monitored 40 individual trees in the high density plot and 31 individual trees in the low-density plot. These individuals were randomly selected within each plot and measured each year from 2002 to 2005. We first measured the diameter at 1.3 meters ($DBH_{i,t}$) for each individual tree i and each year t. Annual basal area increment ($BAI_{i,t}^{\mathrm{obs}}$) was computed as : $BAI_{i,t}^{\mathrm{obs}} = (\pi \times DBH_t^2/4) - (\pi \times DBH_{t-1}^2/4)$.

Male cones abundance ($M_{i,t}$) was recorded as a qualitative ordered variable, consisting in a score ranging from 0 to 4: "0" means no male cone was observed; "1" means few male cones are dispersed in the canopy; "2" means male cones are abundant in one branch; "3" means male cones are abundant on two branches and "4" means male cones are abundant over the whole tree canopy. These scores were converted into multinomial observations $IMC_{i,t}^{\mathrm{obs}}$ as follows:

$$\begin{cases} M_{i,t} = 0 \Rightarrow IMC_{i,t}^{\mathrm{obs}} = [1,0,0,0,0] \\ M_{i,t} = 1 \Rightarrow IMC_{i,t}^{\mathrm{obs}} = [0,1,0,0,0] \\ M_{i,t} = 2 \Rightarrow IMC_{i,t}^{\mathrm{obs}} = [0,0,1,0,0] \\ M_{i,t} = 3 \Rightarrow IMC_{i,t}^{\mathrm{obs}} = [0,0,0,1,0] \\ M_{i,t} = 4 \Rightarrow IMC_{i,t}^{\mathrm{obs}} = [0,0,0,0,1] \end{cases} \tag{1}$$

Female cones ($FC_{i,t}^{\mathrm{obs}}$) were individually counted over the whole canopy from the ground with binoculars and at two seasons each year (in spring then in late summer). The identification and distinct count of one-year-old versus two-years-old cones allowed us to determine the number of cones produced each year. The raw relation between $FC_{i,t}^{\mathrm{obs}}$ and $BAI_{i,t}^{\mathrm{obs}}$ in Fig. 2 suggests a positive correlation between growth and female reproduction.

3.3 Climate data

A meteorological station (Hobos ProV2 micro-loggers) at 1.96 km from the study site allowed to measure local climatic variables from 1999 to 2005. Then, local precipitations

and mean temperature were extracted from long-term national meteorological data from 1960 to 2013 and down-scaled using statistical regression on local climatic measurements (Quintana-Seguí *et al.*, 2008). In this study, we used the precipitations accumulated from April to August ($RAIN_t$, in mm) and the mean temperature between April and June ($Tmean_t$, in T°C). These selected months have been previously acknowledged to affect tree development (Aussenac and Finkelstein, 1983; Till, 1987; Linares *et al.*, 2013).

3.4 Bayesian statistical analyses

We developed a Bayesian hierarchical model linking resources to three energetic sinks: growth, reproductive buds initiation and female cones survival. Potential correlations between these sinks are accounted for by correlated random effects. The model is composed of two layers (Fig. 3 for a general overview): the process model which describes how resources are acquired and allocated to each sink, and the data model which describes the links between the process-model and the observations. The observations typically consist in repeated counts of male and female organs to characterize the reproductive sink and repeated measure of size increment to characterize the growth sink.

3.4.1 Process model

Resources: The level of resources ($R_{i,t}$) for individual i the year t is considered as a latent variable conditioning the budget potentially allocated to the different energetic sinks. We modeled $R_{i,t}$ as dependent on observed climatic variables ($RAIN_t$ and $Tmean_t$) and on observed individual tree diameter ($DBH_{i,t}$) through the following linear model:

$$\begin{cases} \log(R_{i,t}) = \alpha_0 + \alpha_1 * DBH_{i,t} + \alpha_2 * RAIN_t + \alpha_3 * Tmean_t + w_{i,t} \\ w_{i,t} \sim \mathcal{N}(\mu_i^R, \sigma_t^R) \\ \mu_i^R \sim \mathcal{N}(0, \tau_i^R) \end{cases} \tag{2}$$

where α_0 is the intercept, α_1 is the slope parameter for tree diameter, α_2 is the slope parameter for precipitations and α_3 is the slope parameter for mean temperature. $w_{i,t}$ is an individual residual term, corresponding to a temporal random effect (with variance

σ_t^R) whose mean μ_i^R varies across individuals, according to a centered normal distribution with a variance τ_i^R. Note that the log link-function is used to ensure $R_{i,t}$ remains positive.

Resource allocation to energetic sinks: The level of resources ($R_{i,t}$) for individual i the year t determines growth ($BAI_{i,t}$), the number of initiated reproductive buds ($IB_{i,t}$) and the probability of female cones survival ($p_{i,t}^{FCS}$), through the following model :

$$\begin{cases} BAI_{i,t} = \gamma * R_{i,t} + \epsilon_{1,i} \\ IB_{i,t} = X_{i,t} * (\beta_1 * R_{i,t} + \epsilon_{2,i}) \\ \text{logit}(p_{i,t}^{FCS}) = \beta_0 + \beta_2 * R_{i,t} + \epsilon_{3,i} \\ \boldsymbol{\epsilon} \sim \mathcal{N}_3\,(0, \sum) \end{cases} \tag{3}$$

where γ is the slope parameter and $\epsilon_{1,i}$ the individual residual term for the effect of $R_{i,t}$ on growth increment $BAI_{i,t}$; β_1 is the slope parameter and $\epsilon_{2,i}$ the individual residual term for the effect of $R_{i,t}$ on bud initiation ($IB_{i,t}$); β_2 is the slope parameter and $\epsilon_{3,i}$ the individual residual term for the effect of $R_{i,t}$ on female cones survival ($p_{i,t}^{FCS}$). $X_{i,t}$ is a Bernoulli variable ($X_{i,t} \sim \mathcal{B}\,(p_X)$), indicating if individual i produced ($X_{i,t} = 1$) or not ($X_{i,t}$=0) reproductive buds at year t, allowing to consider null values in the observations. The intercept β_0 is fixed to constrain $p_{i,t}^{FCS} \approx 0$ when $R_{i,t} = 0$.

This model explicitly considers that individual random effects on the three sinks, $\epsilon_{1,i}$; $\epsilon_{2,i}$; $\epsilon_{3,i}$, are related to each other through the variance-covariance matrix $\sum$. The pairwise correlations between them can thus be used to investigate constrains in the allocation of resources to the three sinks. Indeed, for a given amount of resources $R_{i,t}$ available for an individual i, the sign of the correlation between $\epsilon_{l,i}$, and $\epsilon_{k,i}$ indicates how resources are respectively allocated to sinks l and k. Correlations were computed as $\rho_{l,k} = \Sigma_{l,k} / (\Sigma_{l,l}\Sigma_{k,k})$.

Contrary to resource budget models used to investigate non-linear patterns of fruit production (Isagi *et al.*, 1997; Ye and Sakai, 2016), our model does not explicitly impose a trade-off between energetic sinks through the partitioning of resource ($R_{i,t}$) among them; for instance, there is no constraints on the triplet $\gamma; \beta_1; \beta_2$. Instead, modeling trade-off

through the correlated individual random effects allow more flexibility, e.g. for possible synergies or antagonisms between sinks. Also, note that the model does not account for pollen limitation and its potential effect on female cone survival.

Male and female reproduction: The model consider that initialized buds ($IB_{i,t}$) then develop into a number of initiated male cones ($IMC_{i,t}$) and a number of initiated female cones ($IFC_{i,t}$) according to the phenotypic gender ($PG_{i,t}$) of individual i at year t, using the following model:

$$\begin{cases} \text{logit}\left(PG_{i,t}\right) \sim \mathcal{N}\left(\bar{PG}, \sigma_{PG}\right) \\ IMC_{i,t} = PG_{i,t} * IB_{i,t} \\ IFC_{i,t} = (1 - PG_{i,t}) * IB_{i,t} \end{cases} \tag{4}$$

3.4.2 Data model

The model use repeated observations of growth, male reproduction and female reproduction, such as presented in our case in the section 3.2. We assume that observed growth ($BAI_{i,t}^{\text{obs}}$) is related to the latent growth variable of the process-model ($BAI_{i,t}$) through :

$$BAI_{i,t}^{\text{obs}} \sim \mathcal{N}\left(BAI_{i,t}, \sigma_{BAI}\right) \tag{5}$$

The number of initiated male cones ($IMC_{i,t}$) is a continuous variable while the observed abundance of male cones ($IMC_{i,t}^{\text{obs}}$) is a categorical ordered variable as described in section 3.2. To link $IMC_{i,t}$ and $IMC_{i,t}^{\text{obs}}$ we used the following observational model:

$$\begin{cases} \boldsymbol{\pi_{i,t}} = [F(s_0), F(s_1) - F(s_0), F(s_2) - F(s_1), F(s_3) - F(s_2), 1 - F(s_3)] \\ IMC_{i,t}^{\text{obs}} \sim \text{Multinomial}\left(\boldsymbol{\pi_{i,t}}, 1\right) \end{cases} \tag{6}$$

where $F(.)$ denotes the cumulative distribution function of a normal distribution with mean $IMC_{i,t}$ and variance σ_{IMC}. $\{s_0, s_1, s_2, s_3\}$ is a set of fixed thresholds determining the boundaries between each value of the notation, and are derived from $F(.)$. Note that this approach is equivalent to consider a probit link in the case of binary data.

Finally, the observed count of female cones ($FC_{i,t}^{\text{obs}}$), is linked to the latent variable describing number of initiated female cones ($IFC_{i,t}$) through the following binomial observational model:

$$\begin{cases} IFC'_{i,t-1} \sim \mathcal{P}(\lambda * IFC_{i,t-1}) \\ FC_{i,t}^{\text{obs}} \sim \mathcal{B}(p_{i,t}^{FCS}, IFC'_{i,t-1}) \end{cases} \tag{7}$$

Initialized female cones $IFC'_{i,t-1}$ are first drawn according to a Poisson distribution depending on $IFC_{i,t-1}$ and λ, a scale parameter. Then the female cones initialized year $t-1$ survive with probability $p_{i,t}^{FCS}$ between year $t-1$ and year t.

3.4.3 Model implementation

The prior distributions for all the parameters of interests are presented in Supporting Information, Table S1. Estimation of parameters was performed using the `JAGS` software (Plummer, 2003) in the `R` environment (R Core Team, 2018). We ran three parallel chains with 2,500,000 iterations, a burn-in of 2,500,000 and a thinning rate at 2500. In the result section, posterior median along with the 95% credible interval of parameters are presented. We conducted posterior predictive checks to evaluate the accuracy of our model in fitting the data. Replicated data were simulated under the fitted model and compared with the observed data. We then calculated a Bayesian p-value for quantitative variables, $BAI_{i,t}^{\text{obs}}$ and $FC_{i,t}^{\text{obs}}$. A value near 0.5 indicate that the model fit correctly data (Gelman *et al.*, 1996). For male cone notation ($IMC_{i,t}^{\text{obs}}$), which only takes 0 and 1 values, we used the Brier score to determine it accuracy. This score varies between 0 and 1, a score below 0.25 indicating that the model predicts better than expected by chance.

We used the predictions of $\epsilon_{x,i}$ with $x = 1, 2, 3$, corresponding to the individual random effects, to investigate individual strategies. No parameters where integrated to distinguish both competitor densities. We tested the correlation between predictions of residual terms (i.e. $\epsilon_{1,i}$ with $\epsilon_{2,i}$, $\epsilon_{1,i}$ with $\epsilon_{3,i}$ and $\epsilon_{2,i}$ with $\epsilon_{3,i}$) and density, to check if similar trends were present in both competitor densities with an analysis of covariance (ANCOVA). The ANCOVA was applied on each model iterations retained (i.e. 3000 iterations) to estimate

P value of the interaction terms $\epsilon_{x,i} \times$ density (with $x = 1, 2, 3$). We reported probability to obtain a significant interaction $P < 0.05$ from each iteration. Then, we defined two ellipses, i.e. one for each densities, corresponding to circle integrating all individuals points in order to identify similar or contrasting strategies between densities. We determined the centroïd ellipse for each density. We computed the overlap area between two ellipses, corresponding to the matching area between these two ellipses, and converted them in percent. For both densities, ellipses center were determined with mean value of axis x and y, and scaled with standard deviation. Lastly, we also checked how phenotypic gender ($PG_{i,t}$) influence ϵ terms with linear regression for each iterations and reported probabilities to obtain $P < 0.05$. Parameters values were reported with median posterior and credible interval. Ellipses were estimated with the package `ellipse` (Murdoch and Chow, 1996), and we determined their size and overlap area with the `rgeos` package (Bivand and Rundel, 2017). Linear regressions were performed with `stats` package (R Core Team, 2018)

4 Results

4.1 Posterior predictive checks

The posterior predictive checks of the hierarchical Bayesian model are presented in Table 1 for all observed variables. The model fitted accurately both growth and female cones production with values closed to 0.5. Male fecundity based on number of male cones also fitted well to the data, with Brier score values closed to 0 for all levels factor, corresponding to male notation (i.e. ranging from 0 to 4). Posterior parameters are described in the following part and in Supporting Information (Table S2).

4.2 Resources and phenotypic gender differences between densities

The modeled level of resources $R_{i,t}$ varied between years, in relation with variations in precipitation and mean temperature, and between individuals, due to variations in tree

size. The model identified a negative effect of mean temperature (α_3, posterior median [CI95%] = -0.03 [-0.06;-0.009]) and positive effects of tree diameter (α_1, posterior median [CI95%] = 0.54 [0.48; 0.59]) and precipitations (α_2, posterior median [CI95%] = 0.16 [0.14; 0.19]) on $R_{i,t}$.

The modeled level of resources $R_{i,t}$ also varied between sites, consistently with variations in tree size. The posterior median value of $R_{i,t}$ at low density was estimated at 0.03 (unitless, [CI95%] = [0.01; 0.06]) as compared to 0.014 (unitless, [CI 95%] = [0.005; 0.031]) at high density (Figure 4 a). Observed growth, $BAI_{i,t}^{\text{obs}}$ was also twice stronger at low density (median [CI95%] = 34.14 [15.2, 65.21] cm^2) than at high density (median [CI95%] = 12.57 [3.00, 26.56] cm^2). Both resources and individual residual term of resource (w_{it}) fluctuated but present more variation in low density than high density (Figure S1). Furthermore, all trees had a high probability to be reproductive in both plots (p_X, posterior median [CI95%] = 0.99 [0.96; 0.99]). There was no difference in the phenotypic gender between the two density conditions, with a median phenotypic gender $PG = 0.11[0.0037; 0.80]$ for the high-density plot and $PG = 0.11[0.004; 0.81]$ for the low-density plot (Figure 4 b).

4.3 Correlation between allocation terms

The pairwise variations in individual residual terms $\epsilon_{1,i}$; $\epsilon_{2,i}$; $\epsilon_{3,i}$ are reported in Fig. 5 (d), (e) and (f), and the posterior distribution of correlations is shown in Fig. 5 (a), (b) and (c). The estimated correlation between growth ($BAI_{i,t}$) and reproductive buds initiation ($IB_{i,t}$) was negative ($\rho_{1,2} = -0.51[-0.89, 0.15]$). The posterior probability that $\rho_{1,2}$ is negative was 0.95, clearly indicating a trade-off between growth and reproductive buds initiation (Fig. 5 a,d). Secondly, the estimated correlation between growth ($BAI_{i,t}$) and female cones survival ($p_{i,t}^{FCS}$) was not significant ($\rho_{1,3} = 0.14[-0.56, 0.77]$ with $pr(\rho_{1,3} > 0) = 0.66$, Fig. 5 b,e). Lastly, the estimated correlation between reproductive buds initiation ($IB_{i,t}$) and female cones survival ($p_{i,t}^{FCS}$) was negative ($\rho_{2,3} = -0.90[-0.99, -0.70]$, $pr(\rho_{2,3} < 0) > 0.99$), indicating a clear trade-off between bud initiation and cone survival (Fig. 5 c,f).

4.4 Density and phenotypic gender effects on individual strategies

The ANCOVA analyses did not find any significant interaction effects between the $\boldsymbol{\epsilon}$ terms and density plots. These results indicate that the correlation structure of resource allocation between the three sinks was the same for the two density plots. Furthermore, the high values of ellipse overlap areas (around 70%, see Figure S2) for all the correlation among posterior median of $\boldsymbol{\epsilon}$ in both competitor density, show that individual strategies did not differ neither in both densities. Finally, the phenotypic gender did not affect individual strategies. Indeed, probabilities to obtain a significant $P < 0.05$ between phenotypic gender (PG) and $\epsilon_{1,i}$ was equal to 28.1%, to 50.7% for $\epsilon_{2,i}$ and to 49.8% for $\epsilon_{3,i}$.

5 Discussion

In this study, we estimated the correlations between growth and several fecundity components in a coniferous tree species, using a Bayesian hierarchical model accounting for the (unobserved) level of resource and its allocation to growth and reproduction throughout the phenological cycle. Although similar models have been previously used in other species (Buoro *et al.*, 2010), this is the first time to our best knowledge that such an approach is used in tree species. It is particularly importance as the trade-offs between growth and reproduction is a main factor to predict the forests dynamics under environmental change.

5.1 Trade-offs between growth, current and future reproduction in trees

The first estimated correlation revealed a trade-off between growth and initiation of reproductive organs: trees which invest more in reproduction have a lower growth. This result was obtained while our model does not specify any hierarchy among sinks or competing resource. Hence, these results suggest that the resources allocated to growth and repro-

duction are competing in the studied system. This supports the hypotheses of resource allocation hierarchy (Wardlaw, 1990; Suzuki, 2001) or competing resource (Koenig and Knops, 1998; Martín *et al.*, 2015; Lebourgeois *et al.*, 2018).

Secondly, we did not find any significant correlation between growth and cone survival. This suggests that resources invested in growth are not in competition with resources invested in cone maturation. This is consistent with other studies reporting that high numbers of maturated cones do not impact tree growth (Cremer, 1992; Yasumura *et al.*, 2006; Żywiec and Zielonka, 2013). However, this relationship may vary among species; for instance a recent study in the European beech, *Fagus sylvatica* demonstrated that reproduction was the determinant factor of inter-annual growth variability and that years of high reproductive effort were responsible of growth reduction (Hacket-Pain *et al.*, 2018).

Lastly, we also found a clear inter-individual trade-off between buds initiation and female cones survival. This is consistent with removal experiments which demonstrated a developmental constraint between current and future reproduction (see for instance in *Pinus halepensis*, Santos-del Blanco and Climent (2014)). Other processes not considered in this study may contribute to the existence of trade-offs. Knops *et al.* (2007) mentioned nevertheless a "putative trade-off" for wind pollinated species induced by pollen limitation. During years of high precipitation, tree size increases but pollen flow and fertilization are reduced, suggesting that growth and reproductive are not linked because they use independent resources.

5.2 Evolutionary implications the observed trade-offs

Trade-offs among sinks were identified in this study by the use of individual random effects, which integrate the genetic and plastic variation among individuals in traits involved in growth and reproduction. In the studied system, Cedar trees displayed different strategies in terms of resource allocation (e.g., some individuals allocated resources preferentially to growth an others to reproduction pool), while they had the same age and similar climatic conditions. Among-individual variations in individual strategies of quantitative allocation of energy are expected to affect population dynamics, such as growth and stability of

the population (Bjørnstad *et al.*, 1994; Bolnick *et al.*, 2011). Moreover, the principle of allocation Cody (1966) assumes that an organism has a certain limit of available energy for expenditure and that genotypes optimizing allocation are positively selected. In this view, the coexistence of several individual strategies of quantitative allocation of energy is expected to be either a transient state towards fixation of the best strategy, or to indicate that several strategies optimize fitness (Harper and Odgen, 1970; Fridley, 2017; Bontemps *et al.*, 2017). However, interpreting the trade-offs observed in this experiment is difficult without detailed knowledge of genotypic variation, because both individual plasticity and genetic variation can be involved in the patterns of correlation (Stearns, 1989). In this study, all of the estimated correlations were not affected by competitor density, suggesting that the level of competition may affect the level resource acquisition but not strategies of resource allocation.

In the studied system, Cedar trees were also systematically male-biased, contrary to a previous study suggesting the existence of male or female individuals (Krouchi *et al.*, 2004). Allocation to male function in plants is expected to require a lower amount of resources (Elmqvist *et al.*, 1991; Obeso, 2002). Based on this hypothesis, we expected more males to be produced at higher density, due to the lower level of resources per individual. However, both low and high density plots were found to be male-biased, and this appears relatively constant across years. Even if the low-density plot tends to produce more female cones, they also produced more pollen. These results are consistent with (Ne'eman *et al.*, 2011) study for which *Pinus halepensis* growth is accompanied by an increase in male biased sex allocation. Moreover, we did not detect any significant effects of phenotypic gender on the correlations among growth and reproductive sinks. Individuals that initiated more buds (or individuals that maturated more cones) were not more male (or more female).

In this study, individual strategies of resource allocation were assumed to be constant among years. However, longer time-series could be used to investigate the evolution of trade-offs by taking in account among-year variation of resource allocation for a given individual, to investigate the evolution of trade-offs, particularly in response to climate

change.

5.3 The advantages of explicitly modelling resources

A main advantage of the hierarchical Bayesian model used in this study is to account explicitly for the unobserved level of resource, through a latent variable ($R_{i,t}$). Although we were unfortunately unable here to measure proxys of the resources available and validate the model, the estimated resource patterns were nevertheless consistent with biophysical and ecophysiological expectations.

In particular, the model accounted well for the differences of resource levels between plots at different competitor densities, even though the model did not included any specific parameter to discriminate resources levels among plots. Higher level of resources per individual were estimated for the low density plot, consistently with the reduced competition. Consequently, increase of thinning intensity improves resource availability and tree growth (Guillemot *et al.*, 2015).

Our hierarchical model also detected positive effects of precipitation with tree size and negative effect of temperature on resources. Consistently with past studies, summer climate and tree size are main drivers resource pool. Indeed, bigger individuals can accumulate more resources, and precipitations increase the amount of resource, which is consistent with the fact that the duration of drought strongly determines growth in Mediterranean type trees (Linares *et al.*, 2013; Lempereur *et al.*, 2015). The negative effect of temperature on resource is also due to drought or direct effect of heat wave on growth. Drought stress are also known to directly impact ecosystem productivity at a larger scale (Kljun *et al.*, 2007).

Globally, resources enhanced both growth and reproduction, but our model can not estimate quantitatively if resource are more important for growth or reproduction. This is one of the limitations of our approach, as many studies have demonstrated a direct impact of drought on reproduction (Pérez-Ramos *et al.*, 2010; Bykova *et al.*, 2018; Bogdziewicz *et al.*, 2017; Oddou-Muratorio *et al.*). In this model, resource is a black-box which integrates climate and competition effects, where tree size combines density effect and individual

variation. Beyond this black-box, resource is refereed here as energy and nutrients and can combine several things as for example water, light, carbon, nitrogen, hormones, etc.

5.4 Resource modelling and their allocation scheme

Our results suggest that trade-offs between traits can be detected if resources are explicitly considered and modeled. Based on the model from van Noordwijk and de Jong (1986), we modeled the level of resource acquisition and their allocation to growth and reproductive sinks, and revealed the existence of trade-offs between growth and reproduction, and between current and future reproduction. Importantly, these trade-offs emerged from the estimation, without any constraints on resource allocation included in the Bayesian model. This is not the case of other models integrating more precisely the mechanisms driving resource acquisition and allocation, such as Dynamic Energy Budget model (DEB) or Resource Budget model (RBM). In DEB models for instance, reserves used for growth can not be used for increasing maturation or reproduction, even though direct competition occurs only among reserves used for building structure versus paying maintenance costs (Kooijman, 2009). In RBM models, resources are allocated to reproduction only when they exceed a threshold (Isagi *et al.*, 1997). Indeed, RBM models consider that plants cannot have high fruit production during several years due to resource depletion (Crone and Rapp, 2014). Our results support the modeling choice used in DEB and RBM models, and suggest that modeling explicitly the variation of resource partitioning between growth and reproduction across the phenological cycle could improve these models.

We also found here that accounting for reproductive phenology, which determines the timing of resource allocation, can improve the estimation of trade-off among growth and reproductive sinks, and can highlight the idiosyncratic patterns of correlations observed in trees so far. Indeed, the sign of the correlation between growth and fecundity can differ depending of the reproductive stage (initiation or maturation). Process-based models can be useful tools to investigate reproductive and growth sinks, because they integrate species behavior through their ecophysiological characteristics, and can also combine them to reproductive phenology. However, processes involved in tree reproduction are not well

understood and most models assume a constant fraction of resource for reproduction (Vacchiano *et al.*, 2018). Further improvements of resource allocation are needed to understand how trees growth and reproduction respond to climate change.

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7 Author Contribution

F.L., H.D. & V.J. initiated the idea. F.L & F.C. provided experimental data. J.P. & E.W. designed the Bayesian model with advice from all authors. V.J., E.W. and J.P. ran simulation. V.J. started the redaction with improvement from all the authors.

8 Data accessibility statement

Data used and hierarchical Bayesian model code will be available from the Dryad Digital Repository.

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9 List of Tables and Figures

9.1 Tables

Table 1: Summary posterior predictive check. For growth and female cone number we reported Bayesian p-values with a value at 0.5 for a perfect fit. For male notation, we reported the Brier score with median and 95%CI, with value closed to 0 for correct fit.

Observed variable	**Bayesian posterior p-value**
Growth ($BAI_{i,t}^{\text{obs}}$)	0.36
Female cone number ($FC_{i,t}^{\text{obs}}$)	0.60

Observed variable	**Brier score**
Male notation ($IMC_{i,t}^{\text{obs}}$)	
note 0	0.15 [0.12; 0.18]
note 1	0.08 [0.08; 0.09]
note 2	0.11 [0.10; 0.12]
note 3	0.08 [0.07; 0.09]
note 4	0.05 [0.03; 0.09]

Table 1

9.2 Figures

Figure 1: Overview of the reproductive and growth cycle of *Cedrus atlantica*. Male reproduction and growth is carry on in one year. The duration of female reproduction is longer, when the fecundation and the maturation of female cone start the next year after the cone apparition.

Figure 2: Observation data of female cone and growth from both density. Mean value with standard deviation of female cone number ($FC_{i,t}^{\text{obs}}$) and mean growth increment ($BAI_{i,t}^{\text{obs}}$, refereed here as BAI or Basal Area Increment in $\text{cm}^2\,\text{year}^{-1}$) for each individuals. Blue color is for high density (1200 $\text{stems}\,\text{ha}^{-1}$) and red for low density plot (250 $\text{stems}\,\text{ha}^{-1}$).

Figure 3: Graphical representation of Bayesian hierarchical model used with the process

and data model. Right angles boxes represent observed variables and elliptic boxes represent unobserved variable (i.e. latent variables). We represent the previous year (t-1) in gray color and current year (t) in black color. Resources are simulated with a relationship between tree diameter ($DBH_{i,t}$), sum of precipitation ($RAIN_t$) and mean temperature ($Tmean_t$). Resources are then allowed for radial growth ($BAI_{i,t}$) and reproduction, which initiates buds ($IB_{i,t}$). Buds differ then between male ($IMC_{i,t}$) and females ($IFC_{i,t}$) according to phenotypic gender (no presented in the figure, $PG_{i,t}$). According to the data model, males cones is achieved during the same year ($M_{i,t}$). Females cones maturation is finally achieved with resources produce next year and are presented with the red box ($FC_{i,t}$). Note that these future resource are also allowed for growth, male production and future female cones initiated.

Figure 4: Estimation of resources and phenotypic gender from the Bayesian model. (a) Boxplot of resources (unitless) estimated with the Bayesian process model for both density and years (b) Boxplot of phenotypic gender estimated for both density and years, ranging in y-axis from maleness (0) to femaleness (1). For both graphics, red color is for the low density (250 stems ha^{-1}) and blue for the high density plot (1200 stems ha^{-1}).

Figure 5: Correlation among sinks. (a) Density plot of $\rho_{1,2}$ correlation is negative (b) Density plot of $\rho_{1,3}$ correlation is non significant (c) Density plot of $\rho_{1,2}$ correlation is negative. The red line represent the median value for these three graphics. (d) Negative correlation between growth (ϵ_1) and number of buds initiated (ϵ_2) (e) Non significant correlation between growth (ϵ_1) and female cone survival (ϵ_3) (f) Negative correlation between number of buds initiated (ϵ_2) and female cone survival (ϵ_1). Dots represent individual values, with red color for low density and blue for high density. Regression are presented for both densities, with their confidence intervals. Dashed line for non significant correlation.

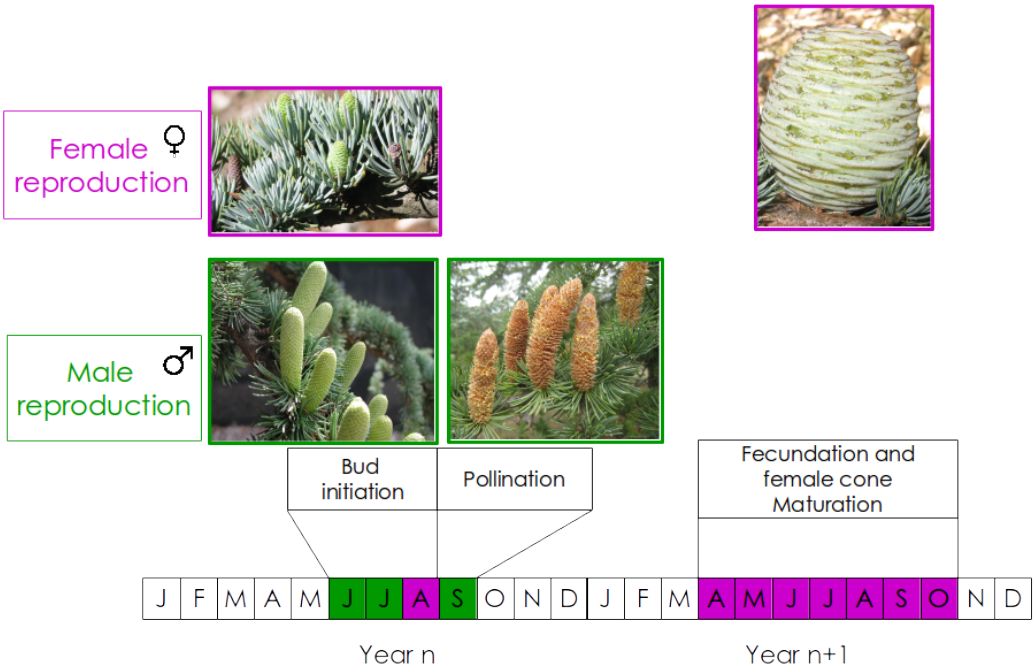
Female ♀ reproduction
Male ♂ reproduction
Bud initiation
Pollination
Fecundation and female cone Maturation
J F M A M J J A S O N D J F M A M J J A S O N D
Year n
Year n+1

Figure 1

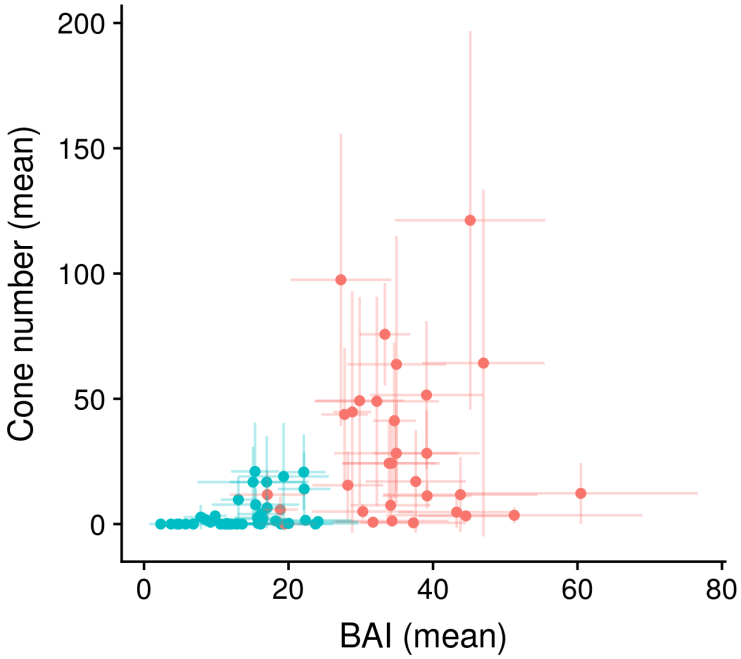

Figure 2

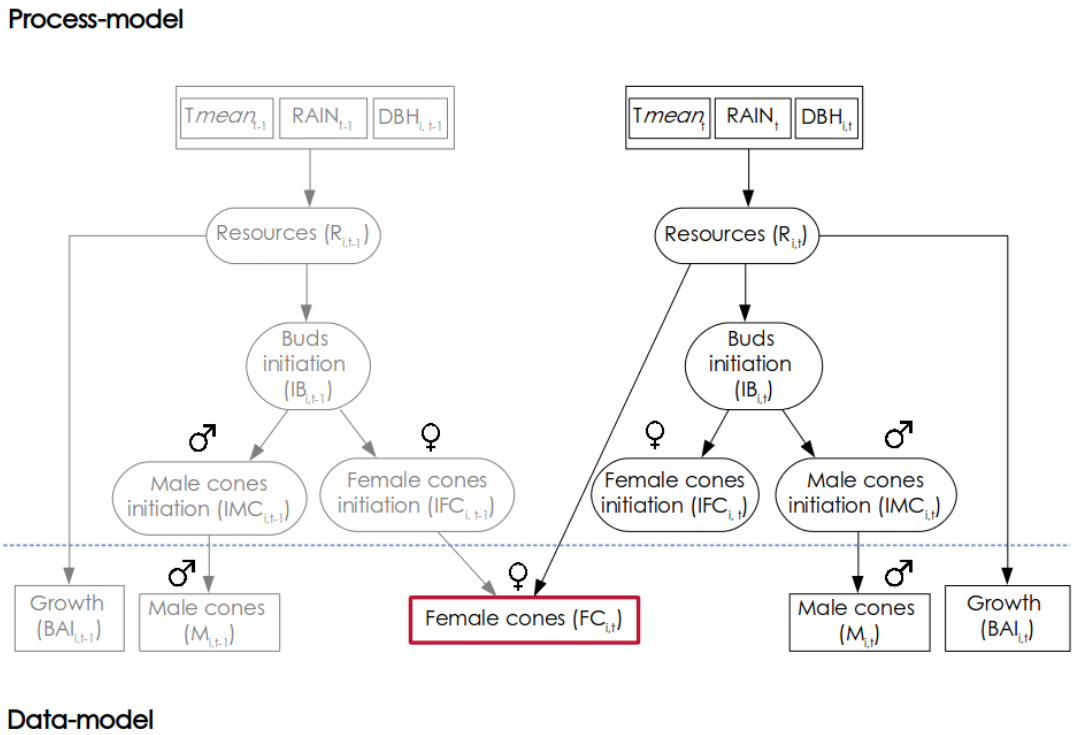
Process-model
Tmean t-1
RAIN t-1
DBH i, t-1
Resources (R i,t-1)
Buds initiation (IB i,t-1)
Male cones initiation (IMC i,t-1)
Female cones initiation (IFC i, t-1)
Growth (BAI i,t-1)
Male cones (M i,t-1)
Female cones (FC i,t)
Tmean t
RAIN t
DBH i,t
Resources (R i,t)
Buds initiation (IB i,t)
Female cones initiation (IFC i, t)
Male cones initiation (IMC i,t)
Male cones (M i,t)
Growth (BAI i,t)
Data-model

Figure 3

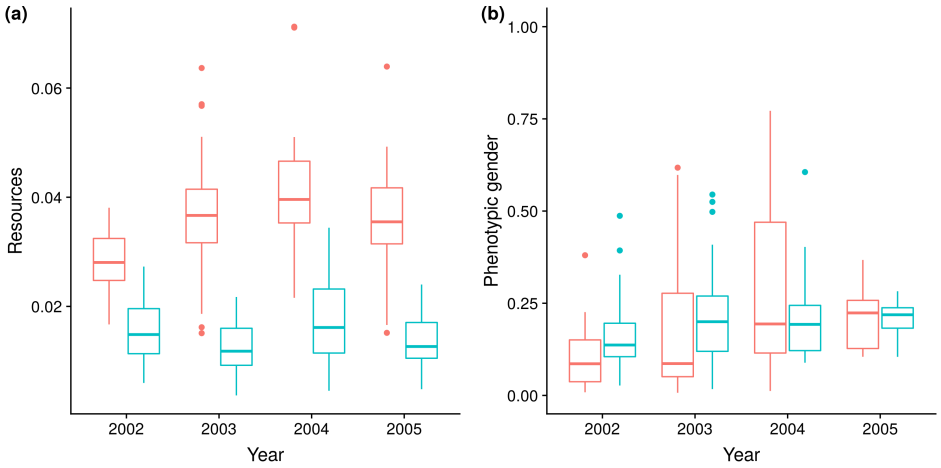
(a)
Resources
0.06
0.04
0.02
2002
2003
2004
2005
Year
(b)
Phenotypic gender
1.00
0.75
0.50
0.25
0.00
2002
2003
2004
2005
Year

Figure 4

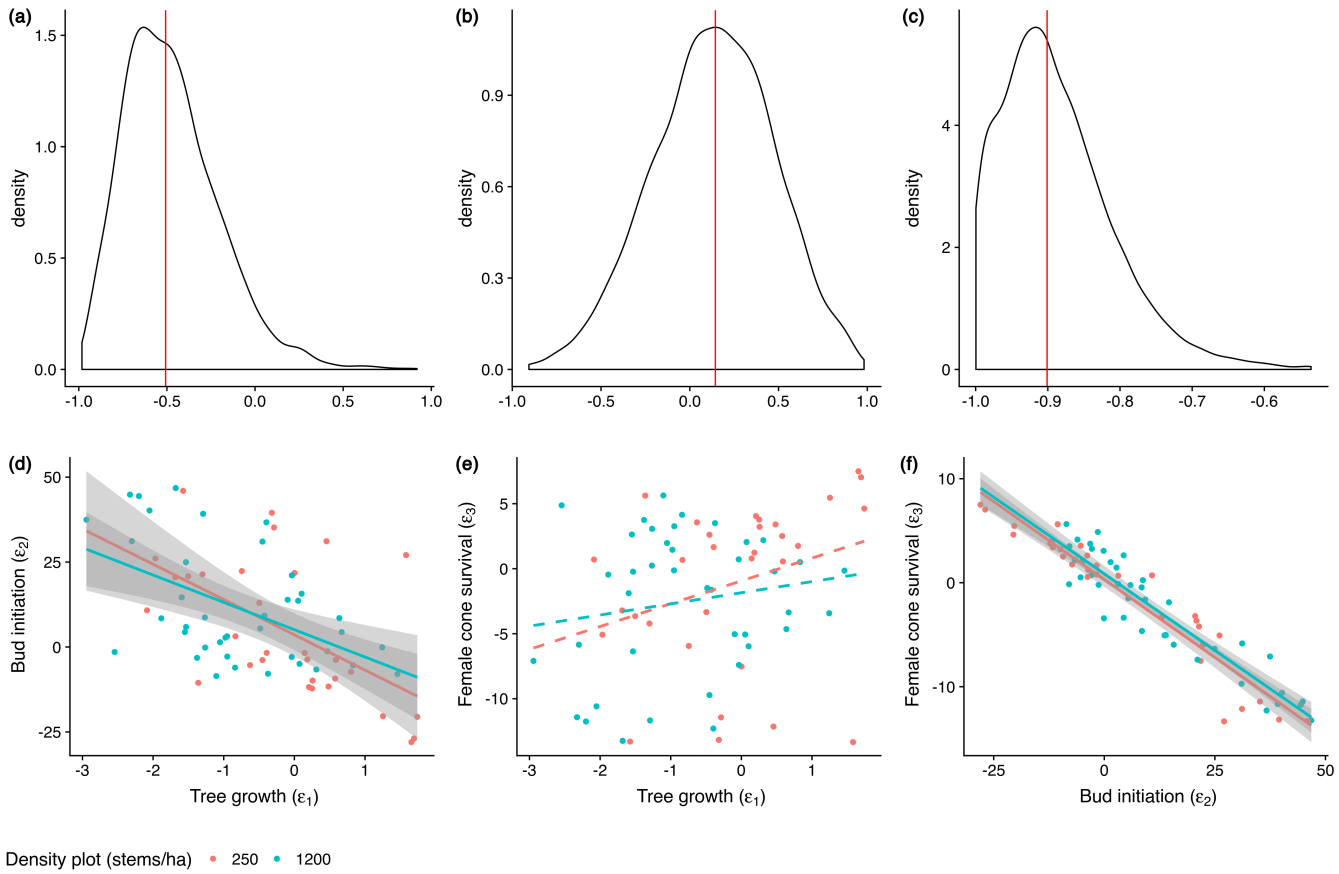
(a)
(b)
(c)
density
(d)
(e)
(f)
Bud initiation (ε_2)
Female cone survival (ε_3)
Tree growth (ε_1)
Bud initiation (ε_2)
Density plot (stems/ha)
250
1200

Figure 5

Supporting Information

Article title: A hierarchical Bayesian resource model to investigate trade-offs between growth and reproduction in a long-lived plant

Authors: Valentin Journé, Julien Papaïx, Emily Walker, François Courbet, François Lefèvre, Sylvie Oddou-Muratorio, Hendrik Davi

Table S1: Prior distribution definition or fixed values
Table S2: Summary of posterior distribution for remaining parameters.
Fig. S1: Variation among year and density of $w_{i,t}$.
Fig. S2: Ellipse area for three correlation.

Parameters	**Prior distribution**
α_0	$\alpha_0 \sim \mathcal{N}(0, 0.001)$
α_1	$\alpha_1 \sim \mathcal{N}(0, 0.001)$
α_2	$\alpha_2 \sim \mathcal{N}(0, 0.001)$
α_3	$\alpha_3 \sim \mathcal{N}(0, 0.001)$
PG	$PG \sim \mathcal{N}(0, 0.001)$
β_1	$\beta_1 \sim \mathcal{U}(0, 10000)$
β_2	$\beta_2 \sim \mathcal{U}(0, 10000)$
p_X	$p_X \sim \mathcal{U}(0, 1)$
λ	$\lambda \sim \mathcal{U}(0, 10000)$
σ_{PG}	$\sigma_{PG} = 1/\sigma^2$ with $\sigma \sim \mathcal{U}(0, 10)$
Σ	$\Sigma \sim \mathcal{W}(Id3, 4)$
γ	$\gamma = 1000$
β_0	$\beta_0 = -10$

Table S1: Description of prior distribution. $\mathcal{N}$ for $Normal$ distribution, $\mathcal{U}$ for $Uniform$ distribution and $\mathcal{W}$ for the inverse $Whishart$ distribution

Parameters	**Median and CI values**
α_0	-3.88 [-3.94; -3.82]
β_1	880.8 [580.0; 1193.3]
β_2	501.9 [390.8; 729.5]
λ	8.01 [4.22; 21.74]

Table S2: Summary of posterior distribution (medians and credible intervals) for parameters used in our model.

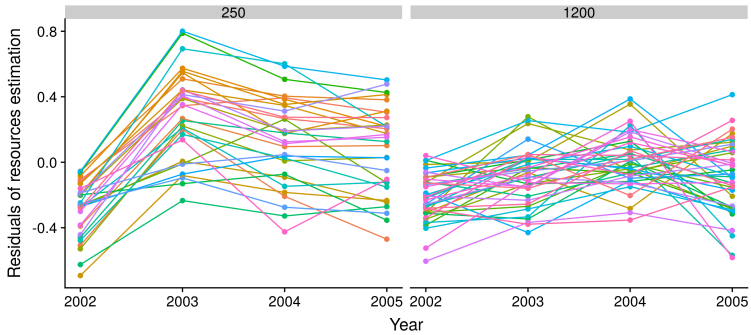

Figure S1: Variation of residual term of resource estimation (w_{it}). Individual values for each year and it covariation among years. These variations are presented for low and high density plots.

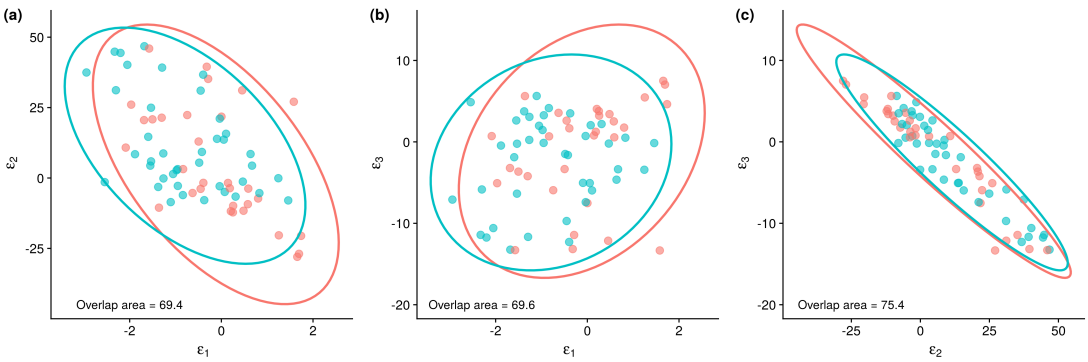

Figure S2: Ellipse area for high density (blue) and low density (red) for each three correlation. (a) Negative correlation between growth (ϵ_1) and number of buds initiated (ϵ_2) (b) Non significant correlation between growth (ϵ_1) and female cone survival (ϵ_3) (c) Negative correlation between number of buds initiated (ϵ_2) and female cone survival (ϵ_1). Dots represent individual values, with red color for low density and blue for high density. Overlap area in percent is indicated for each correlation

3 Synthèse et Discussion

Dans cette étude, nous avons estimé les relations entre croissance et reproduction en utilisant un modèle bayésien hiérarchique, qui intègre les ressources et l'allocation entre les deux puits. Nous avons démontré, chez le Cèdre de l'Atlas, un compromis entre croissance et la production de bourgeons reproducteurs. Des individus qui produisent beaucoup de bourgeons reproducteurs sont aussi des individus qui grossissent moins et réciproquement. Nous avons aussi trouvé un compromis entre survie des cônes et production de bourgeons. Des individus qui investissent beaucoup dans l'initiation des bourgeons sont aussi des individus qui produisent moins de cônes matures. Cependant, nous n'avons pas trouvé de corrélation significative entre croissance et survie des cônes. Ces différentes corrélations ne changent pas quand le niveau de compétition change, et ne sont pas dues à de potentiels biais sexuels et à des différences entre les individus plutôt mâles ou femelles (Krouchi et al., 2004). La modélisation des ressources et leurs variations spatiales et temporelles pourrait être améliorée en s'inspirant d'autres modèles tels que les Resource Budget Models (RBMs), pour mieux tenir compte des contraintes sur l'allocation entre les puits de croissance et de reproduction (Isagi et al., 1997).

De plus il pourrait être intéressant d'avoir une meilleure estimation de la ressource, qui dans notre étude est estimée par une régression entre le climat et la taille de l'individu. Par exemple des modèles écophysiologiques, qui intègrent à la fois les caractéristiques du site, de l'espèce et des individus pourraient permettre d'avoir une meilleure estimation de la ressource. Nous avons commencé à développer une version du modèle écophysiologique CASTANEA pour le Cèdre. Nous avons une version assez satisfaisante du modèle pour le moment, avec des croissances simulées bien corrélées sur les deux placettes (Figure IV.1).

Une des perspectives sera d'utiliser les ressources simulées par CASTANEA, tel que la productivité primaire nette (*Net Primary Productivity*, NPP) et comparer les sorties que nous avons avec le modèle bayésien hiérarchique (Figure IV.2). Cependant, une intégration directe de la reproduction au sein du modèle CASTANEA permettrait d'intégrer les effets des différents événements climatiques, mais aussi de tester des hypothèses d'allocation des ressources lors de la reproduction.

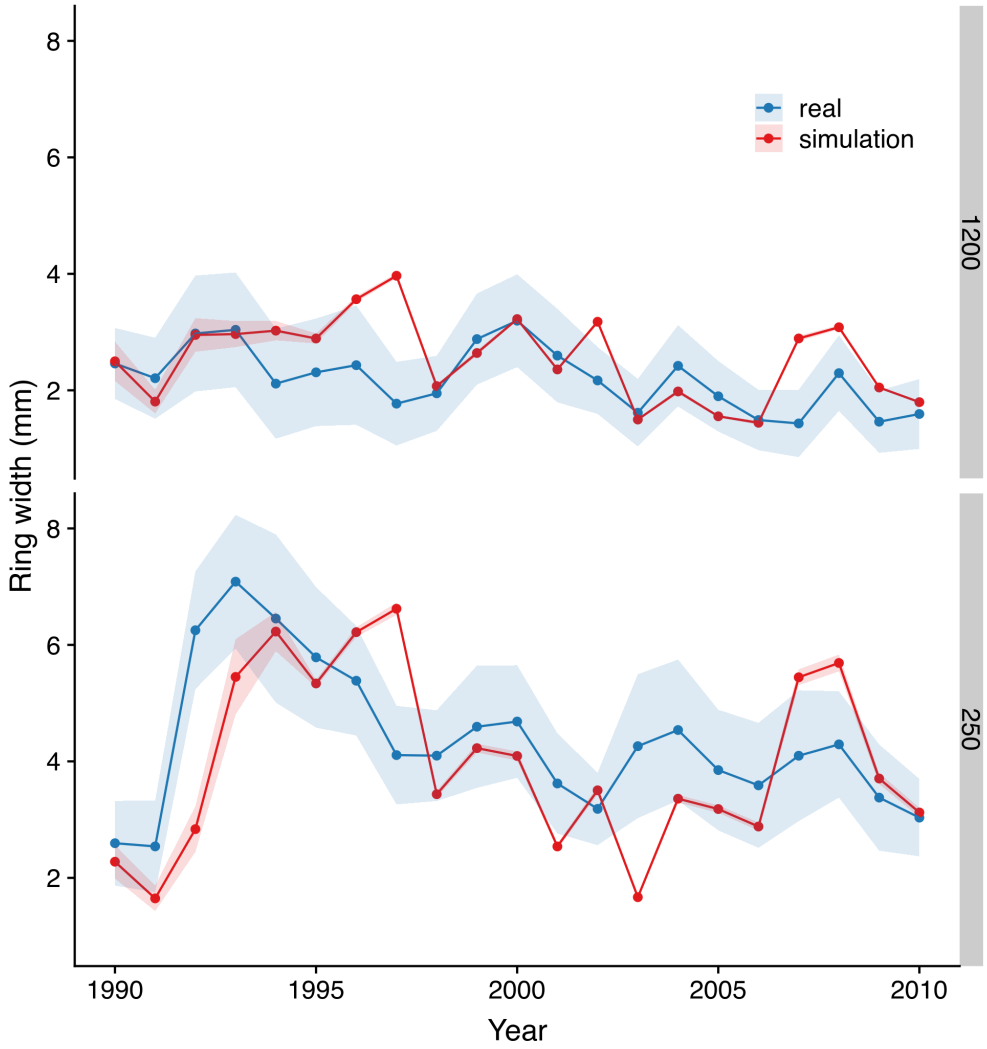

Figure IV.1: Simulation de la croissance moyenne des placettes avec le modèle CASTANEA (rouge pour les simulations et bleu pour les observations) de 1990 à 2010 pour le Cèdre (Site Sault) à l'échelle individuelle. Pour la faible densité (250 ind.ha^{-1} en bas) ; RMSE = 1.34, Pearson Correlation Coefficient (PCC) = 0.56. Pour la forte densité (1200 ind.ha^{-1} en haut) ; RMSE = 0.76, PCC = 0.42.

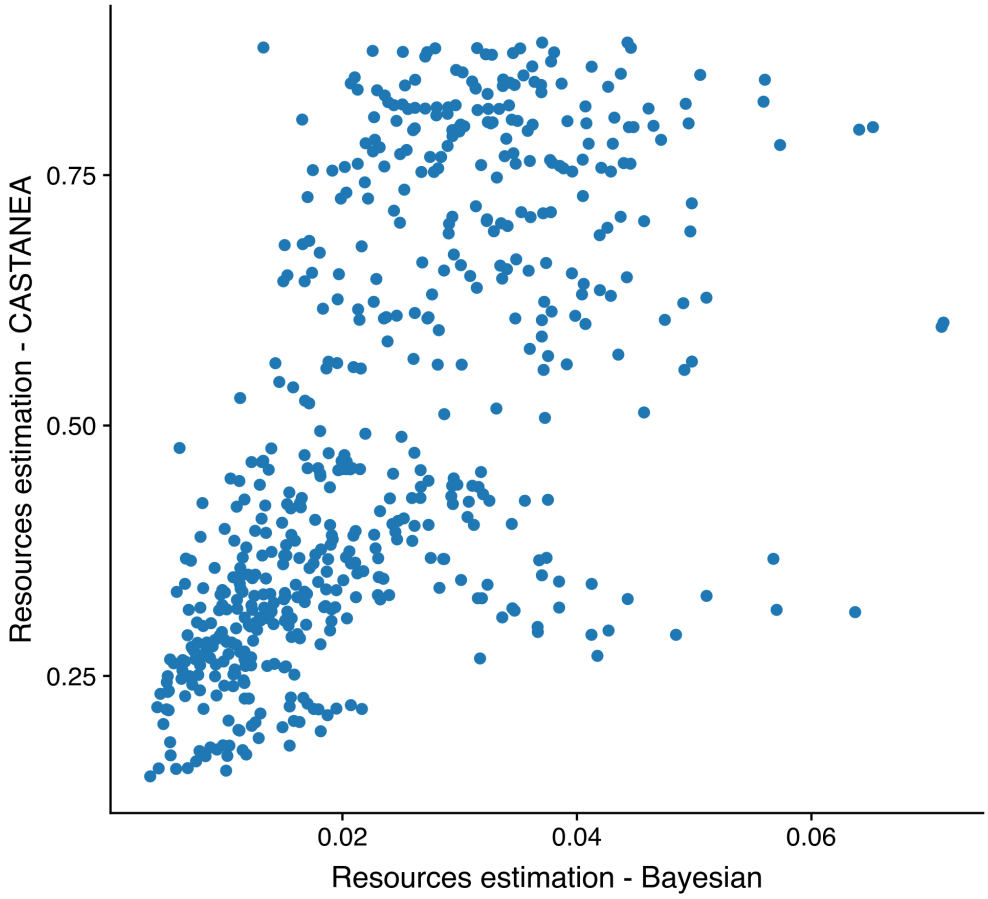

Figure IV.2: Comparaison des ressources entre CASTANEA (NPP normalisée) et le modèle bayésien hiérarchique (P<0.001 ; R2 = 0.39).

Chapitre V

Allocation des ressources lors de la reproduction à l'aide d'un modèle écophysiologique

1 Contexte

L'utilisation de modèle prédictifs pour anticiper les effets du changement climatique sur la biodiversité est devenue une approche majeure en écologie (Mouquet et al., 2015). Pour les forêts, l'utilisation de modèles peut ainsi améliorer notre compréhension des déterminants de la dynamique des forêts et leur sensibilité au climat, mais aussi permettre la projection dans le futur de l'état des forêts suivant divers scénarios de changement climatique (Prentice et al., 2007). Plusieurs modèles mécanistes ont été développés, intégrant la croissance et la survie des arbres. Cependant, la formalisation de la reproduction dans les modèles mécanistes reste parfois simpliste, voir absente (Vacchiano et al., 2018). Or, la reproduction des arbres est une composante majeure, impactant la dynamique des populations, ainsi que les interactions entre espèces (Clark et al., 2019). De plus, les conséquences du changement climatique sur les processus liés à la reproduction ne sont pas tous très bien connus. Nous avons ici étendu le modèle écophysiologique CASTANEA pour simuler la reproduction des arbres, et plus spécifiquement la quantité de biomasse de fruits produite par unité de surface au sol. Le nouveau modèle simule l'allocation du carbone à la reproduction, de l'initiation des bourgeons, jusqu'à la maturation des fruits, en tenant compte de la phénologie et des effets de sécheresse et de gelées sur les fruits. Nous avons utilisé ce modèle sur le Sapin pectiné (*Abies alba*) en région méditerranéenne, où nous disposons d'observations de phénologie, de croissance et du nombre de cônes. Après l'étape de calibration-validation du modèle, nous avons utilisé une analyse de sensibilité pour identifier les paramètres les plus sensibles de notre modèle, avant de prédire la production future de cônes dans la région.

Ce projet a été amorcé en 2017, suite à la connexion avec le modèle de phénologie, puis repris en décembre 2018. L'article est en préparation pour une soumission à *Ecological Modelling*.

2 Resource allocation to reproduction in forest trees : an ecophysiological model to predict cones production for silver fir (*Abies alba*)

Auteurs : Valentin Journé, Isabelle Chuine, Sylvie Oddou-Muratorio & Hendrik Davi
Mots-clés : *Abies alba*, allocation du carbone, CASTANEA, PHENOFIT, modèle basé sur les processus, reproduction, réserves

Resource allocation to reproduction in forest trees: an ecophysiological model to predict cones production for silver fir (*Abies alba*)

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Highlights

- We updated an ecophysiological model by integrating fruit and seed production
- Fruit production depends of the quantity of resources and phenology events
- The model is used for a coniferous species under current and future climate scenario
- The model partially simulated temporal variation of fruit and seed production

Summary

Tree reproduction is a major process impacting population dynamics and species interactions. However, predicting the response of tree reproduction face to ongoing climate change is still challenging. In this study, we improved and used a process-based model, CASTANEA, to simulate fruits production at stand scale. We implemented a reproductive module that simulates phenology of reproductive structures, carbon allocation to buds and seeds depending on both sources and sinks dynamics, and abortions of the reproductive buds. The number of initiated buds depends on the level of carbohydrates resources, following the accumulation of resources hypothesis. We then model each of the phenological events of the reproduction and determine the temporal growth curves of the fruits or cones. We applied this model to a coniferous species, Silver fir (*Abies alba*), to a population located in the Mediterranean region. We calibrated the model across an elevation gradient and validated the model with a 10 years reproduction data-set. We found that the model was able to partially simulate temporal variation of cone production. However, it was not possible to reproduce both mean cone production and all the masting years. The level of reserves is maybe not the only factor explaining variation of the initiated buds and other mechanisms must be investigated to explain masting patterns.

Keywords: *Abies alba*, carbon allocation, CASTANEA, PHENOFIT, process-based model, reproduction, reserves

1 Introduction

The increasing awareness that ongoing climate change may jeopardize the abilities of major tree species to growth, survive and reproduce has fostered the development of predictive ecology approaches. Theses approaches are used to better understand the determinants of forest dynamics and functioning and their sensitivity to climate, and also to forecast possible futures for forest under climate change scenarios (Makela et al., 2000; Prentice et al., 2007). Different models have been developed by different scientific communities to address different issues, but a better integration of these efforts is required for improving the predictive power of models. While the processes of growth and survival have been the subject of numerous developments, the reproduction process received less attention. Yet, sexual reproduction, a major process of tree population dynamics, determines forest regeneration and species composition of forest communities at ecological timescale, and the abilities of species to adapt to changing environmental conditions at evolutionary timescale.

Four different types of process-based models (PBMs) incorporate reproduction with variable levels of detail (Table 1). First, reproduction is one of the key processes incorporated in forest dynamic models (e.g. gap models, see review example in Bugmann 2001) to simulate forest succession and species diversity from stand to landscape scale. A major strength of some of these models is to represent the different processes shaping tree regeneration, from seed production to seed dispersal and seedlings establishment and survival, and to combine them with growth and mortality processes across the whole tree life cycle. Second, Resource Budget Models (RBMs, (Satake and Iwasa, 2000; Crone and Rapp, 2014) have been specifically developed to represent the processes driving fruit and seed production and to understand the determinants of masting patterns (i.e., the spatio-temporal variation in the amount of seed produced). The major strength of RBMs is their generality, which allows them to investigate different evolutionary or ecological theoretical hypotheses that could explain masting (Pearse et al., 2016). However, a general limitation of both forest dynamic models and RBMs is that they do not explicitly account for the effect of climatic variation on the resources available for reproduction and tree phenology.
Third, some physical and ecophysiological PBMs, called Dynamic Vegetation Models (DVMs)

include a representation of reproduction. These models explicitly link together the physical and physiological processes such as radiative transfer, evapotranspiration, photosynthesis, respiration or carbon allocation to simulate biogeochemical cycles (water, carbon and nitrogen fluxes) between the canopy, the atmosphere and the soil (Prentice et al., 2007). Different DVMs have been proposed to simulate forest functioning, from detailed stand-scaled DVMs accouting for species ecophysiology (see review example in Le Roux et al. 2001), to forest ecosystem models at global scale with a plant functional type representation (e.g. Dynamic Global Vegetation Model, see review example in Prentice et al. 2007). The major strength of these DVMs is their ability to simulate the physiological responses of tree, growth and mortality in response to climate variation at fine ecological timescale. However, most of them include a very simplistic representation of resource allocation to reproduction (Vacchiano et al., 2018).

A last category of PBMs aim at simulating survival and reproductive success as a function of pedoclimatic daily variables and the aggregation of different functional traits: phenological traits, frost and drought resistance. They have been mainly used to simulate tree species distribution (PHENOFIT, Chuine and Beaubien 2001). The specificity of such PBMs is to account for both vegetative and reproductive phenologies and resistance to abiotic stresses, which play a major role in reproductive success and overall plant fitness (Morin et al., 2007; Duputié et al., 2015). Indeed, phenology determines the length of the fruit maturation period, and mediates the effect of stressing meteorological conditions, such as frost and drought, which can limit seeds and fruits production either by stopping the resource allocation or by destroying the reproductive organs (Chuine, 2010; Pearse et al., 2016; Bogdziewicz et al., 2017, 2018). However, such models simulate a relative reproductive success and not the number of seed or fruits produced each year because they do not integrate carbon (and other nutrients) allocation to reproductive organs.

The objective of this study is to improve the DVM CASTANEA (Dufrêne et al., 2005) to simulate tree reproduction, in term of fruit biomass, and its impact on growth and survival. Indeed, existing DVMs have several well-known limitations to represent reproduction, beginning with the modelling of resource allocation to growth and reproduction. For instance, the literature recurrently reports the weak abilities of DVMs to simulate forest growth accurately

(Cramer et al., 2001; De Kauwe et al., 2014). Uncertainties in carbon allocation scheme are suspected to be responsible for the weak accuracy of predictions of forest growth (see for examples; Babst et al. 2013; Guiot et al. 2014) and inter-annual Net Primary Productivity (NPP, see for example; Collalti et al. 2016), leading to unrealistic futures predictions (Gea-Izquierdo et al., 2017). While the links between NPP and radial growth tend to become better documented, allocation to reproductive structures remains one of the least advanced fields of research, at least for forest trees (but see Grossman and DeJong 1994 for fruits trees). Some DVMs consider that allocation to reproduction depends on the level of carbon reserve, such that reproduction occurs only if enough resources remains after allocation to other compartments. The threshold level of reserve is often based on Non Structural-Carbohydrates (NSC) concentrations (e.g. PDG model, Oddou-Muratorio and Davi 2014, TREEDYN model Bossel 1996, KM2000 model Kleidon and Mooney 2000) or on NPP (e.g. SEIB-DGVM, Sato et al. 2007). Alternatively, other DVMs consider that reproduction occurs every year with a constant fraction of resources allocated to reproduction (e.g. Moorcroft et al. 2001; Sitch et al. 2003; Krinner et al. 2005). Improving the modelling of carbon allocation is thus likely to benefit the predictions of a large number of variables, such as productivity, tree growth and reproduction (Le Roux et al., 2001). For example, it has been argued that lagged effects observed in tree growth could be due to drought events (Anderegg et al., 2015), but also to changes in resource allocation schemes responsible for trade-offs between growth and reproduction (Hacket-Pain et al., 2018).

Another limitation of DVMs lies in the simplified representation of the reproductive phenology, from initiation of flowers to fruit maturation. The phenology of reproductive organs is usually tightly coupled to the phenology of vegetative organs, first because lots of forest trees have mixed buds containing both flowers and leaves, second because fruits and seed growth depend on carbohydrates produced by nearby leaves in normal conditions (Hoch, 2005; Hoch et al., 2013; Delpierre et al., 2016). Reversely, the phenology of reproductive organs has an impact on the seasonal dynamics of carbon allocation scheme within the tree, since it determines the periods of cell multiplication and growth, and carbohydrates accumulation in the fruits and seeds (Delpierre et al., 2016), and also on the temporal dynamics of their respiration costs (Koppel et al., 1987). In

forest tree species, factors and mechanisms involved in flower initiation versus fruit maturation differ (Han and Kabeya, 2017). In temperate trees, reproduction usually spreads over two years, from bud initiation which takes place in summer to final fruit production with occurs in autumn of the next year (Fig. 1). According to RBMs, flower buds production occurs when plants have built up enough resources (Satake and Iwasa, 2000). Resource depletion due to both flowering and fruit production can then impact the initiation of new buds and the reproduction of the next year (Satake and Iwasa, 2000; Wiley et al., 2017). Stored NSC can to be used at the beginning of fruit growth, when leaves are not fully matured, otherwise, carbohydrates accumulated in the fruits come preferentially from nearby leaves (Hoch et al., 2013; Ichie et al., 2013). Carbon is the principal limiting nutrient for fruit growth, whereas nitrogen seems rather limiting flower buds production (Hoch et al., 2013; Ichie et al., 2013; Miyazaki et al., 2014; Igarashi et al., 2019).

In this paper, we present an augmented version of the DVM CASTANEA (Dufrêne et al., 2005; Davi et al., 2005; Davi and Cailleret, 2017) aiming at simulating fruit set and growth of forest trees on a yearly basis depending on the climatic conditions. In this new model, we refined the carbon allocation sub-model by including a new compartment representing the reproductive structures, and we modelled the processes related to this compartment from bud initiation to fruit maturation. This was achieved by adding some components (phenology and frost resistance) from the PHENOFIT model to CASTANEA within the CAPSIS plateform. We also explicitly modelled the effects of drought on fruit production. The model was calibrated and validated for a population of the coniferous species, *Abies alba* in Southern France, based on observations of ring width, phenology and cone production. Using this model, we ran a sensitivity analysis to identify which parameters or processes are the most likely to drive temporal variations in fruit production (including masting). Finally, we illustrate how this new model can be used to predict future fruit set and understand possible reproduction failure.

2 Material and Methods

2.1 General overview of CASTANEA model

To develop our new model, we took advantage of the community modelling platform CAPSIS (Dufour-Kowalski et al., 2012), which hosts several forest dynamics models and library of processes, including the CASTANEA and PHENOFIT libraries. The CASTANEA library available in CAPSIS corresponds to an updated version of the DVM CASTANEA, originally developed to simulate water and carbon fluxes in forest ecosystems (Dufrêne et al., 2005; Davi et al., 2005, 2009). Different physiological processes are modelled at a temporal scales ranging from hour to years for monospecific stands, with more than 100 species-sites parameters. The original CASTANEA model considers an average tree, represented by six compartments: leaves, branches, stem, reserves, fine roots and coarse roots. Climate variables, species and site parameters drive carbon acquisition, and respiration of the tree. Then, CASTANEA can simulate forest productivity (NPP), and tree growth (tree ring increment). To run the simulations, the model needs daily climate data, with temperature, solar radiation, precipitations, wind speed and relative humidity. Other updates information of the model are present in the article from Davi and Cailleret 2017 and Petit-Cailleux et al. 2019

2.2 The new CASTANEA model with reproduction

Here, we connected the CASTANEA library to part of the PHENOFIT model (which is based on the PHELIB library) to simulate leaf and flower phenology processes, as well as dynamic frost hardiness of these different organs. We also included a new reproductive carbon compartment for buds and fruits in the CASTANEA library (Figure 2). The new model include 16 new species-specific parameters (Table 2). Site characteristics values are presented in the site description and are reported on <ZENODO link>.

We modelled all the stages of reproduction from buds initiation to fruit maturation, accounting for the reproductive phenology and carbon allocation to reproduction at each stage. We included in the carbon allocation sub-model of CASTANEA a new carbon pool representing the

reproductive structures with three new state variables: the numbers of flower buds, fruits and seeds. Our first hypothesis is that the number of flower buds is determined by the resources, here the level of reserves. The second hypothesis is that allocation to reproductive structures takes priority over the growth of wood and roots, as it is already the case in CASTANEA for the leaves. Consequently, after their initiation, the growth of the reproductive organs is largely determined by the dynamics of the reproductive sink, which is itself controlled by its phenology and its own growth rules.

We detail hereafter the different stages of this new carbon allocation model, working at a daily time step (Fig. 1).

2.2.1 Carbon allocation to a potential maximal number of buds

For the first stage, we modelled the potential number of vegetative buds (Pot_{Nbuds}) as a function of tree size and available resources, as in Davi et al.(2009). The level of available resources is computed from the ratio between the biomass available in Non-Structural Carbohydrates (NSC) reserves at the time of budset (noted Res_{buds}) and the theoretical biomass in reserves (BSS_{th}). BSS_{th} modeled as :

$$BSS_{th} = TGSS \times B_{AliveWood} \tag{1}$$

With $TGSS$ the initial concentration of NSC and $B_{AliveWood}$ the total alive wood biomass.

Hence, at the time of budset at the end of each year, Pot_{Nbuds} is computed as :

$$Pot_{Nbuds} = \begin{cases} c_{LAI1} \times DBH^{c_{LAI2}} \times (\frac{Res_{buds}}{BSS_{th}})^{c_{LAI3}} \times \frac{1}{LA} & \text{if } Res_{buds} > 0 \\ 0 & \text{if } Res_{buds} \leq 0 \end{cases} \tag{2}$$

where LA is the average area of one leaf, c_{LAI1} is a slope of a relationship between Leaf Area Index (LAI) and tree diameter (DBH), c_{LAI2} is a power coefficient of the relationship between LAI and DBH, and c_{LAI3} a power coefficient on reserve effect.

2.2.2 Carbon allocation to flower buds

In a second step, we modelled carbon allocation to flower buds. The ratio between flower buds and vegetative buds (R_{fbvb}) is modelled following :

$$R_{fbvb} = \begin{cases} \frac{Res_{buds}}{BSS_{th}} \times \frac{CC_{repro}}{c_1} & \text{if } Res_{buds} > Res_{repro} \\ 0 & \text{if } Res_{buds} \leq 0 \end{cases} \tag{3}$$

where the coefficient c_1 quantifies the mass of female flowers produced per gram of reserves used, and CC_{repro} is the construction cost for reproductive organs. R_{fbvb} is assumed to be linearly proportional to the biomass of alive wood (Res_{buds}) simulated from the model divided by the initial NSC concentration (BSS_{th}), meaning that the level of reserves directly affects the number of flower buds. Note that we did not include carbon allocation to male reproductive buds.

The potential number of flower buds ($Pot_{NbudsFlowers}$) is then computed from the potential number of vegetative buds (Pot_{Nbuds}), following :

$$Pot_{NbudsFlowers} = R_{fbvb} \times Pot_{Nbuds} \tag{4}$$

In total, the carbon allocation to flower buds submodel has three new parameters (Table 2).

2.2.3 Leaf phenology and flowering

In this part, we present how we coupled different phenological models of the PHENOFIT library with CASTANEA model. We used here a two-phase sequential phenology model to simulate both budburst and flowering dates. The model describe a first phase of endodormancy which is released when a certain amount of chilling has been accumulated. Then a second phase of ecodormancy follows during which buds growth respond positively to increasing temperature. The daily rate of chilling is calculated with a threshold function of the mean temperature of the julian day (T_d), with the threshold temperature (T_b) which is a species specific parameter

(Chuine, 2000). The threshold function is defined as:

$$R_c(T_d) = \begin{cases} 1 & \text{if } T_d < T_b \\ 0 & \text{if } T_d \geq T_b \end{cases} \tag{5}$$

The end of the endodormancy phase (t_c) occurs when the sum of daily rates of chilling (R_c) reaches a threshold of chilling units (C_{crit}), which is a species-specific parameter.

$$\sum_{t_0}^{t_c} R_f(T_d) \geq C_{crit} \tag{6}$$

Then, bud growth rate depends on the accumulation of so called forcing units (R_f) modelled with a sigmoïd function (Chuine, 2000) :

$$R_f(T_d) = \frac{1}{1 + \exp\left(-d_T(T_d - T_{50})\right)} \tag{7}$$

With d_T a positive slope parameter and T_{50} defines the mid-responses temperature of the sigmoïd function. The budburst date (t_f) occurs when a critical amount of forcing units (F_{crit}) has been accumulated since t_c:

$$\sum_{t_c}^{t_f} R_f(T_d) \geq F_{crit} \tag{8}$$

In total, the new flower phenology submodel has six parameters (Table 2).

2.2.4 Seeds abortion due to regular mortality

The model simulates the daily number of fruits (Nb_{seeds}) from the potential number of flowers of the previous day. Next, the number of seeds is computed from the number of fruits and a number of seeds per fruit assumed to be constant by species. We included a species specific parameter to quantify the daily seed mortality ($Seed_{md}$). Each day, a constant fraction of seeds is removed:

$$Nb_{seeds_t} = \begin{cases} Nb_{seeds_{t-1}}(t) \times (1 - Seed_{md}) & \text{if } t = t_f \text{ and } Nb_{seeds}(t) = Pot_{NbudsFlowers} \\ 0, \text{otherwise} \end{cases} \tag{9}$$

With $Seed_{md}$ is the daily seed mortality.

2.2.5 Bud and seed abortion due to climatic events

We modelled both the effects of frost and drought on reproduction.

Frost effect on seed production

The proportion of flower buds can be reduced by frost damage (hereafter FD). FD was assumed to have similar effects on leaves and seeds. As in the PHENOFIT model, FD was model following Leinonen 1996. FD is calculated on a daily basis based on daily minimum temperature and frost hardiness of each organ, which itself depends on temperature, photoperiod and the stage of development of each organ. Damage to flower buds is then directly converted into a reduction of the number of final seeds.

$$Nb_{seeds_t} = Nb_{seeds_{t-1}} \times (1 - \text{FrostDamage}_t) \tag{10}$$

With $\text{FrostDamage}_t = FD_t - FD_{t-1}$

Frost damage is calculated as:

$$FD = \frac{1}{1 + \exp\left(B(R_t - T_{min})\right)} \tag{11}$$

with B a slope parameter, R_t the daily rate of frost hardiness and T_{min} the daily minimum temperature. The level of frost hardiness at day t depends on the level of the previous day and on the minimum temperature (dFH_{ti}), night length (dFH_{pi}), and the hardening competence of the organ, which itself depends on its development state (endodormant, ecodormant or active)

(CR):

$$R_t = \frac{4}{5} \times R_{t-1} + \frac{1}{5} \times (FH_{min} + CR \times (dFH_{ti} + dFH_{pi})) \tag{12}$$

with FHmin the maximum level of frost hardiness of the organ, homogeneous to a temperature (i.e., the minimum temperature that can be sustained), dFHti the increase in frost hardiness induced by temperature, and dFHpi the increase in the stationary level of frost hardiness induced by night length (photoperiod). dFHti is calculated as:

$$dFH_{ti} = \begin{cases} FHtfemax - \frac{FHtfemax}{T_{e1}-T_{e2}} \times (T_{min} - T_{e2}) & \text{if } T_{e2} \leq T_{min} \leq T_{e1} \\ FHtfemax & \text{if } T_{min} < T_{e2} \\ 0 & \text{if } T_{min} > T_{e1} \end{cases} \tag{13}$$

where T_{e1} and T_{e2} are upper and lower limits of the temperature range necessary to increase frost hardiness, T_{min} is the minimum daily temperature, and $FHtfemax$ is the maximum level of frost hardiness induced by temperature.

dFHpi is calculated as :

$$dFH_{pi} = \begin{cases} \frac{FHpfemax}{NL_2-NL_1} \times (NL_t - NL_1) & \text{if } NL_1 \leq NL_t \leq NL_2 \\ FHpfemax & \text{if } NL_t > NL_2 \\ 0 & \text{if } NL_t < NL_1 \end{cases} \tag{14}$$

With NL_t the night length, NL_1 and NL_2 the lower and upper limits of the effective night length range required to increase frost hardiness. $FHpfemax$ is the maximum level of frost hardiness induced by night length.

Drought effect on seed production

The number of alive seeds each day is linearly affected by the percent loss of hydraulic conductivity (PLC) following Martin-StPaul et al. 2017 :

$$Nb_{seeds_t} = Nb_{seeds_{t-1}} \times (1 - \text{droughtDamage}_t) \tag{15}$$

With $\text{droughtDamage}_t = PLC_t - PLC_{t-1}$

The daily percentage of loss of conductivity, PLC, is calculated as follows:

$$PLC = \frac{1}{1 + \exp^{\frac{s1}{25}(\psi_{midday} - \psi_{50})}} \tag{16}$$

where $s1$ is a slope parameter for the exponential function, and ψ_{50} is the mid response parameter for which 50% of vessels are embolized. The last term ψ_{midday} is the midday leaf water potential, simulated at the daily scale.

$$\psi_{minsoil_t} = max(-1 \times (\frac{1}{REW_t}^{\frac{1}{m}} - 1)^{\frac{1}{n}} \times \frac{10000}{\alpha}; -10) \tag{17}$$

The relative extractable water (REW) is obtained with

$$REW_t = \frac{R_{sol_t} - R_{wilt}}{R_{fc} - R_{wilt}} \tag{18}$$

where R_{wilt} is the soil water content at wilting point and R_{fc} at field capacity.

2.2.6 Carbon allocation to seed growth

We used a Gompertz growth function to model the biomass (M_{sg}) allocated to seed growth through time (t). This exponential-family function is widely used in biology to describe growth rates (Zwietering et al., 1990; Paine et al., 2012), and fruit growth (Bertin, 1995; Jullien, 2001). This function includes a lag time period and allows non-zero initial masses (Paine et al., 2012). The mass seed growth a time t writes as follows:

$$M_{sg_t} = M_{seed} \times \exp(-\exp(\frac{\mu_m \times e}{M_{seed}} \times (\lambda - t) + 1)) \tag{19}$$

With λ the length of the lag time period for seed growth, also corresponding to the flowering date simulated by the phenology model. This model includes three parameters (but only two new ones): μ_m is the growth rate (i.e. slope parameter); M_{seed} is the median value of seed mass; and e is set to $exp(1)$. In coniferous species, fertilization usually occurs a few months after the pollination date, but seeds and fruits already start growing before the fertilization (Singh and

Owens, 1981, 1982).

Then, total biomass invested in reproduction (B_{Repro}) at time t is obtained using the equation:

$$B_{Repro_t} = \frac{Nb_{seeds_t} \times M_{sg_t}}{1 - Str_{Aux}} \tag{20}$$

With Str_{Aux} the proportion of auxiliary reproductive structures, such as cupule or scale.

The total seed number by square meter of soil is converted into a number of seeds per individual, based on tree crown projection.

$$TreeNb_{seeds_t} = Nb_{seeds_t} \times \frac{\pi \times (a_{GF} \times DBH^{b_{GF}})^2}{RDI} \tag{21}$$

With DBH for tree diameter, a_{GF} for the slope of the height-DBH relationship, b_{GF} is a power coefficient of the height-DBH relationship, RDI is the relative density index and Nb_{seeds} is the number of seeds. In our study case, we finally converted the $TreeNb_{seeds}$ into a $TreeNb_{cones}$ by dividing $TreeNb_{seeds}$ by the mean number of seeds per cones, which is equal to 253.9 seeds per cone for *Abies alba* in Ventoux (Davi et al., 2016).

2.3 Studied species and sites

Silver fir, *Abies alba* Mill., is a major European coniferous tree (Vitasse et al., 2019). This monoecious species produces male flowers (called catkins) and female flowers and fruits (called cones) on the same tree. Both pollen and seed are wind-dispersed. Vegetative and flower buds are initiated at the end of spring/early summer of year t (Fig. 1). Both types of buds open during spring at year $t + 1$. Cone and seed development starts just after pollination and until the autumn of the same year $t + 1$ (Singh and Owens, 1981, 1982).

We used environmental and ecological data from previous studies on Mont-Ventoux, a Mediterranean mountain in southeastern France (44°10'28"N; 5°16'16'E). We ran simulations across five sites at different elevation (Dvx 1 at 995m, Dvx 2 at 1020m, Dvx 3 at 1117m, Dvx 4 at 1247m and Dvx 5 at 1340m), and simulated one mean tree per site (Fig. 3). We also run simula-

tions along a longitudinal transect at an elevation of 1117m (with climatic conditions similar to Dvx3), where we simulated a total of 16 different mean trees. We ran simulations for the period 1959-2015 at all sites, except site Dvx3 where simulations were run for the period 1966-2015. This allowed us to simulate only trees with a DBH value > 5cm, and to avoid wrong simulation of ring width when trees are too young. We followed the same procedure as described in Davi and Cailleret 2017 to account for within and among-sites variation environmental, ontogenetic and phenotypic characteristics. All site characteristics and climate used for the simulations are presented in <ZENODO link> and in Supplementary material, Fig. S1. Temperatures decreased by -0.7°C/100m whereas precipitation increased by 14mm/100m towards higher elevation.

To evaluate the model, we used several data sets collected in the sites Dvx1 to Dvx5: budburst date, ring width and cone production (see Table 3). Budburst was monitored at two sites (Dvx 3 and Dvx 5) from 2008 to 2015 (see Table 3). Ring width was measured at the five sites and along the transect from 1959 to 2009 (Cailleret et al., 2014; Davi and Cailleret, 2017). Cone production was monitored at individual scale from 2008 to 2015 in 30 plots in the Mont-Ventoux region (altitude ranging from 965m to 1524m). Data from the 30 sites were aggregated for model evaluation. More details about study sites monitored for cone production are presented in Davi et al. 2016 and in Supplementary materials, Section A.1.1. For each of the five study sites, local temperature, precipitation and relative humidity were measured with local climatic station from 2008 to 2015 (Cailleret and Davi, 2011). Daily local climatic conditions were estimated from 1960 to 2015 with long-term national meteorological data, down-scaled to the local sites using statistical regressions (Quintana-Seguí et al., 2008) (Supplementary material, Fig. S1).

2.4 Calibration of budburst, frost hardiness and carbon allocation sub-models

Most previously existing species-specific or site-specific parameters were taken from (Dufrêne et al., 2005; Davi et al., 2005), or from Davi and Cailleret 2017.

2.4.1 Calibration of budburst and frost hardiness

We calibrated the most sensitive parameters of the budburst sub-model (C_{crit} and F_{crit}, Gauzere et al. 2017) on our study sites to improve the accuracy of budburst dates prediction. To that aim, we ran 5000 simulation with varying C_{crit} and F_{crit} values, drawn in a uniform distribution: $C_{crit} \sim \mathcal{U}(52.5, 87.5)$ and $F_{crit} \sim \mathcal{U}(9.7, 16.1)$. Then, we compared the simulated budburst dates to the observed budburst date (at sites Dvx3 and Dvx5) using the *Root Mean Squared Error* (refer as RMSE), which gives the standard deviation of model prediction error (Supplementary material, Fig. S3). This procedure allowed us to select the best C_{crit} and F_{crit} values (i.e., the ones minimizing RMSE). For frost hardiness, we used all parameters values from Gauzere et al. sub.

2.4.2 Calibration of the carbon allocation model

We used the French national inventory dataset (RENECOFOR, Ulrich 1995) to estimate the construction costs of all organs: branchs, leaves and reproduction. The equations used to model the construction costs CC_{repro} are presented in Supplementary materials, Section A.1.2. We estimated the initial concentrations of NSC (parameter $TGSS$) for above-ground and bellow-ground tree biomass based on previous results from Hoch 2005. Daily abortion rate of seeds in *Abies*, $Seed_{md}$, was fixed to 0.003 (details in Supplementary material, based on measurements in Mont-Ventoux sites Section A.1.3). We estimated parameter c_1, the ratio between flower and vegetative buds as follows: $c_1 = \frac{1}{RateExp_{Cone} \times CC_{repro}} = \frac{1}{0.028 \times 1.38} = 25.75$ where $RateExp_{Cone}$, the total number of buds and cones per branch, is estimated to 0.028 from measurements (Szabadi & Fady, unpublished data), and CC_{repro}, the reproductive construction cost, is estimated to 1.38. After the calibration of leaf phenology and tree growth, we estimated the level of reserves needed for flower bud production (parameter Res_{repro}), by running 9000 simulations for all sites with varying Res_{repro} values. Res_{repro} was drawn in a uniform distribution $Res_{repro} \sim \mathcal{U}(0, 1000)$ (see Supplementary material, Fig.S4, Fig.S5). We then computed the mean simulated cone production ($TreeNb_{cones}$) per year from all sites, compared it to the observed yearly cone production, and selected the Res_{repro} value which provided the minimum RMSE value.

2.5 Model validation and sensitivity analyses

For each sites, we assessed the ability of the model to predict tree ring width (rw) and cone production ($TreeNb_{cones}$) using three different metrics: the *Nash-Sutcliffe Efficency* (NSE), the *Pearson correlation coefficient* (r) and the RMSE. The NSE is ranging from $-\infty$ to 1, with a value closed to 1 for most accurate model and bellowed 0 indicated that model simulations are worst than mean observed data. The r Pearson is the correlation between observations and simulations, ranging between -1 for negative correlation to 1 for positive correlation. All these metrics were computed from the average values of observations or simulations over all years. Note that for the cone production the validation was done by combining all years and sites.

Then, we ran a sensitivity analysis to identify the parameters of the carbon allocation model to reproduction that have the strongest effects on the prediction of cone production, and to quantify uncertainty of this prediction. Sensitivity analysis is one of the major steps to evaluate model and to highlight model limitations and directions of further improvements (Cariboni et al., 2007). For each of the seven parameters of the carbon allocation model to reproduction (Table 2), we simulated a range from ±35% of the optimal value defined in Table 2. We ran simulation at each site (5 sites on the elevation gradient and 16 sites on the longitudinal transect) for the period 1959 to 2015 (except for site Dvx3, with a starting date in 1966). Then, we computed average values of cone production over all sites for each vector of parameters. Model parameters were treated as independent random variables and their uncertainty was characterised by a uniform or a Gaussian distribution (only for the parameter c_1). Such distribution are appropriate when the lack of knowledge on parameters does not allow assigning a well-defined distribution (see for example in Pappas et al. 2013).

Sensitivity indices were computed based on the Sobol decomposition (Sobol, 1993), which estimates separately the main effect (first order) and the total effect of each parameter on the response variable (i.e. cone production). The total effect of a parameter is defined as the sum of its main effect and of all the interactions involving that parameter. A value closed to 1 indicates a strong effect of a given parameter on the response variable. The sensitivity indices were estimated using a regression-based approach to model the response variable (Sudret, 2008). Besides cone production, we also analysed other output variables, such as the Net Primary

Productivity and NSC concentrations in Fig. S7.

2.6 Predictions of silver fir fruit set in future climatic conditions

Finally, we ran simulations for future climatic conditions to identify consequences of climate change on tree growth and cone production in our study sites. We used climatic data simulated with HadGEM climate model for the historical period (1959 to 2013) and future period (2017 to 2099) under RCP4.5 and RCP8.5 scenarios for all sites. The Hadley Centre Global Environmental Model version 2 (HadGEM2) family models was designed to simulate and understand the centennial scale evolution of climate including biogeochemical responses (Collins et al., 2011). Additional information on the model is given by Collins et al. 2011 and The HadGEM2 Development Team et al. 2011. HadGEM2 is one of the warmest future climate model and can foretell a decrease in rainfall. Simulated climatic data were downscaled for our sites using local climate data. Downscaling is carried out in two stages. The data from the HadGEM2 model were first corrected for bias and downscaled using the R package "meteoland" (De Cáceres et al., 2018) at the SAFRAN point closest to the plots studied. Then, the local climate station data recorded locally are used to transform the climatic data according to the altitude of the plots (method described in Gauzere et al. 2019).

3 Results

3.1 Model evaluation

The among-year variations of budburst dates were predicted with a relatively high accuracy at both sites (r = 0.77 and NSE = -1.86 for Dvx3; r = 0.94 and NSE = 0.75 for Dvx5). For site Dvx3, the model however simulated an earlier budburst date as compared to the observations (RMSE = 13.45 for Dvx3, Fig. 4).

The new model was also able to predict accurately tree ring widths for most of the sites (r correlation ranging from 0.31 to 0.68, see Fig. 5), except at sites Dvx5 (r = -0.20, Fig 5, E) and Dvx2 (r = 0.12, Fig 5, B). Overall, the model tended to simulate higher tree growth than expected (RMSE ranging between 0.4 and 0.91).

The model was able to simulate some of the variations of the observed cone production, with high peak and null cone production (r = 0.56, Fig. 6). Note that we used here a value of the parameter Res_{repro} that allowed us to predict accurately the mean cone production. However, with this value of Res_{repro} fixed at 243 gC.m^{-2}, some mismatches occurred between predictions and observations after the main mast year (2010), and we predicted too many years without cone production. The frequency of reproduction failure (no cone production) decreased if the parameter (Res_{repro}) was set to a lower value (see Supplementary material, Fig.S4, Fig.S5). However a lower Res_{repro} also increased the frequency of mast years.

3.2 Sensitivity analyses

The parameter of Res_{repro} was the most sensitive parameter, and explained respectively 85% and 86% of the variation in cone production, when considering respectively the main or total effect of this parameter (Fig. 7). The other five considered parameters all explained less than 10% of cone production variation.

3.3 Effects of climate change

The model predicted less variability of cones production and higher cone production during mast year under future climate as compared to current climate (Fig. 8, A). For the current climate,

the model predicted a cone production per tree of 5.14 cones (sd = 17.6), while the mean cone production increased to 13.9 cones (sd = 41.4) per tree under the RCP 4.5 scenario, and to 21.6 cones (sd = 61.2) under the RCP 8.5 scenario. The predicted coefficient of variation was higher for the current climate (cv = 0.34) than for the future climates (0.29 and 0.28 for RCP4.5 and RCP8.5 respectively). Since we began the simulations with trees of mean age of 50 years and mean DBH of 18 cm, the trees were quite old and big at the end of the simulations, and were expected to produce more cones. Lastly, we found that the frequency of reproduction failure did not change between the current (91%) and future climates (87% with RCP4.5 and 84% with RCP8.5). The model predicted an increase of mean tree growth from 2.09 mm (sd = 0.86mm) to 2.55 mm (sd = 0.95mm) and 2.87 mm (sd = 1.06mm) for climate scenario RCP 4.5 and RCP 8.5 respectively (Fig. 8, B).

4 Discussion

We developed in this study an augmented version of the DVM CASTANEA, able to simulate fruit set and growth of forest trees on a yearly basis depending on the climatic conditions. This new DVM assumes that reproduction can only occur when enough resources have been accumulated, as also hypothesised in RBMs. Following this hypothesis, our model overpredicted the risk of reproduction failure, but was nevertheless able to predict the among-year variation of cone production, and the masting events in the coniferous species, *Abies alba* in Southern France. The model also predicted an increase of cones production in future climatic conditions. We first discuss in details how our new DVM can improve the prediction of tree growth and reproduction, before reviewing future perspective for its use and development.

4.1 Predictions of tree growth and reproduction with an augmented eco-physiological model

Our new PBM overall simulated accurately tree growth. However, some sites were affected by human disturbance, which could strongly affect ring width observations. For example, at the high-elevation sites Dvx4 and Dvx5, stand thinning occurred in 1995 and 1999. The subsequent

reduction of competition and its consequences on tree growth was not predicted accurately because CASTANEA model represents the stand as an average tree, without a spatially explicit representation of competition. Furthermore, environmental control of carbon allocation could also affect the simulation of tree growth, by modulating the sink demand after, for example, a drought period (Guillemot et al., 2017). However, consistently with a previous study on the same study sites using the CASTANEA model, we did not simulate here major events of hydraulic failure (Davi and Cailleret, 2017). Consequently, loss of conductance did not impact tree growth nor cone production in our simulations.

The model was able to reproduce accurately the among-year variations in budburst dates, but underestimated the date of budburst at low altitude (Dvx3). Different hypotheses can be advanced to explain this bias, beginning with genetic differentiation of budburst parameters between sites. Indeed, when we calibrated the budburst model separately for each site, we found a higher value of F_{crit} for the site Dvx3 as compared to Dvx5 (Supplementary material, Fig. S1). This may indicate that the population at site Dvx3 required an higher forcing temperatures for budburst. This finding in not consistent with a seedlings common garden study based on the same study sites, which did not found genetic differentiation for budburst parameters along the elevation gradient (Latreille and Pichot, 2017). Nevertheless, it is possible that the genetic differentiation between the populations at the two contrasted elevations is too small to be observed in the common gardens with a weekly monitoring of the date of budburst. A second hypothesis might be that at low elevation, the observed decline of *Abies alba* (Cailleret et al., 2014; Davi and Cailleret, 2017) delays budburst. In all cases, this is probably a specificity of Ventoux, since the observed budburst cline with elevation is lower at Ventoux than at other sites such as in the Pyrenees (Gauzere et al., sub).

Depending on the Res_{repro} parameter value, our new model simulated either too frequent events of reproduction failure or too frequent masting events as compared to observations (Supplementary material, Fig.S6). Furthermore Res_{repro} was found to be the most sensitive parameter, impacting much more fruit production than other parameters such as mortality rate

or the ratio between flower and vegetative buds. Depending on the carbon reserve threshold for flower initiation, trees could either produce no cone during several years (high threshold), or produce cones each year (low threshold) (Supplementary material, Fig.S5). The model therefore presented some limits to simulate accurately both the mean cone production and it variation among years. Note that the model predicted cone production for a mean tree, whereas observations concern individual trees, which show a large variation in cone production (Davi et al., 2016). Some individuals, which could be refer to as super-producers (Hacket-Pain et al., 2019), produced many cones while the majority of individuals produced no cone (Supplementary material, Fig.S2). Therefore, the overestimation of the number of years with no cone production might be due to an underestimation of the cone production of the super-producers during the bad years.

4.2 Prediction of tree growth and reproduction under future climate

With our new model, both tree mean growth and mean cone production were predicted to increase whatever the future climatic scenario considered (ie., RCP 4.5 or RCP8.5). This is consistent with other previous PBM simulation studies which also predicted an increase of tree growth under RCP 8.5 scenario, due to the positive fertilisation effects of CO_2 concentration (Davi et al., 2006; Gea-Izquierdo et al., 2017). Recently, Caignard et al. 2017 also found that temperature warming was associated to increasing fruit set in temperate oaks. An increase of CO_2 concentration has also been found to reduce age at maturity and increase cone production in *Pinus* (*P. taeda*, LaDeau and Clark 2001). Our model predicted years with no cone production, as already reported by other studies: for example on another coniferous genus *Pinus*, a reduction of cone production was expected with less variability (Mutke et al., 2005; Redmond et al., 2012) due to negative effects of increasing temperature on seed fertilisation (Flores-Rentería et al., 2018).

4.3 Perspectives to improve the modelling of resource allocation to reproduction and growth

A first challenge for the use of CASTANEA model in general and of our augmented version in particular is the large number of parameters to estimate. Parameters estimation is particularly challenging when some of them have major impact on a given output variable (here, cone production), when several combination of parameters result in the same output variable value, or/and when data on some parameters are limited, for instance the threshold of reproduction or seed maturation. Although this was out of the scope of this study, a solution to achieve parameter inference in such case would be inverse modelling, where observations are used for both calibration and validation of the model (Hartig et al., 2012). Based for example on Bayesian methods, we could specify a prior information of ours parameters, then compare model outputs with observed data and obtain a posterior estimate on each parameter. This posterior estimate of model parameters could be used to calculate model uncertainty and improve model predictions (Hartig et al., 2012). A recent study on tree mortality found that inverse modelling presents good performance and could improve ecological forecasts (Cailleret et al., 2019).

A perspective to improve our DVM is to refine the mechanisms of carbon allocation to reproduction. Our model is based on the allocation scheme proposed by RBM, such that cone production occurs only when sufficient reserves are available. RBM also include different mechanisms such as veto effects, i.e. extreme events limiting cone production, and can also take into account the effects of pollen limitation, and carbon or nitrogen resources (see for example; Abe et al. 2016; Schermer et al. 2019). The drawback of RBMs is however their limited ability to account for the effect of environmental conditions on reproductive processes, whereas this is a major strength of ecophysiological PBMs such a CASTANEA. In this study, our CASTANEA model was able to simulate masting patterns, although the balance between masting and reproduction failure events remain to be improved. To that aim, other carbon allocation schemes could be tested, for example by including potential competition of carbon sinks between growth and reproduction, or by including a climatic cue which could favour fruit production (Kelly et al., 2013). Incorporation of these additional processes could improve

carbon allocation and the predictions of climate change effects on forest ecosystems (Franklin et al., 2012).

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6 Author Contribution

V.J. & H.D. initiated the idea. V.J. & H.D. developed the model. V.J. ran simulations and started the redaction of the initial draft. All authors contributed to the improvement of the result interpretation and redaction.

7 Data accessibility statement

All inventory and climate files used for simulations are available from the Zenodo Digital Repository <link>.

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8 List of Tables and Figures

8.1 Tables

Table 1: The main process-based model incorporating reproduction of trees.

Category	Example	Reproductive feature included processes	Target process	Scale
Forest dynamic models	FORCLIM	Seed production, seed dispersal, seedlings establishment and survival	Demographic dynamics over the whole life-cycle	From stand to landscape
Resource budget model	-	-	Temporal and spatial variation in seed production (i.e. masting)	Individual/stand
Ecophysiological model (or DVM)	CASTANEA	Seed production	Biogeochemical cycle, effects of climate on forest dynamics	From stand to species range
Developmental threshold models	PHENOFIT	Flower and fruit phenology	Reproductive success as a function of phenology	Species range

Table 2: List of parameters for the phenology and reproductive carbon allocation models for *Abies*. National data obtained from the RENECOFOR network, local data obtained from local monitoring on the Mont-Ventoux.

Parameter	Abbreviation	Units	Value	Sources
Leaf and flower Phenology Model				
Critical amount of forcing units	F_{crit}	°C	10.3	This study
Critical amount of chilling units	C_{crit}	°C	63	This study
Medium responses of the forcing temperature accumulation	T_{50}	°C	21.28	national data
Beginning of endo or ecodormancy	t_0	days	-62	national data
Threshold temperature for rate of chilling	T_b	°C	10	national data
Sigmoid parameter for forcing state	d_T	-	-0.19282	national data
Allocation Model				
Coefficient used in carbon allocation for the ratio between flower buds and vegetative buds allocation	c_1	-	25.75	unpublished local data
Seed mass (median value)	M_{seed}	mg	50.5	unpublished local data
Threshold level to allow reproduction	Res_{repro}	$gC.m^{-2}$	243	This study
Rate of auxillary reproductive structure	Str_{Aux}	-	0.337	unpublished local data
Construction cost of reproductive organs	CC_{repro}	$gC.gC^{-1}$	1.38	national data
Daily seed mortality rate	$Seed_{md}$	-	0.0037	unpublished local data
Growth rate of the Gompertz function (slope)	μ_m	-	2.11	unpublished local data

Table 3: Data used for model calibration and validation for *Abies* on the Mont-Ventoux.

Observations	Nb of sites	Nb of individuals	Nb of years	mean values (sd)	median values (CI95%)
Budburst date	2	46	7 (from 2008 to 2015)	138.8 (7.6)	138 (126, 156)
Ring width	6	116	50 (from 1959 to 2009)	1.47 (0.9)	1.27 (0.29, 3.75)
Cone production	30	1152	17 (from 1998 to 2015, miss 2001)	15.9 (26.4)	6 (0, 90)

8.2 Figures

Figure 1: Reproductive cycle from a bud to a mature fruit in a forest tree species such as *Abies alba*. Buds are initiated during the year $t-1$ (stage 1), with differentiation of vegetative versus reproductive buds occurring later during the year $t-1$ (stage 2). Budburst and flowering occur at spring of year t, (phenology event, stage 3). Note that abortion can occur at all stages, from buds (stage 3) to fruit maturation (stages 4 and 5). Lastly, cone (or fruit) with seeds grow from spring after pollination until autumn at year t (stage 6).

Figure 2: General overview of the augmented CASTANEA model with reproduction. The light blue box represents environmental variable used as input by CASTANEA (i.e. temperature, precipitation, global radiation, wind speed). The dark blue box represents the standard CASTANEA model, with its model of carbon allocation to different compartments (in pink). Here, we added a new reproductive compartment CASTANEA for bud initiation and fruits (including seeds). The orange box represents the PHENOFIT model, which we connected here to CASTANEA to model the timing of carbon allocation to leaves and fruits. Blue arrows represent environmental effects on CASTANEA and PHENOFIT. Black arrows represent carbon allocation to tree compartments and the influence of phenology processes.

Figure 3: Map of the study sites on Mont-Ventoux, South-Eastern France. We studied five sites (Dvx1 to Dvx5) at elevations ranging from 995m to 1340m (elevation gradient), and 16 sites along a transect at 1100m in elevation (closed to the site Dvx3).

Figure 4: Comparison of simulated versus observed budburst dates among years for the sites Dvx3 (A) and Dvx5 (B). Black dots and lines represent observations (mean and sd), while red dots and dashed line represent simulations.

Figure 5: Comparison of simulated versus observed tree growth across years for the 5 elevation sites and the transect (A for Dvx 1, B for Dvx2, C for Dvx3, D for Dvx4, E to Dvx 5, and F for the transect). Black dots and line represent observations (mean) with their standard deviation (in grey). Red dots and line represent simulations, with standard deviation in the graphic (F). Smaller graphics represent simulation data in comparison to observation data with 1:1 line (black dotted), significant regression line (solid blue line) and non significant regression (dashed blue line). Note that for the site Dvx3 (C) simulations started in 1966.

Figure 6: Comparison of the simulated mean and standard deviation of cone production (in red) and counts of cones (black line and dots, with grey area) from 1998 to 2015 on the Mont-Ventoux region. The inside plot presents simulations and observations with the 1:1 line (black dotted) and the linear regression in blue with distribution of values.

Figure 7: Sensitivity analysis of the mean cone production (as output variable) to seven parameters of the carbon allocation model.

Figure 8: Predictions for growth (A) and reproduction (B) under future climatic scenario (RCP4.5 and RCP8.5). Solid lines are the mean and standard deviation of each output variable, averaged over the the five sites of the elevation gradient and the 16 sites of the transect.

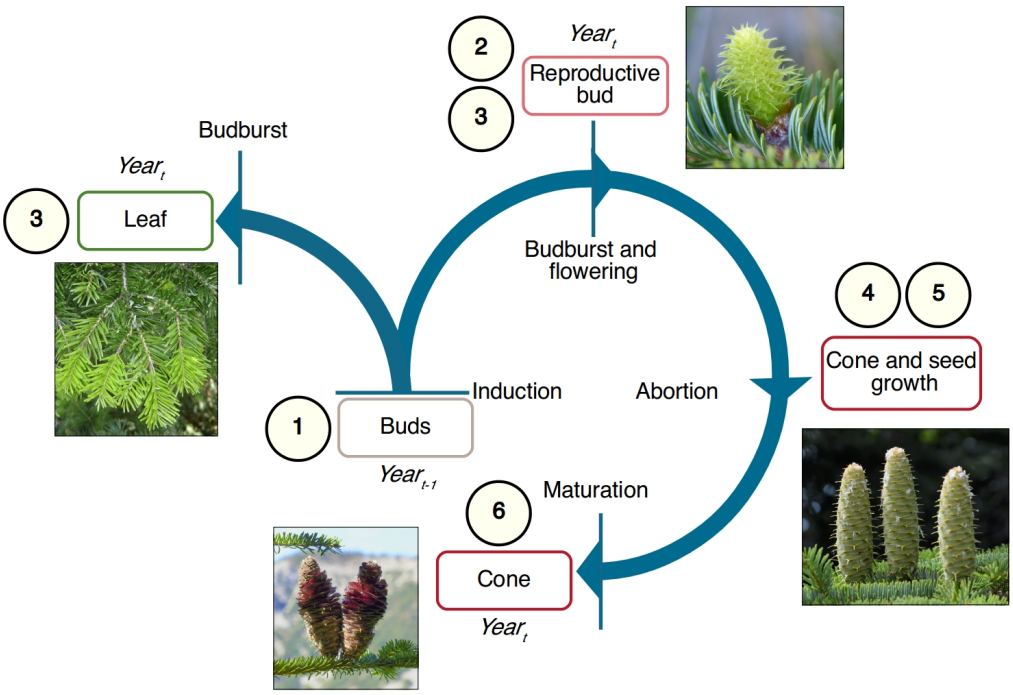
2
3
Year$_t$
Reproductive bud
Budburst
Year$_t$
3
Leaf
Budburst and flowering
4
5
Cone and seed growth
Induction
Abortion
1
Buds
Year$_{t-1}$
6
Maturation
Cone
Year$_t$

Figure 1

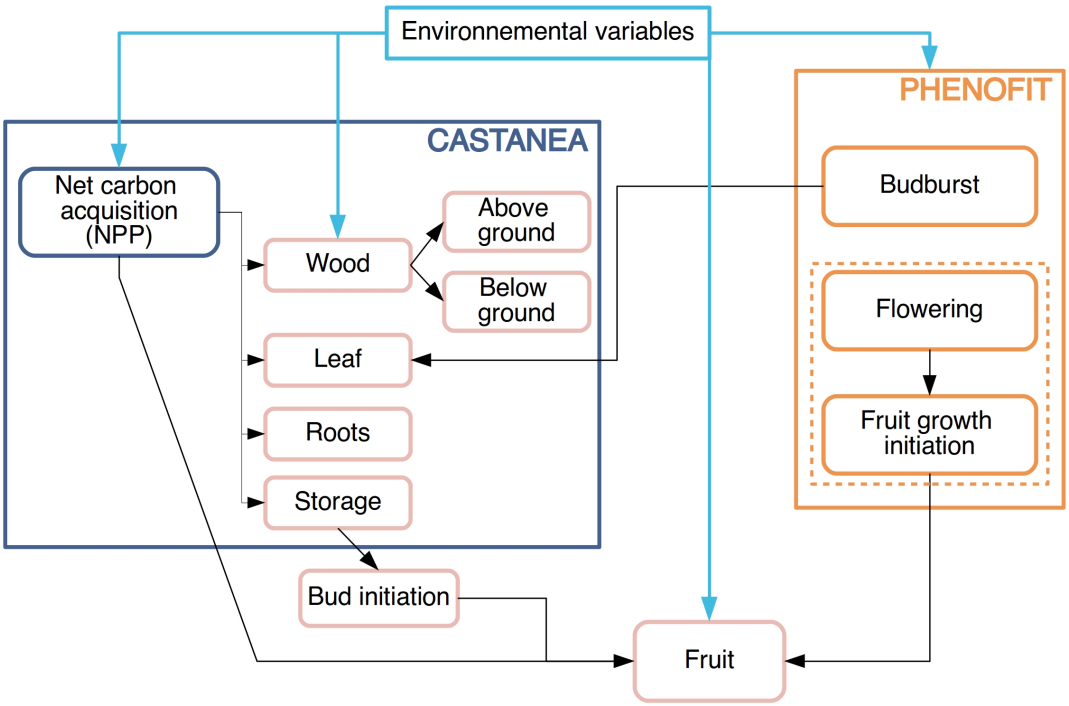
Environnemental variables
PHENOFIT
CASTANEA
Net carbon acquisition (NPP)
Wood
Above ground
Below ground
Leaf
Roots
Storage
Bud initiation
Budburst
Flowering
Fruit growth initiation
Fruit

Figure 2

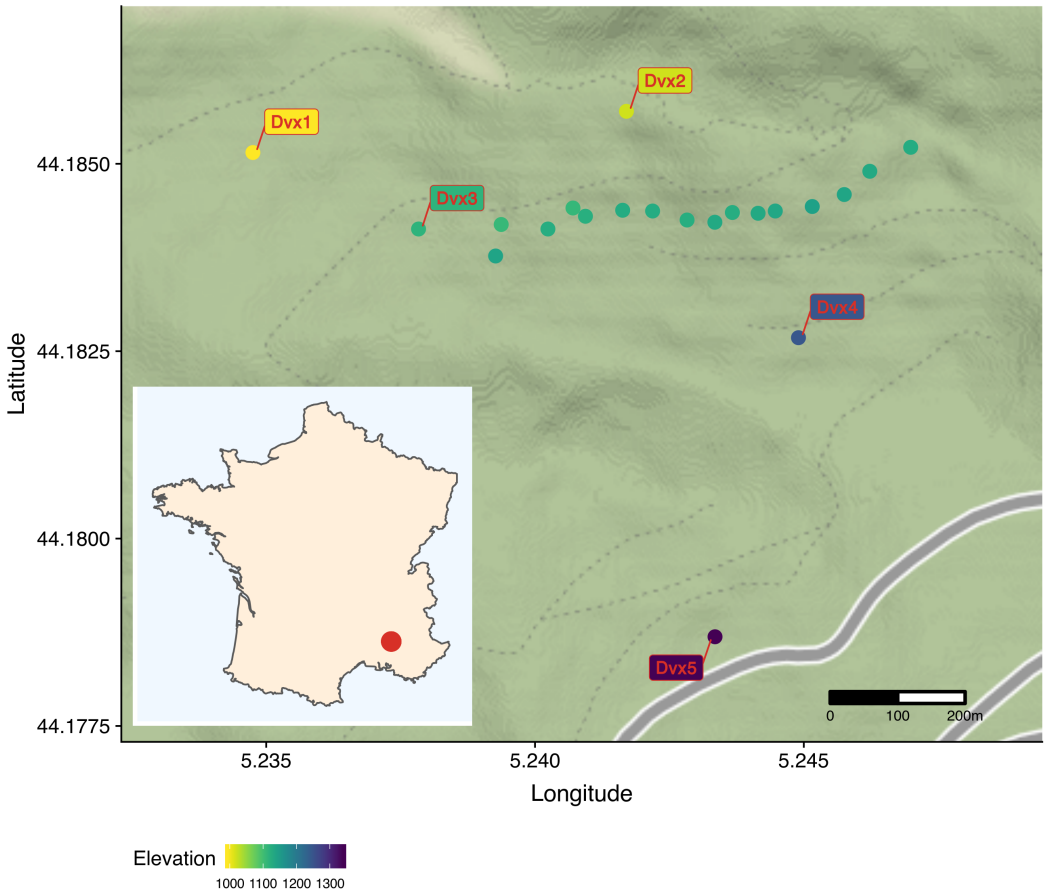
Dvx1
Dvx2
Dvx3
Dvx4
Dvx5
44.1850
44.1825
44.1800
44.1775
Latitude
5.235
5.240
5.245
Longitude
0
100
200m
Elevation
1000 1100 1200 1300

Figure 3

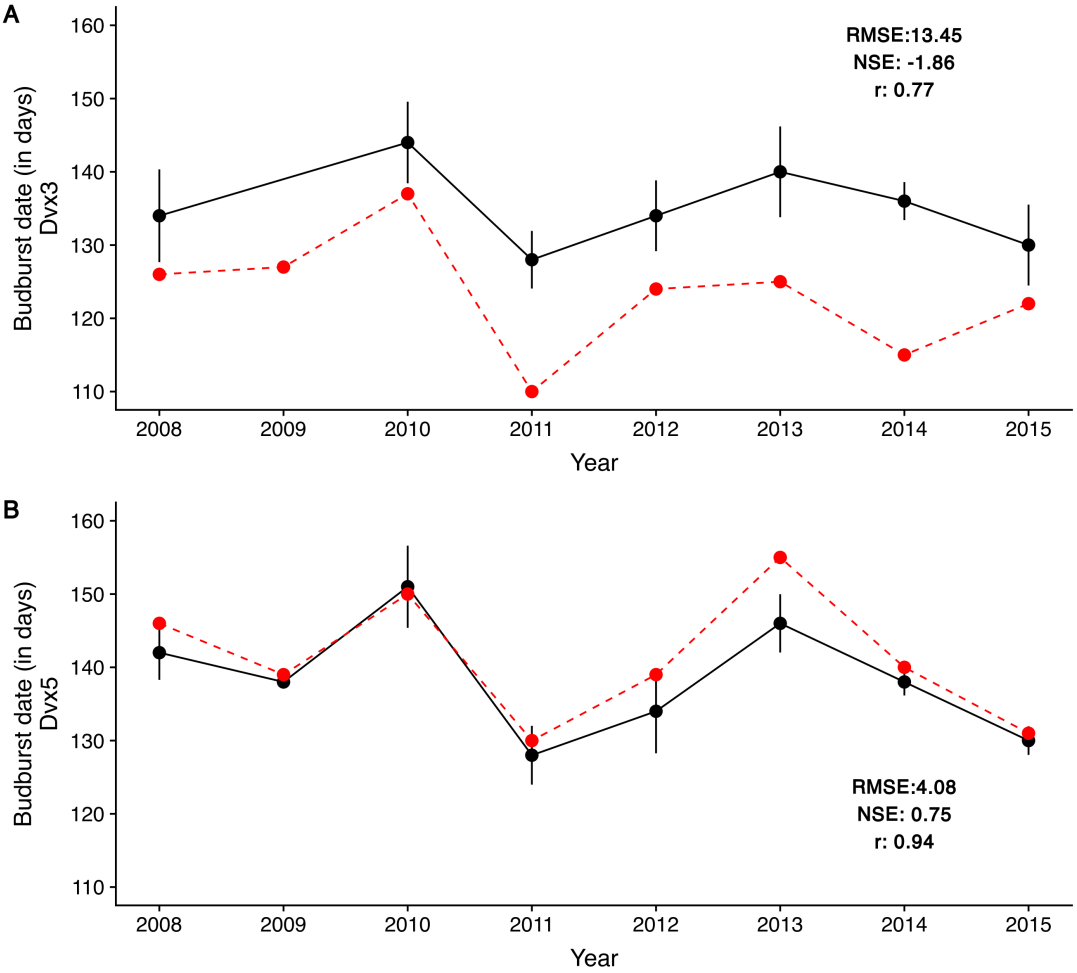
A
Budburst date (in days)
Dvx3
160
150
140
130
120
110
RMSE:13.45
NSE: -1.86
r: 0.77
2008
2009
2010
2011
2012
2013
2014
2015
Year
B
Budburst date (in days)
Dvx5
160
150
140
130
120
110
RMSE:4.08
NSE: 0.75
r: 0.94
2008
2009
2010
2011
2012
2013
2014
2015
Year

Figure 4

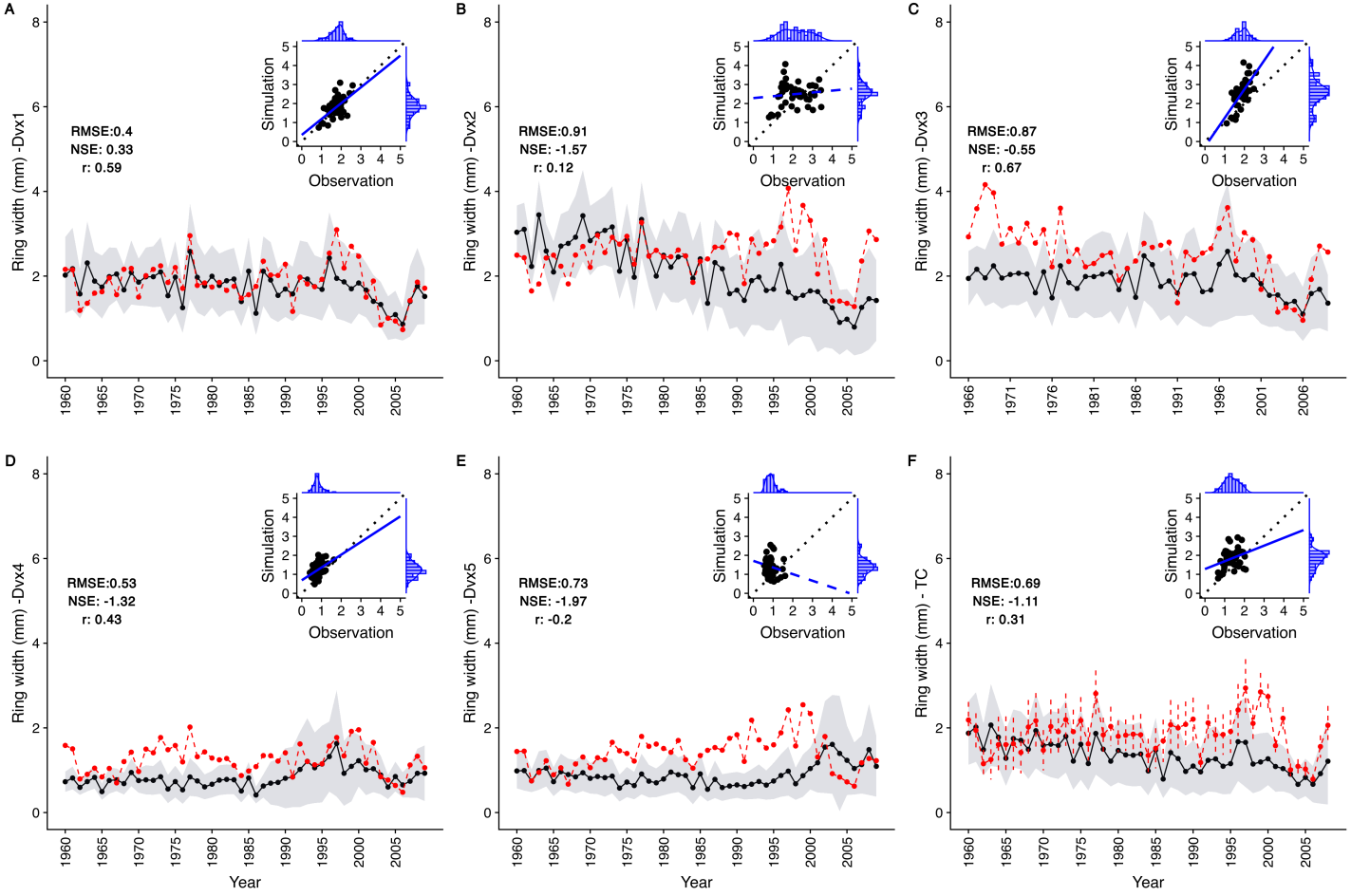
A
RMSE:0.4
NSE: 0.33
r: 0.59
Ring width (mm) -Dvx1
B
RMSE:0.91
NSE: -1.57
r: 0.12
Ring width (mm) -Dvx2
C
RMSE:0.87
NSE: -0.55
r: 0.67
Ring width (mm) -Dvx3
D
RMSE:0.53
NSE: -1.32
r: 0.43
Ring width (mm) -Dvx4
E
RMSE:0.73
NSE: -1.97
r: -0.2
Ring width (mm) -Dvx5
F
RMSE:0.69
NSE: -1.11
r: 0.31
Ring width (mm) - TC
Simulation
Observation
Year

Figure 5

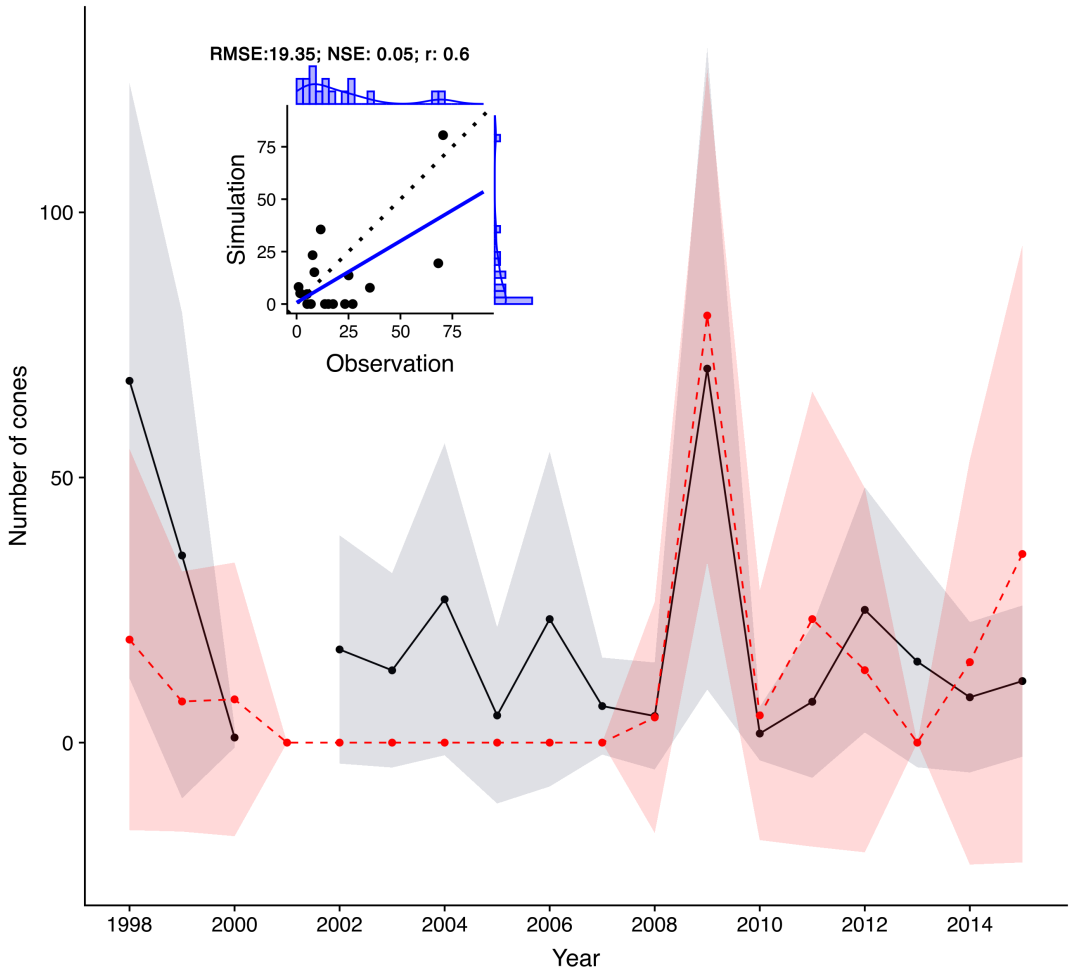
RMSE:19.35; NSE: 0.05; r: 0.6
Simulation
Observation
0
25
50
75
Number of cones
100
50
0
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year

Figure 6

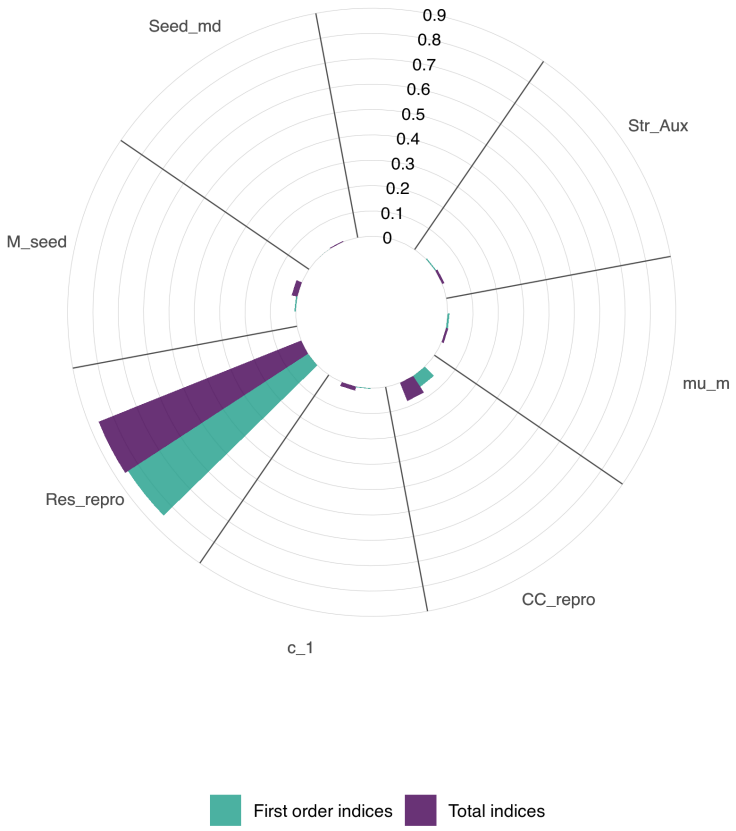
Seed_md
Str_Aux
mu_m
CC_repro
c_1
Res_repro
M_seed
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
First order indices
Total indices

Figure 7

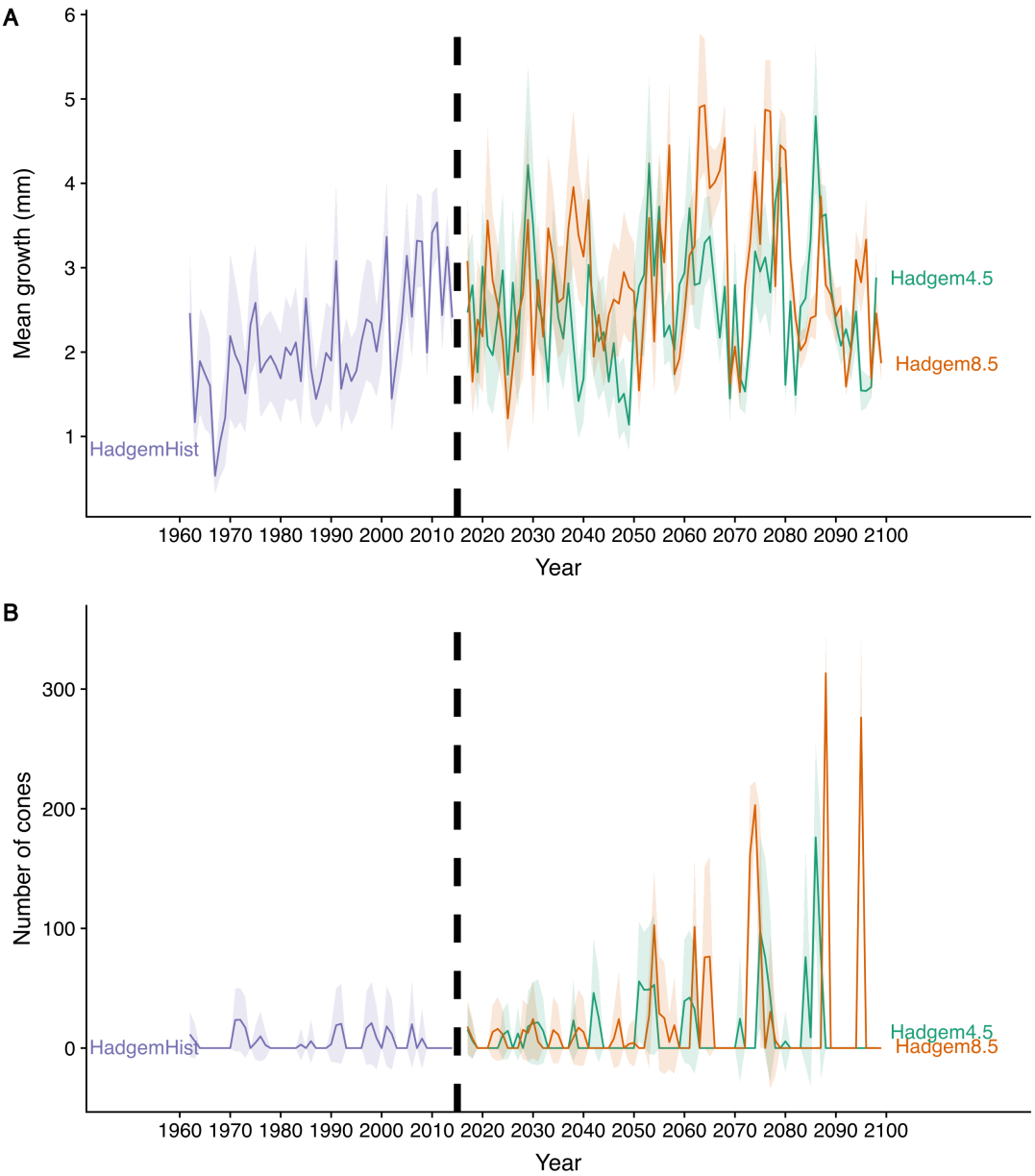
A
Mean growth (mm)
6
5
4
3
2
1
HadgemHist
Hadgem4.5
Hadgem8.5
1960 1970 1980 1990 2000 2010 2020 2030 2040 2050 2060 2070 2080 2090 2100
Year
B
Number of cones
300
200
100
0
HadgemHist
Hadgem4.5
Hadgem8.5
1960 1970 1980 1990 2000 2010 2020 2030 2040 2050 2060 2070 2080 2090 2100
Year

Figure 8

A Supplementary material

Article Title: Resource allocation during reproduction in forest trees: a process-based model to simulate variation in cone production with silver fir (*Abies alba*)

Authors: Valentin Journé[1], Isabelle Chuine[2], Sylvie Oddou-Muratorio[1] & Hendrik Davi[1]

A.1 Supplementary Sections

A.1.1 Cone production datasets

In this study we compiled dataset of cone production on the Mont-Ventoux region, also presented in the article from (Davi et al., 2016) and cover a total period from 1998 to 2015 (miss 2001). Each year, brown and ripened cones were counted using binoculars at the end of the summer prior to seed release. Note that aborted cones were not included in these datasets. First, we used data from three different stand named "P34" (at 1310m), "Contrat" (at 1418 m), and "Mont-Serein" (between 976 and 1424m) from 1998 to 2007. Second, the cones of 73 trees located on a continuous elevation transect (Ventoux CET from 965 to 1524m) were counted in 2006 and 2007. Third, 129 trees located inside or near five $400m_2$ plots at different altitudes (995, 1020, 1117, 1247 and 1340m, collectively called the discontinuous elevation transect or Ventoux DET) were identified and mapped, and the cones were counted every year from 2007 to 2015. Fourth, the cones of 243 trees located along a contour line transect (Ventoux CLT with an average elevation of 1120m) were counted in 2007, 2008 and 2012.

A.1.2 Determination of construction costs for silver fir

Construction costs are defined as the amount of glucose necessary to construct 1 gram of biomass, from resources (i.e. minerals and photoassimilates), and can be obtained for each organ such as leaf, stem and cones (Vertregt and Penning de Vries, 1987). Majority of studies defined construction costs for leaves and stem, but no values are present in the literature for cones of temperate tree species. This parameter is necessary for our process-based model. Here, we used a national network (RENECOFOR, Ulrich 1995) where they analysed litter fall and leaves

elements. We used an equation from Wullschleger (1997), based on elements concentration and ash to calculate construction costs for all tree organs species. The equation to calculate construction cost, defined as V_G (gGlucose.gDM^{-1}), is:

$$V_G = (5.39C + 0.80A + 5.64 f_{N,h}N - 1.191)(1 + r_T) \tag{1}$$

where C is is tissue carbon content (g/g), A is ash content (g/g), N is nitrogen content (g/g), $f_{N,h}N$ the fraction of nitrogen used in growth (fixed at 0.5 for leaves and 1 for others parts), r_T the added cost of translocating photosynthates from sources to sink (fixed at 5.3%).

The construction cost V_G can be convert in gC.gC^{-1} with the following equation :

$$\begin{cases} V_G[gC/gC] = \frac{(V_G[gGlu/gDM])*propC}{tc} \\ propC = \frac{(6*MM_C)}{MM_{C_6H_{12}O_6}} \end{cases} \tag{2}$$

where MM_C is molar mass of carbon, MM_O is molar mass of oxygen, $MM_{C_6H_{12}O_6}$ molar mass of glucose. The parameter tc corresponds to the carbon content in dry mass. We calculated mean values for each elements concentration per tree and use dry mass matters. For example, supposed that for 100g of dry matters, we calculated mean ash mass with $\frac{\%Ash}{100}$. All construction costs were calculated for reproduction (i.e. reproductive structures), branch leaves from litterfal and also leaves extracted directly from the tree. Values are presented in Table S1. Note that we estimate reproductive cost of reproduction mainly based on fruit production collected from litterfal.

Table S1: Construction costs obtained from equation for tree species. Values presented are in gGlucose.gDM^{-1} for glucose, and in gC.gC^{-1} for carbon for each organs : branchs, reproduction (i.e. reproductive structures) and leaves directly sampled in the tree or in litterfal.

Species	Construction Cost	Branchs	Leaves (Tree)	Leaves (Litterfal)	Reproduction
Abies alba	glucose	1.910	1.804	1.796	1.855
	carbon	1.409	1.370	1.368	1.384

A.1.3 Equation to determine a daily seed mortality rate : $Seed_{md}$

To calculated this rate, we used data from annual mortality rate (refer as $Seed_{ma}$) and period between beginning of seed growth initiation (refer as d) to final seed maturation which is describe as:

$$N_{t+1} = N_t \times (1 - Seed_{md}) \tag{3}$$

$$N_m = N_0 \times (1 - Seed_{md})^d \tag{4}$$

$$1 - \frac{N_m}{N_0} = (1 - Seed_{md})^d \tag{5}$$

$$1 - Seed_{ma} = (1 - Seed_{md})^d \tag{6}$$

With $\frac{N_m}{N_0} = Seed_{ma}$ and corresponds to the ratio between the initial number of seeds (N_0) and the final number of seed after mortality (N_m). However the parameter of interest, is $Seed_{md}$. To isolate this parameter we can used a log transformation of the equation describe as follows:

$$\ln(1 - Seed_{ma}) = \ln((1 - Seed_{md})^d) \tag{7}$$

$$\ln(1 - Seed_{ma}) = d \ln(1 - Seed_{md}) \tag{8}$$

$$\ln(1 - Seed_{md}) = \frac{\ln(1 - Seed_{ma})}{d} \tag{9}$$

$$Seed_{md} = 1 - \exp \frac{\ln(1 - Seed_{ma})}{d} \tag{10}$$

Based on local data, cone growth initiation starts from 160 days to the maturation date at 205 days ($d = 205 - 160 = 40 days$), and the annual seed mortality is $Seed_{ma} = 0.21$

References in Supplementary material

Vertregt, N. and Penning de Vries, F. (1987). A rapid method for determining the efficiency of biosynthesis of plant biomass. *Journal of Theoretical Biology*, 128(1):109–119.

Wullschleger, S. (1997). Energetic Costs of Tissue Construction in Yellow-poplar and White Oak Trees Exposed to Long-term CO2Enrichment. *Annals of Botany*, 80(3):289–297.

A.2 Supplementary Figures

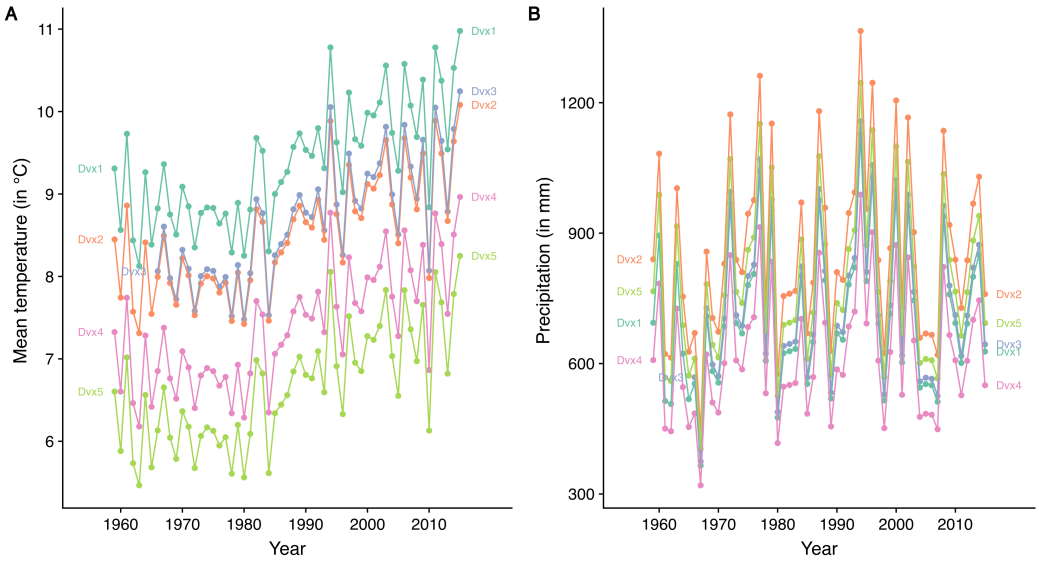

Figure S1: Variation of climatic variables for mean yearly temperature and rainfall for all study sites. Note that for the transect we used climate from the site Dvx 3. We observed an increase of mean temperature since 1960 and it fluctuates between 6°C and 11°C. Precipitation fluctuates between 380 and 1600mm per year

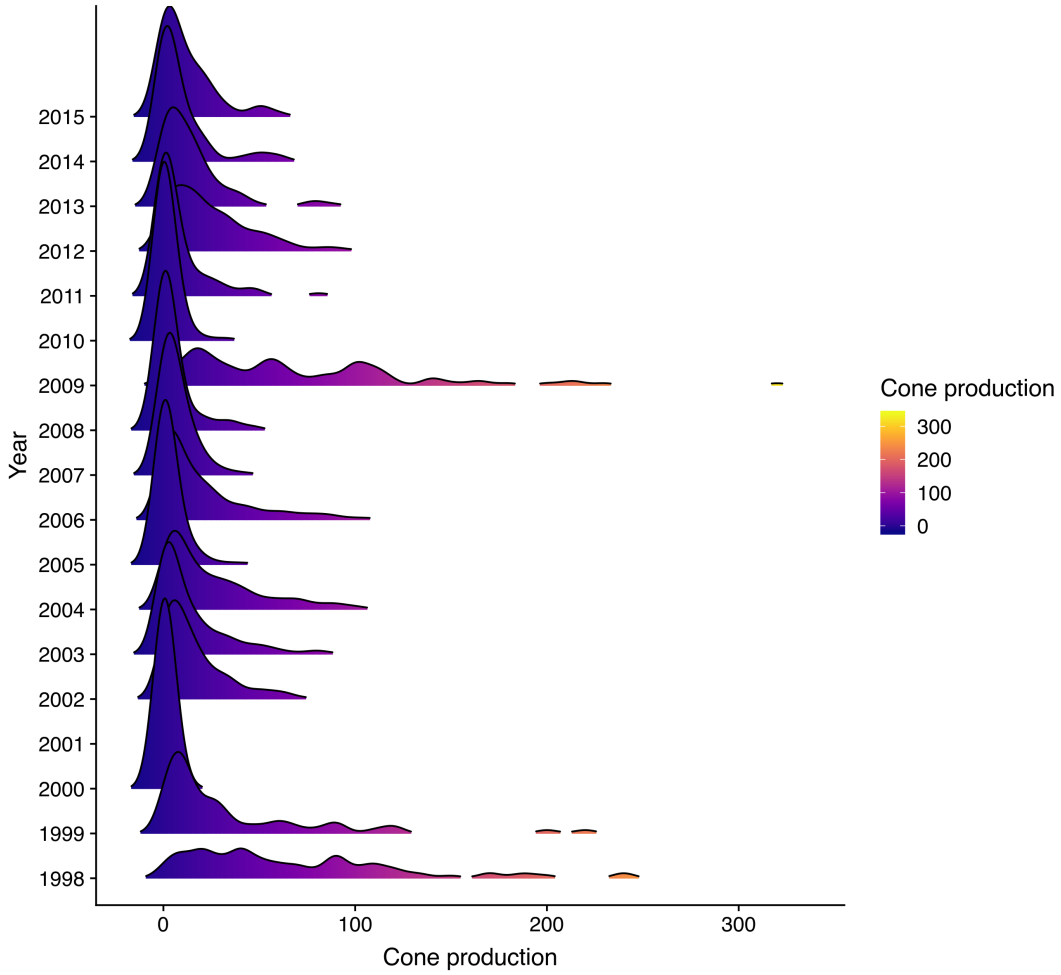

Figure S2: Distribution of cone production (i.e. number of counted cone) observations during the study period (1998-2015, missing year 2001) on the Mont-Ventoux.

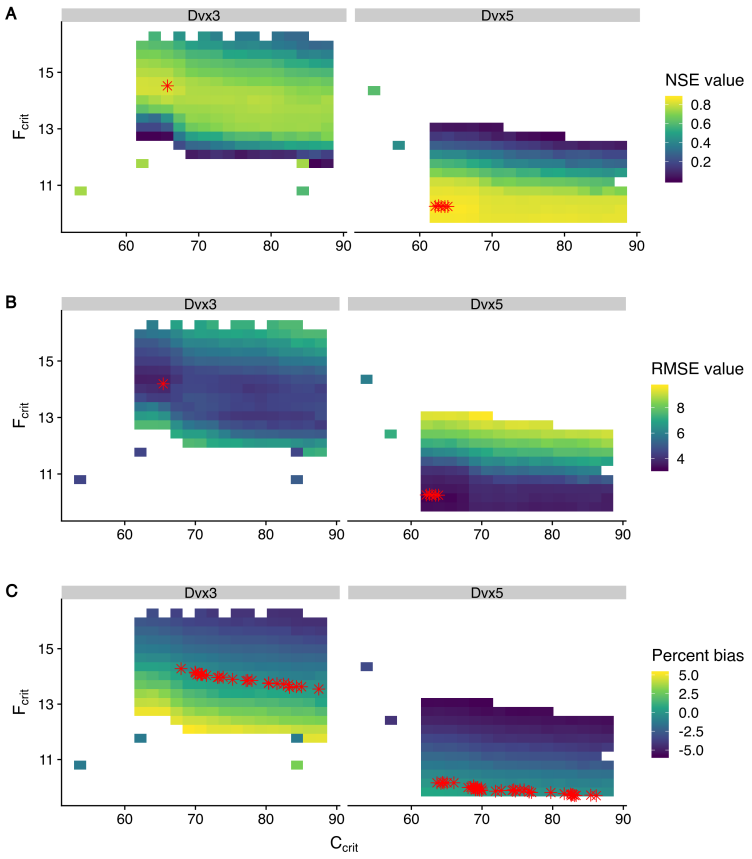

Figure S3: Model fit validation of the leaf phenology model (parameters C_{crit} and F_{crit}). Comparison between simulation with different values of C_{crit} and F_{crit} for sites Dvx3 and Dvx5, and with budburst date observation. We calculated NSE value (A), RMSE value (B) and Percent bias in (C). Red dots present in all graphics present the maximal value of NSE for each sites in (A), the minimal value of RMSE in (B) and zero values of percent bias in (C).

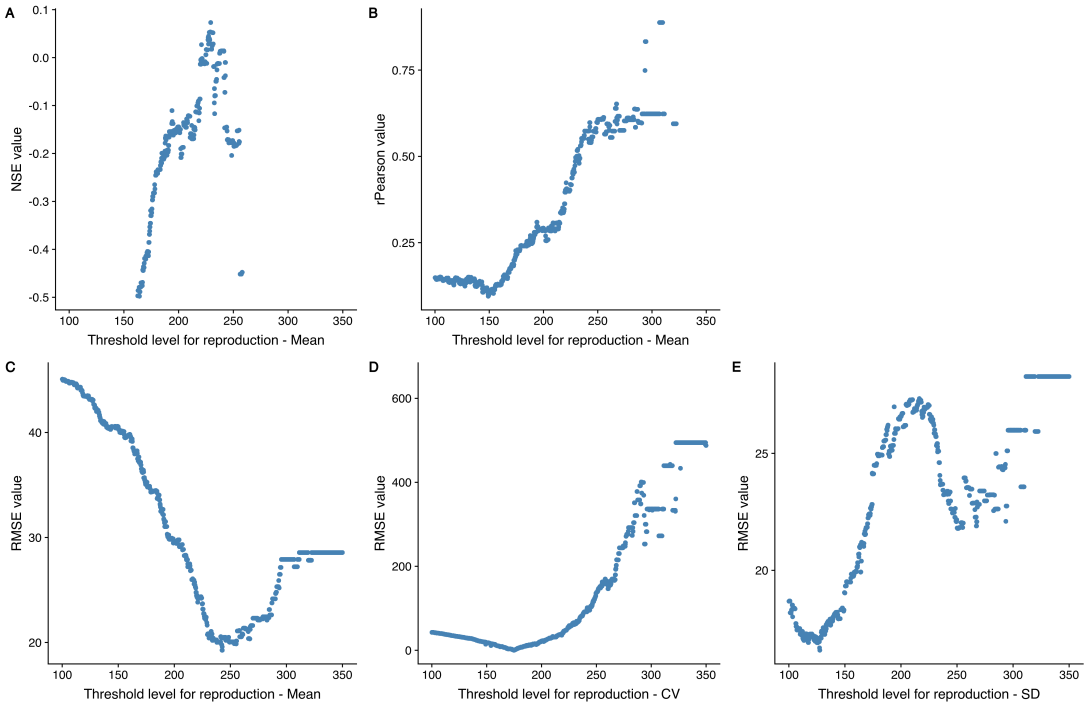

Figure S4: Model fit validation for tree cone production to determine potential value of threshold level for reproduction. Comparison between simulation (10000 simulations) and real cone production from all study sites. We calculated NSE value (A), RMSE value (B) and Pearson correlation (C). We estimated the optimal value based on RMSE for parameter Res_{repro} at 236 to predict accurately a mean cone production. We also compared simulation and observations with a coefficient of variation of cone production (D) and with a standard deviation of cone production (E).

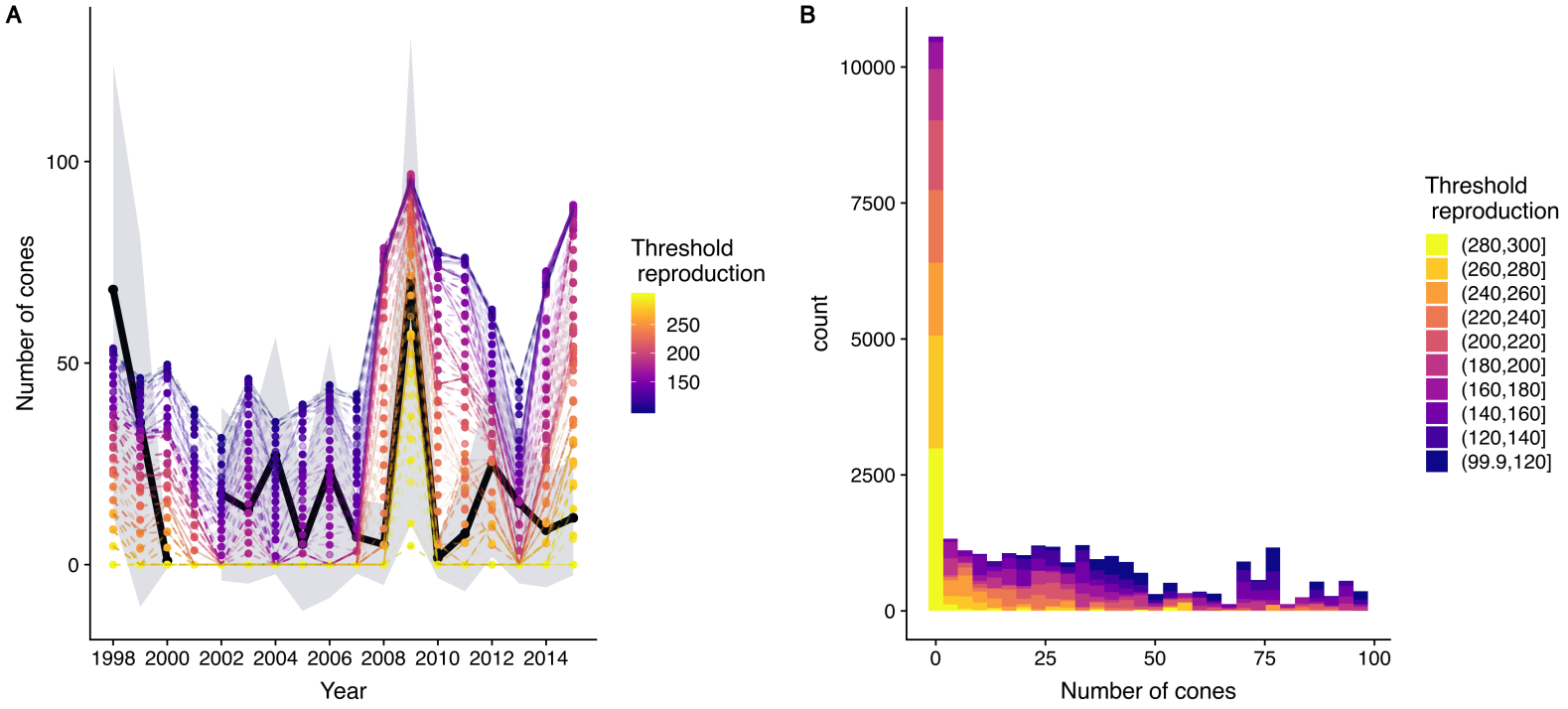

Figure S5: Variation of the parameter Res_{repro} from 100 to 300. In (A) average of observed cone production is presented in balck with standard deviation in grey. All simulations with different values of parameter is present with dashed lines. In (B) distribution of cone production for each values of Res_{repro} (division into 10 class of the parameter Res_{repro}).

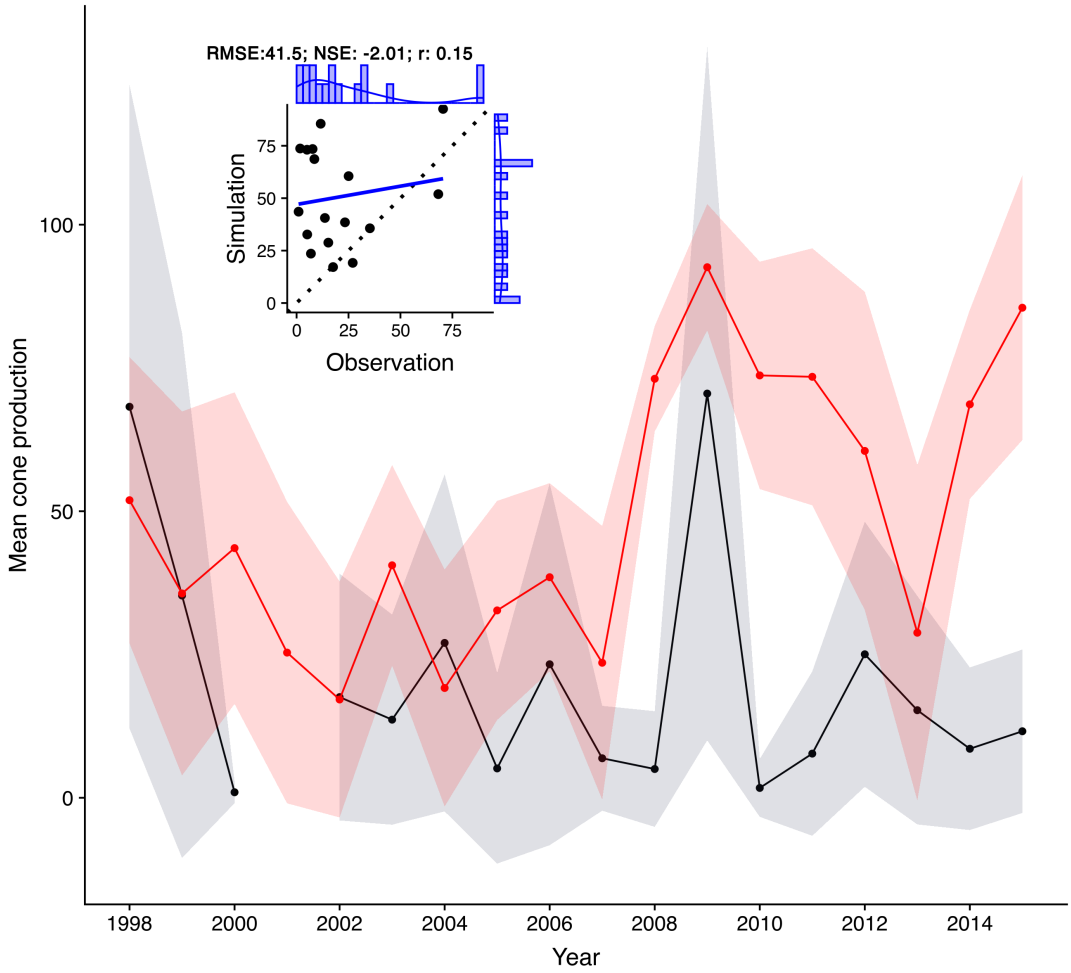

Figure S6: Simulation based on RMSE selected from standard deviation of cone production (see Fig. S4) . The Res_{repro} was fixed to a value at 128.

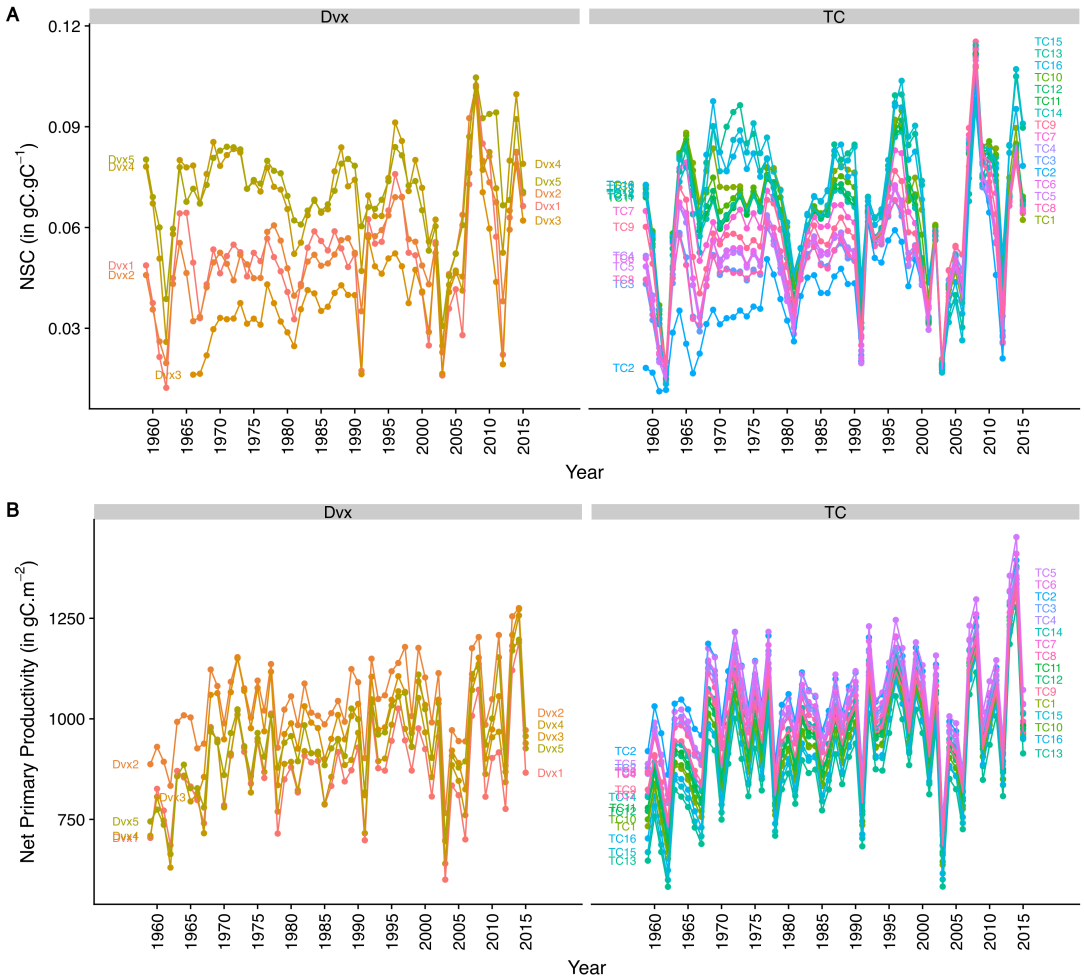

Figure S7: Simulation of the CASTANEA model for the (A) Variation of NSC concentration (in $gC.gC^{-1}$) and (B) Variation of NPP (in $gC.m^{-2}$) from the altitudinal gradient (Dvx) and the transect study (TC).

3 Synthèse et Discussion

Dans notre modèle, l'initiation des bourgeons floraux, l'année n , a lieu si le niveau de réserves dépasse un seuil donné, et ensuite le nombre de bourgeons floraux est proportionnel à ce niveau de réserve. Cette approche est inspirée des RBMs (Resource Budget Models, Isagi et al. 1997; Crone & Rapp 2014), où les fortes années de reproduction n'ont lieu que s'il y a dépassement d'un seuil de reproduction. Après la floraison, le printemps suivant en $n + 1$, le taux d'avortement floral réduit la quantité de fruits matures. Notre modèle prédit plusieurs années sans aucune production de cônes. Il est donc capable de reproduire un comportement de type « *masting* » et prédit aussi que la production de fruits moyenne sera plus importante dans le futur. Cette augmentation de la reproduction moyenne est due aux effets positifs du réchauffement (allongement de la durée de végétation) et à l'effet fertilisant du CO_2. L'effet de l'augmentation du CO_2 est effectivement un facteur qui peut entraîner l'augmentation de la reproduction. Des expériences d'enrichissement en CO_2 ont par exemple conduit à une biomasse plus importante de fruits produits, avec une masse par fruit plus importante (Way et al., 2010) ou bien une augmentation générale de la quantité de fruits produits sur l'arbre (LaDeau & Clark, 2001; Stiling et al., 2004). Des simulations ont aussi trouvé que pour la croissance, l'augmentation du CO_2 a un effet « fertilisant » permettant un accroissement plus important de la biomasse des arbres (Davi et al., 2006; Gea-Izquierdo et al., 2017).

Cependant, le seuil de réserves induisant la production de bourgeons floraux est le paramètre où nous avons le plus d'incertitudes. Un seuil faible assure une production de fruits chaque année, et un seuil élevée augmente la fréquence de production nulle de cônes (voir Figure Annexe). Dans notre cas, il n'est pas possible de prédire correctement avec ce modèle à la fois la production moyenne de cônes, ainsi que sa variation temporelle. Ainsi, la mise en place d'expérimentations pourrait réduire l'incertitude liée aux valeurs des paramètres. Cependant, estimer expérimentalement le niveau de ressources nécessaire à l'arbre pour se reproduire peut être difficile, à cause des multiples interactions avec l'environnent lors de l'allocation entre les différents puits (Hoch, 2015; Wiley et al., 2017). Une alternative peut être d'utiliser des méthodes inverses pour réduire l'incertitude des paramètres dans la calibration des paramètres, en utilisant d'autres variables observées à plus large échelle que celle de l'organe (Hartig et al., 2012; Evans et al., 2016). En plus de l'incertitude liée aux paramètres, nous n'avons pas inclus d'autres processus impliqués dans la reproduction, tel que la compétition par exemple entre la croissance et la reproduction. Des années favorables pour la reproduction sont peut-être des années défavorables pour la croissance, où le carbone est principalement alloué à la reproduction (Hacket-Pain et al., 2018; Lebourgeois et al., 2018). De plus, d'autres études ont trouvé que le climat est un élément majeur de la reproduction, car il peut favoriser l'initiation de

la reproduction (Kelly et al., 2013; Yeoh et al., 2017). Une augmentation des températures estivales, et des sécheresses avant la période d'initiation, peuvent augmenter la quantité de bourgeons floraux (Vacchiano et al., 2017). Il pourrait ainsi être intéressant d'intégrer un signal climatique pour induire l'initiation des bourgeons floraux, comme un mécanisme dans le modèle écophysiologique CASTANEA.

Chapitre VI

Discussion générale : De la compréhension des mécanismes à fine échelle vers la prédiction des patrons de reproduction à large échelle

1 Prendre en compte les ressources pour étudier la reproduction des arbres forestiers

L'objectif général de cette thèse était de comprendre et prédire l'effet du climat sur les variations spatiales et temporelles de production de graines chez les arbres forestiers, en prenant en compte l'acquisition et l'allocation des ressources aux différentes fonctions (croissance et reproduction). Pour cela, j'ai utilisé des approches complémentaires de modélisation statistique (à la fois fréquentistes et bayésiennes) et mécanistes, que j'ai mis en oeuvre à différentes échelles, des individus aux populations.

Tout d'abord, j'ai démontré dans le chapitre III que la durée de la saison de végétation affecte la production de fruits chez le Hêtre et les Chênes tempérés. Une avancée de la phénologie foliaire se traduit par une saison de végétation longue, conduisant à une période de photosynthèse et d'accumulation de photoassimilats plus importante, ce qui augmente la production de fruits de manière linéaire chez les Chênes et non linéaire chez le Hêtre. Pour ce dernier, une saison de végétation trop longue (supérieure à 170 jours environ) diminue la production de biomasse des fruits à l'échelle de la population. Ainsi, il est nécessaire de tenir compte de la variation de la phénologie des arbres pour mieux comprendre et prédire la production en biomasse de bois (Nemani, 2003; Vitasse et al., 2009b) et de fruits (Tapper, 1996; Nakamura et al., 2010).

En modélisant explicitement les ressources comme une variable latente, le modèle Bayésien que j'ai utilisé dans le chapitre IV a permis de mettre en évidence des compromis entre croissance et reproduction chez le Cèdre, et ce quel que soit le niveau de densité des peuplements. D'une part, initier un grand nombre de bourgeons reproducteurs diminue la croissance de l'arbre de l'année. D'autre part, les ressources allouées à la maturation des cônes diminuent celles allouées à l'initiation de nouveaux bourgeons, et donc à la reproduction de l'année suivante. La prise en compte des ressources, variable non observée et estimée grâce aux caractéristiques de l'arbre et du climat, a permis de détecter des compromis entre croissance et reproduction, et entre reproductions successives. La modélisation de la relation entre climat et ressources allouées à la croissance et à la reproduction dans cette approche était relativement simple et générale, mais ne tenait pas compte de processus écophysiologiques à l'échelle de l'arbre.

Pour palier ces limites, le modèle mécaniste présenté dans le chapitre V simule le cycle du carbone et de l'eau entre l'arbre, le sol et l'atmosphère, en intégrant des processus liés à la reproduction. Pour le développer, j'ai tout d'abord connecté le modèle écophysiologique CASTANEA (Dufrêne et al., 2005; Davi et al., 2009) et un modèle phénologique, implémenté dans PHENOFIT (librairie

PHELIB, utilisée par le modèle PHENOFIT, Chuine & Beaubien 2001; Morin & Chuine 2005), afin de mieux modéliser la phénologie de l'assimilation du carbone. Cette connexion permet de mieux simuler l'effet des gelées printanières sur la phénologie foliaire et reproductive. J'ai aussi ajouté un nouveau compartiment pour la reproduction au sein du modèle CASTANEA, et j'ai modélisé explicitement l'allocation du carbone des bourgeons aux graines et fruits. Le modèle est inspiré des « Resources Budget Models » (RBMs), qui supposent que le niveau de ressources accumulé par la plante a besoin dépasser un seuil pour qu'elle puisse se reproduire (Vacchiano et al., 2018). L'avantage de mon modèle par rapport aux RBMs est qu'il tient explicitement compte des effets du climat (la température, mais aussi le CO_2, le stress hydrique) sur la dynamique des ressources. Ce modèle prédit une augmentation de la moyenne de production de cônes pour le Sapin sur le Mont-Ventoux face aux changements climatiques. Cependant, il est encore nécessaire de développer ce modèle pour mieux comprendre quelles combinaisons de mécanismes et de paramètres déterminent la variation de production de graines et de fruits. Comme suggéré dans le chapitre III, il se peut aussi que, comme la croissance, la reproduction ne soit pas limitée par le carbone assimilé, y compris au moment de la maturation des fruits, mais qu'elle soit intimement liée à d'autres compartiments comme par exemple la croissance primaire et secondaire du bois. Ainsi, une année de forte production de graines peut réduire fortement l'accroissement des arbres décidus et conifères (Mund et al., 2010; Hacket-Pain et al., 2018; Lauder et al., 2019).

2 Vers une meilleure compréhension des mécanismes impliqués dans le *masting*

Le climat affecte les ressources allouées à la reproduction, de l'initiation des bourgeons jusqu'à la maturation des fruits. Le nouveau modèle écophysiologique développé dans le chapitre V n'a pas permis de simuler de façon complètement satisfaisante les variations de productions de fruits observées. Comme nous l'avons vu dans l'introduction, plusieurs mécanismes peuvent être responsables de variations de reproduction. La production de fruits peut être le résultat d'une production de bourgeons plus importante ou bien un avortement plus faible des fleurs et fruits. Mais avec ce nouveau modèle je pourrai étudier plus en détails les différents déterminants impliqués dans le *masting*, en testant d'autres hypothèses pour expliquer les variations du nombre de bourgeons floraux comme : l'effet du différentiel de températures pendant la saison de croissance (Kelly et al., 2013), l'effet des signaux hormonaux responsables de l'alternance que l'on retrouve chez les arbres fruitiers (Sedgley & Griffin, 1989), ou encore l'effet de stratégies consistant à produire une quantité constante de bourgeons, comme ce que l'on peut trouver a priori pour les Chênes (Pearse et al., 2016; Bogdziewicz et al.,

2017b).

Lors de la maturation, j'ai considéré un taux d'avortement journalier constant, qui réduit la quantité de bourgeons floraux et *in fine* la production de fruits. Mais ce taux d'avortement et le nombre de fruits finaux peuvent aussi être liés à d'autres compartiments de l'arbre, comme par exemple la croissance du bois ou les réserves. Nous savons que pour certaines espèces, il peut y avoir des compromis entre croissance et reproduction (Mund et al., 2010; Hacket-Pain et al., 2018; Lebourgeois et al., 2018; Bogdziewicz et al., 2019a) au niveau individuel, tels qu'une année de forte fructification réduit la croissance de l'arbre, ou entre individus, avec des stratégies d'allocation de ressources différentes entre individus. Il se peut que la reproduction soit liée positivement à la croissance, c'est-à-dire qu'une année où les conditions environnementales sont favorables à la croissance sont aussi favorables pour la reproduction (Pearse et al., 2016; Lebourgeois et al., 2018; Bogdziewicz et al., 2019a). Des études expérimentales ont démontré que la mise en place des fruits réduit la quantité de carbone des réserves disponible, et les fructifications futures (Miyazaki et al., 2002; Crone et al., 2009), mais la fructification dépend avant tout des assimilats de l'année en cours (Hoch et al., 2013; Miyazaki, 2013; Han & Kabeya, 2017). Les différentes combinaisons possibles de mécanismes, qui reposent sur différentes hypothèses d'allocation à la reproduction, de l'initiation des bourgeons floraux à l'avortement des fleurs ou des fruits, sont présentées dans le tableau récapitulatif VI.1 et la Figure VI.1.

En combinant ces différents schémas d'allocation, le modèle CASTANEA peut être utilisé pour mieux comprendre les processus déterminant les variations de productions de graines. A titre d'illustration, j'ai commencé à utiliser ce modèle pour simuler le nombre moyen de graines (en graines.m^{-2}) sur l'ensemble des sites RENECOFOR chez le Hêtre commun. J'ai testé trois schémas d'allocation au moment de l'initiation de bourgeons floraux (Figure VI.2) ; fixe, alterne et dépendant du niveau de réserves. J'ai considéré un taux d'avortement journalier constant (cf chapitre V). Dans ces cas-là, le modèle simule bien l'alternance sur l'ensemble des sites, avec des années de fortes productions suivies de faibles productions, quel que soit le schéma d'allocation (cf chapitre V). Cette alternance peut être induite, par exemple par le ratio entre bourgeons floraux et végétatifs initial ou bien par le taux d'avortement.

Une fois les mécanismes identifiés et le modèle calibré, il pourrait aussi être intéressant d'étudier les conséquences du *masting* en terme de productivité à l'échelle de la forêt. Il a par exemple été estimé que la production de fruits des forêts européennes en terme de NPP est d'environ 10 à 40 gC.m^{-2}.an^{-1}, et peut représenter 3% de la GPP (Fernández-Martínez et al., 2017b). On peut

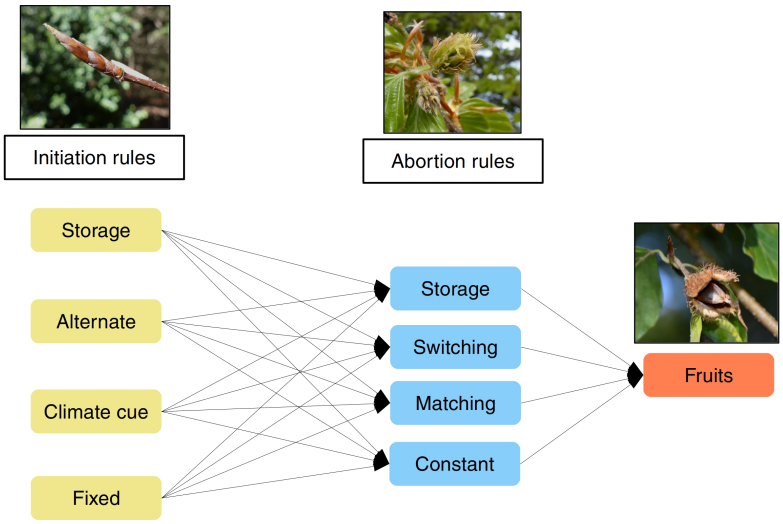

Figure VI.1: Différents schémas d'allocation proposés par le modèle CASTANEA. A noter qu'il est possible de combiner plusieurs hypothèses sur l'initiation des bourgeons floraux et sur l'avortement des fleurs et fruits. Dans le chapitre V, j'ai considéré que l'initiation des bourgeons reproducteurs dépend des réserves et que taux d'avortement journalier est constant. Photos : F. Jean, O. Gilg, S. Cecchini.

voir dans la Figure 2 de Fatichi et al. (2019) que la biomasse de reproduction simulée dans différents biomes (79 sites au total) augmente linéairement avec les précipitations, mais que cette tendance ne se retrouve pas dans les observations, où il y a des sites avec une biomasse de reproduction très faible voir nulle. L'utilisation de notre modèle pourrait permettre d'apporter des précisions sur le coût de la reproduction en terme de productivité pour des forêts tempérées (en utilisant des données issues des tours à flux où il est mesuré la NPP, GPP, etc. Reyer et al. 2019).

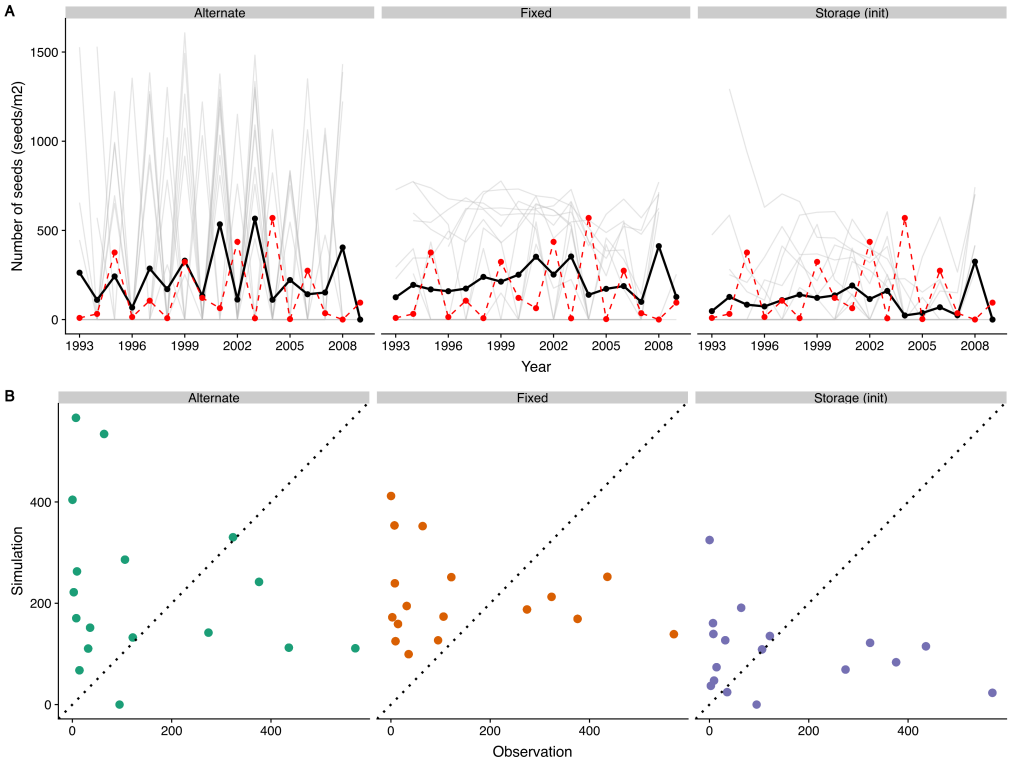

Figure VI.2: Exemple illustrant des simulations de nombre de graines pour différents mécanismes impliqués dans l'initiation des bourgeons floraux chez le Hêtre sur les sites RENECOFOR (20 sites au total). L'avortement est comme dans le chapitre V, constant. A) L'initiation des bourgeons floraux est ici alterne (« Alternate »), fixe (« Fixed »), ou bien dépendant du niveau des réserves (comme dans le chapitre V). En rouge figure la valeur moyenne du nombre de graines mesurées sur l'ensemble des sites par année, en gris, les simulations sur l'ensemble des sites et en noir la valeur moyenne du nombre de graines par année simulée sur l'ensemble des sites. En B) comparaison des valeurs moyennes du nombre de graines (i.e. graines.m^{-2}) simulées et observées par année, et suivant les différents processus liés à l'initiation des bourgeons floraux.

Initiation des bourgeons floraux	Avortement des fleurs/fruits
Réserves (*« storage »*) : le niveau de réserves détermine le ratio entre bourgeons floraux et bourgeons végétatif. Le nombre de bourgeons floraux initiés avec la quantité de réserves	**Réserves (*« storage »*)** : le taux d'avortement des fleurs diminue quand le niveau de réserve augmente.
Alternance (*« alternate »*) : une forte fructification réduit la quantité de bourgeons floraux inities la même année	**Transfert (*« switching »*)** : le taux d'avortement des fleurs augmente quand l'allocation du carbone à croissance augmente
Signal climatique : la quantité de bourgeons floraux augmente quand le différentiel de température entre $T_n - T_{n-1}$ lors de la saison de végétation de l'arbre augmente (inspirée du Δ_T).	**Appariement (*« matching »*)** : le taux d'avortement des fleurs diminue quand l'allocation du carbone à la croissance augmente
Fixe : une quantité de bourgeons floraux est fixée chaque année.	**Constant** : la production finale de fruits dépend d'un taux d'avortement de fleurs journalier constant.

Table VI.1: Les schémas d'allocation implémentés dans le modèle CASTANEA pour modéliser l'initiation des bourgeons floraux et l'avortement des fleurs/fruits.

3 Des données aux modèles

Le principal verrou à la compréhension des variations de reproduction en relation avec le climat reste la disponibilité des données nécessaires pour calibrer et/ou valider les modèles. Comme discuté dans le chapitre V, les modèles basés sur les processus écophysiologiques sont particulièrement gourmands en données, et certains paramètres sont assez difficiles à estimer expérimentalement (par exemple, le taux de réserves nécessaires pour se reproduire, les taux d'avortement, etc.). Un petit nombre de bases de données existantes rassemblent les données de fructification à large échelle, en général espèce par espèce. Il en existe pour les espèces Européennes comme le Hêtre et l'Epicéa commun (Ascoli et al., 2017a). Elle se caractérisent par une grande hétérogénéité des mesures de reproduction (nombre de graines/fruits ou indices de fructification ; nombre d'années de suivi). D'autres données de reproduction sont disponibles dans des base de données plus généralistes issues d'autres réseaux, par exemple ICP forests `<http://icp-forests.net/`, réseau intégrant les données RENECOFOR pour la France> où il est répertorié la quantité en biomasse des fruits à l'échelle de la placette. La base de données TRY comporte des éléments sur la masse des graines (`<https://www.try-db.org/TryWeb/Home.php>`).

En revanche, peu de données sont disponibles sur la phénologie des événements liés à la floraison et à la maturation pour les arbres forestiers (par exemple avec PHENOCLIM <https://phenoclim.org/fr>, PERPHECLIM <https://www6.inra.fr/projet-accaf-perpheclim/Acces-aux-donnees>). Il est aussi difficile de trouver des informations liées aux effets des gelées ou sécheresses sur les organes reproducteurs, leurs développement et leurs physiologie. En effet, les études portant sur l'effet d'événements climatiques extrêmes sont généralement faites sur des espèces herbacées modèles (Hedhly et al., 2009; Zinn et al., 2010) ou sur des arbres fruitiers (Sedgley & Griffin, 1989), mais rarement sur les arbres forestiers (exception par exemple avec Bykova et al. 2018 sur la production de pollen). De même, les données sur la cinétique du développement du fruit et l'effet de variables environnementales sur ce développement restent rares. Dans notre modèle d'accroissement des fruits, la croissance ne varie qu'avec le temps. Ce modèle, couramment utilisé pour la croissance des fruits (Bertin, 1995; Jullien, 2001), est caractérisé par une période de latence suivi d'un accroissement exponentiel avant d'atteindre sa masse finale. Il pourrait être intéressant de tester la validité de ce modèle pour les arbres forestiers. Les informations sur l'effet du climat sur le développement du fruit sont notamment indispensables pour prédire comment le changement climatique peut influencer la vitesse de maturation, mais aussi comment les concentrations en CO_2 peuvent influencer l'allocation du carbone lors de la maturation. Pour les arbres fruitiers cultivés et la vigne, il semblerait que des concentrations plus élevées de CO_2 augmente la taille des fruits et leur masse sans affecter la qualité des fruits (Ito et al., 1999; Bindi et al., 2001). Les travaux menés dans des milieux enrichis en CO_2 ont montré que les cultures allouent plus de biomasse à la reproduction et produisent en général plus de fruits et de graines (Jablonski et al., 2002).

La disponibilité de données, même peu précises (par exemple sous forme d'indices) est cruciale aussi bien dans les approches de modélisation statistique que mécaniste. Dans l'étude de modélisation statistique de Hacket-Pain et al. (2018), les auteurs ont utilisé des indices de fructification et de croissance pour étudier le lien entre croissance et reproduction chez le Hêtre à l'échelle européenne. Les auteurs ont trouvé un lien entre ces deux composantes, les années de fortes productions de fruits étant celles où la croissance est plus faible. Dans le chapitre IV, j'ai aussi utilisé des données d'indice pollinique pour caractériser l'initiation de la reproduction des individus, qui ont contribué à mettre en évidence des compromis entre l'initiation des bourgeons reproducteurs et la croissance des individus.

Les approches de modélisation mécanistes peuvent s'accommoder de jeux de données partiels, notamment pour leur paramétrisation, grâce au développement des méthodes de modélisation inverse (Hartig et al., 2012). Par exemple,

les méthodes Bayésiennes de modélisation inverse permettent de combiner des estimations directes de paramètres et de processus, codées dans des fonctions de vraisemblance des observations (Csilléry et al., 2010). Les approches ABC, *Approximate Bayesian Computation*, en particulier reposent sur (1) la simulation des variables de sorties d'intérêt (par exemple la date de débourrement) en considérant la gamme possible d'un ou plusieurs paramètres à partir de leur loi a priori, puis (2) le calcul de distance entre variables simulées et observées pour choisir les valeurs de paramètres les plus probables. L'objectif de cette méthode inverse dans notre cas est de sélectionner le meilleur vecteur de paramètres. J'ai testé cette approche pour calibrer le modèle de phénologie pour le Hêtre. Pour cela j'ai constitué un vecteur de paramètres (ex. 9 paramètres pour le modèle de phénologie du Hêtre, Gauzere et al. 2017), et où j'ai fait varié chaque paramètre dans une gamme de valeur (suivant par exemple une distribution uniforme). J'ai ensuite utilisé le modèle CASTANEA pour simuler la variable réponse d'intérêt (ici la date de débourrement) et ce pour chaque valeurs du vecteur de paramètres. Il est ensuite possible de comparer les valeurs simulées et observées, en tenant compte des corrélations potentielles entre paramètres, afin de retenir les meilleures valeurs pour le vecteur de paramètre (Figure VI.3). Un des objectifs suivants est de redéfinir les valeurs de paramètres sensibles pour la reproduction et la croissance, mais aussi de sélectionner au sein des différentes hypothèses présentées en tableau VI.1, un des schémas d'allocation qui prédit le mieux les productions de graines et fruits. Cependant cette approche nécessite d'avoir un nombre important de simulations et peut prendre plusieurs mois de simulations (ex. 80 jours de simulations dans Cailleret et al. 2019).

4 Perspectives

Dans le chapitre IV de cette thèse, c'est bien la variation entre individu de la relation croissance-nombre de cônes initiés, ou nombre de cônes initiés-nombre de cônes matures qui a permis de mettre en évidence les compromis. En revanche, dans les deux autres chapitres, je n'ai pas pris en compte la variation entre individus des paramètres/variables de reproduction. Dans le chapitre III, les analyses statistiques de la biomasse de fruits sont faites à l'échelle de la population. Dans le chapitre V j'ai considéré et modélisé un peuplement moyen, en faisant l'hypothèse que tous les arbres d'un peuplement ont les mêmes valeurs de paramètres. Néanmoins, plusieurs études sur la reproduction des arbres forestiers ont montré que certains individus ont tendance à produire beaucoup de graines contribuant ainsi majoritairement aux capacités de régénération des forêts (Davi et al., 2016; Minor & Kobe, 2017; Hacket-Pain et al., 2019). Nous pouvons remarquer dans le chapitre V, que certains individus ont tendance à produire plus de cônes pour le Sapin, alors que la majorité des autres individus n'en produisent pas. La maturation sexuelle, variable suivant la taille et l'âge

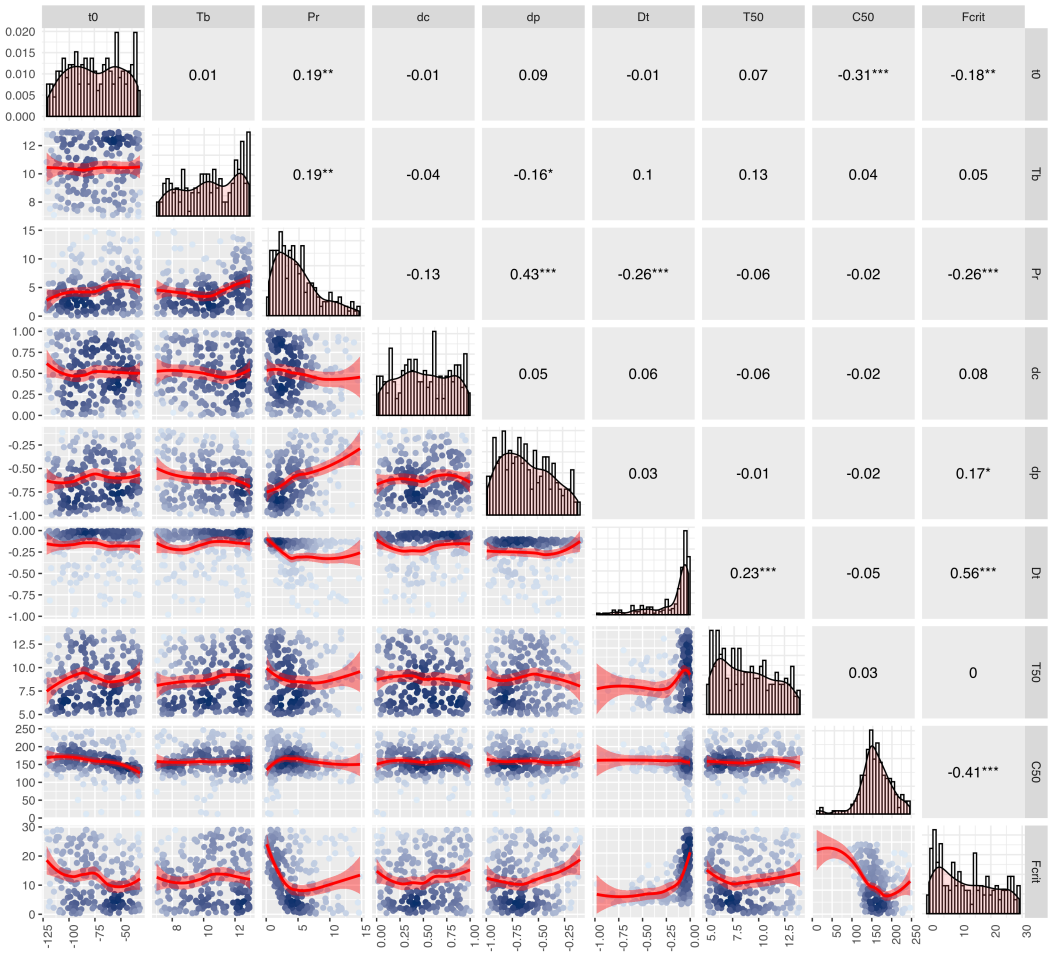

Figure VI.3: Calibration des paramètres du modèle de phénologie du Hêtre (Gauzere et al., 2017). Visualisation de la matrice de corrélation entre les différents paramètres du modèle de phénologie et des distributions a posteriori (génération de 100000 valeurs du vecteur de paramètre $\theta = (F_{crit}, T_{50}, C_{50}, t_0, T_b, d_p, d_c, d_T, P_r)$*, pour les 20 sites suivis sur la période 1993-2015).*

de l'individu, pourra aussi être une composante à intégrer dans le modèle de reproduction CASTANEA.

Dans le futur, nous envisageons de faire varier entre individus les valeurs de paramètres du nouveau module de reproduction de CASTANEA pour étudier comment différentes valeurs de tel ou tel paramètre affecte la valeur sélective des individus (gradients de sélection), ou pour simuler la dynamique adaptative de population dans lesquelles les traits de reproduction peuvent évoluer (Oddou-Muratorio & Davi, 2014). Je n'ai pas non plus pris en considération l'effet de la phénologie et la biomasse reproductive mâle sur la production de fruits, alors que diverses études suggèrent que ces mécanismes peuvent être limitants. Dans l'avenir, il pourrait être intéressant de modéliser la phénologie de l'émission de pollen dans notre modèle, et éventuellement l'effet de la biomasse reproductive mâle. Même avec des concentrations de pollen mâle moins importante, la phénologie de la floraison est aussi un mécanisme majeur qui peut expliquer les variations de productions de graines (Schermer et al., 2018; Bogdziewicz et al., 2019b).

Enfin, j'ai fait l'hypothèse que les ressources carbonées sont primordiales pour assurer la reproduction, et particulièrement la production finale de fruits. Dans le chapitre V j'ai suggéré qu'il y a sûrement d'autres mécanismes impliqués dans la reproduction, car je n'ai pas réussi à simuler l'ensemble des années de fructifications. Nous pouvons nous demander, si la reproduction, comme la croissance, est limitée par le carbone. Certaines études montrent déjà que le carbone n'est pas l'élément limitant la reproduction lors de l'initiation (Hoch et al., 2013; Han & Kabeya, 2017; Igarashi et al., 2019). Il pourrait être intéressant d'utiliser la version CASTANEA développée au laboratoire d'Ecologie, Systématique et Evolution à Paris, qui inclut le cycle de l'azote même si la version n'est pas validée pour l'ensemble du cycle. Pour les arbres fructifères, chez l'espèce *Fagus crenata*, l'azote prélevé dans sol, pendant la saison de végétation, est utilisé pour la croissance des fruits, et diminue ainsi la quantité d'azote dans les feuilles (Han et al., 2019). Il est aussi possible que le carbone soit non limitant lors de la maturation des fruits. Ainsi, il pourrait être intéressant de focaliser davantage sur la phénologie de la reproduction, comme ce qui est fait actuellement avec la croissance (Guillemot et al., 2017; Friend et al., 2019). Par exemple, en utilisant des approches moléculaires, il a été montré que l'expression des gènes impliqués dans l'initiation florale est sensible à la disponibilité des éléments tel que l'azote (Miyazaki et al., 2014; Miyazaki & Satake, 2017), mais est aussi sensible aux signaux environnementaux comme la sécheresse et température (Yeoh et al., 2017). L'étude de Yeoh et al. (2017), pour une espèce tropicale en couplant des approches moléculaires et de modélisation, a trouvée que l'initiation florale dépend de signaux environnementaux (sécheresse et températures fraîches) émis

2-3 mois avant l'activation des gènes liés à la floraison. Même si les déterminants de la floraison sont différents pour les espèces des régions tempérées, la biologie (et physiologie) moléculaire permettrait d'améliorer notre compréhension des effets environnementaux sur la physiologie et la phénologie de la reproduction, et *in fine* sur la reproduction des arbres.

5 Des modèles mécanistes intégrant la reproduction pour comprendre et prédire l'aire de répartition des espèces

La reproduction est une composante majeure de la valeur sélective et impacte les capacités d'adaptation des espèces (Morin et al., 2007; Chuine, 2010; Bykova et al., 2012; Duputié et al., 2015). Actuellement, la majorité des études portant sur les effets du climat sur la distribution des espèces à large échelle se basent sur des modèles corrélatifs de niches bioclimatiques (cSDMs), qui deviennent ainsi un outil majeur dans la communauté des forestiers (Pecchi et al., 2019). Cependant, pour les forêts, ces modèles ont parfois tendance à prédire un déplacement des aires bioclimatique assez massif (Dyderski et al., 2018; Vitasse et al., 2019b). Outre les critiques sur la structure des données utilisées et les méthodes de validation, plusieurs limites conceptuelles des cSDMs ont été identifiées, comme la non prise en considération des interactions entre espèces, de la dispersion, ou de l'adaptation (Hampe, 2004; Bahn & McGill, 2007; Beale et al., 2008; Lozier et al., 2009; Dormann et al., 2012; Fourcade et al., 2018). Inclure des mécanismes dans les cSDMs a été proposé comme une solution pour pallier leur limitation (Kearney & Porter, 2009). Dans une étude pionnière chez une espèce de Moustique (*Aedes aegepty*) en Australie, Kearney et al. (2009) ont intégré un modèle biophysique qui tient compte de l'influence du climat sur les différents stades de vie de l'organisme et un module qui tient compte de la variation de traits en réponse au changement climatique. Il est ainsi possible de savoir quelles variables climatiques affectent le plus le cycle de vie de l'espèce, mais aussi prédire la colonisation de l'espèce dans de nouveaux environnement en tenant compte de l'évolution des traits. Le couplage de cSDMs avec des modèles de dynamiques éco-évolutive (Cotto et al., 2017), ou bien avec l'intégration de la variabilité génétique, en associant le génotype avec l'environnement (Razgour et al., 2019) permettent d'obtenir des prédictions d'aires de répartitions actuelles plus précises et moins pessimistes sur le devenir des espèces pour le futur. Cependant ces approches ne sont encore pas très développées et sont encore des exceptions (voir Annexe 2).

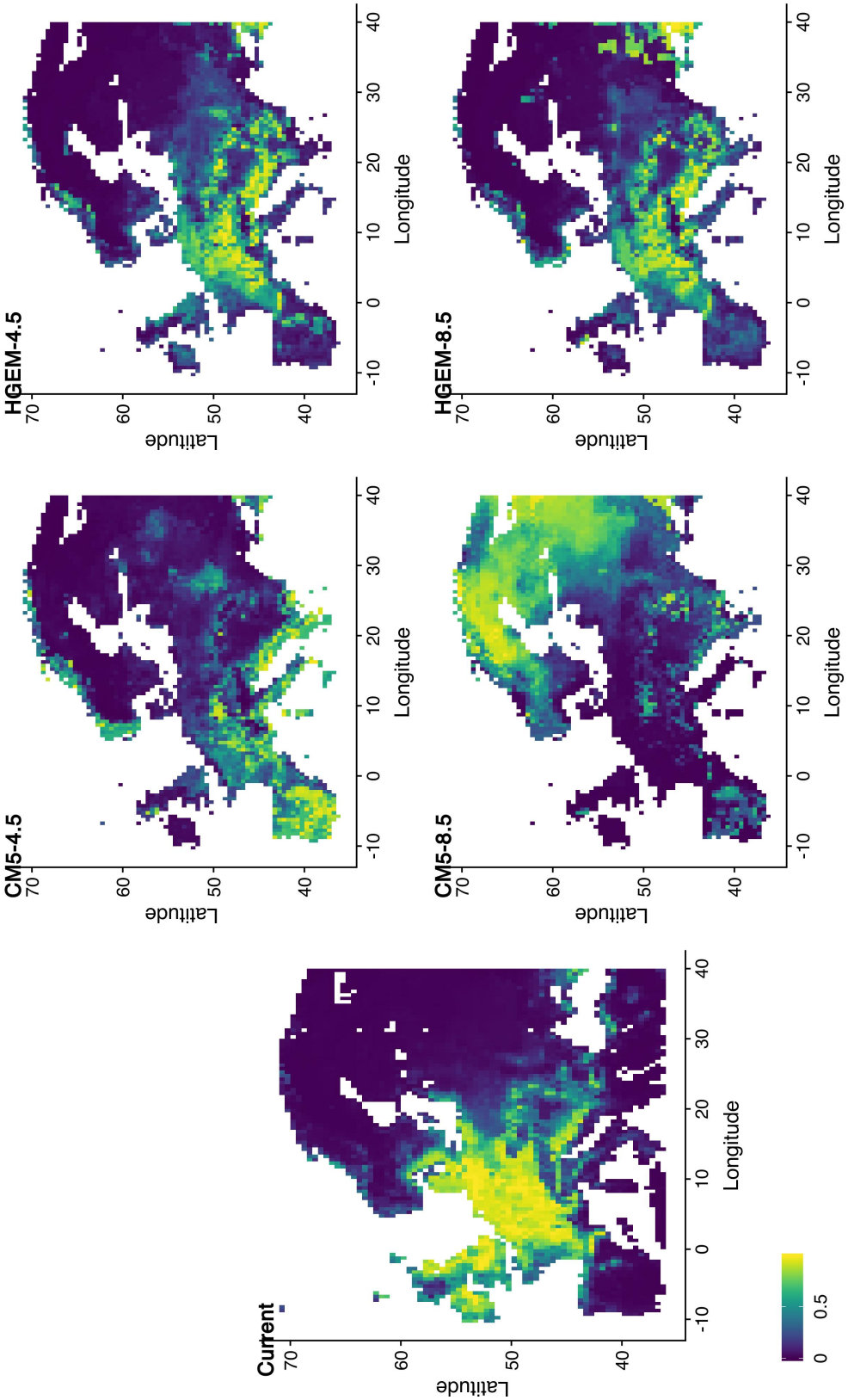

FIGURE VI.4: Prédictions de probabilité de présence issues de modèle de niche corrélatif (cSDMs) pour le Hêtre. Scénario climatique actuel (current) et futur (RCP4.5 et RCP8.5, avec les modèles climatiques HadGEM2 et CM5). Voir annexe pour les détails sur méthodologie.

Pour illustrer la capacités des modèles mécanistes à prédire l'aire de distribution des espèces, nous avons comparé les prédiction de distributions issues de cSDMs avec celle du modèle écophysiologique CASTANEA utilisé à l'échelle de l'aire de répartition du Hêtre en Europe (voir tableau VI.2). Par rapport aux modèles corrélatifs, qui prédisent pour le Hêtre un déplacement important de la niche bioclimatique (Figure VI.4), le modèle écophysiologique CASTANEA prédit une croissance plus forte (Petit-Cailleux et al, in prep) et une production de graines plus importante sur une large partie de l'aire de distribution (Figure VI.5).

Prédictions	**Valeur AUC – métrique d'évaluation**
Modèle écophysiologique CASTANEA	
Croissance (largeur de cernes en mm)	0.85
Nombre de graines (graines.m^{-2})	0.86
NPP (gC.gC^{-1})	0.86
Modèle corrélatif MAXENT	
Probabilité de présence	0.91

Table VI.2: Récapitulatif des valeurs issues des modèles à large échelle, entre modèle corrélatif et modèle mécaniste. Évaluation des prédictions avec l'AUC (Area Under The ROC Curve) à l'aide du climat actuel (données climatiques WATCH).

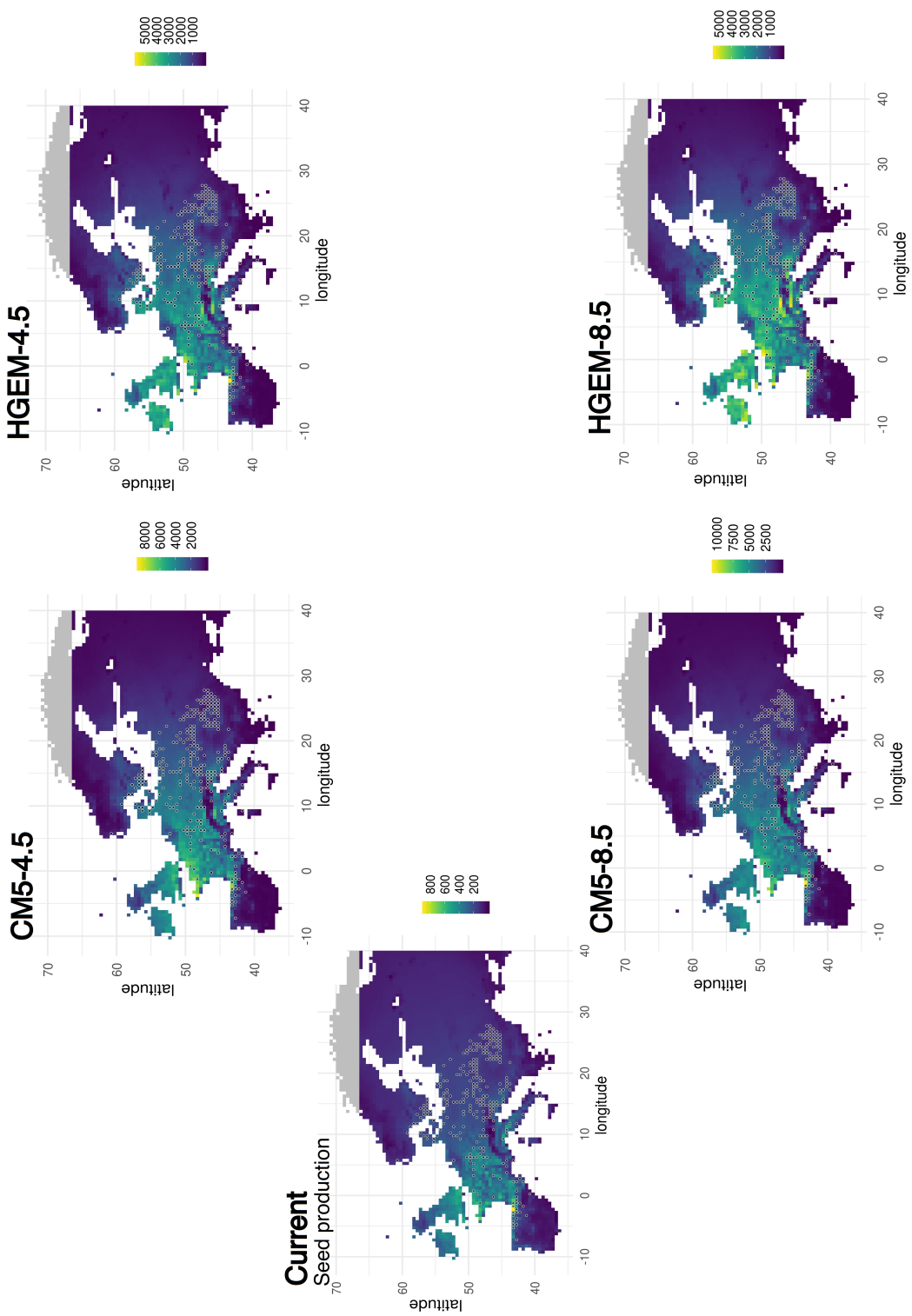

FIGURE VI.5: Prédiction de production de graines (graines/m2) issues du modèle mécaniste CASTANEA pour le Hêtre. Scénario climatique actuel (curent) et futur (RCP4.5 et RCP8.5, avec les modèles climatiques HadGEM2 et CM5).

Plutôt que de simplement comparer ces sorties comme ce qui a déjà été fait (Morin & Thuiller, 2009; Kramer et al., 2010; Keenan et al., 2011; Cheaib et al., 2012; Gritti et al., 2013b; Serra-Diaz et al., 2013), il peut aussi être intéressant de coupler des approches mécanistes et corrélatives pour réduire l'incertitude de la prédiction de la distribution liée aux différentes approches de modélisation (Gritti et al., 2013a; Talluto et al., 2016). Une étude de Talluto et al. (2016) a combiné un modèle corrélatif avec les prédictions d'aires de distribution issues d'un modèle mécaniste (modèle PHENOFIT, prédictions de distribution issues de Morin & Thuiller 2009). Il a pour cela développé un modèle corrélatif simple, où il est prédit la probabilité de présences de l'espèce (en fonction de la température du climat), et a ensuite « informé » les paramètres de ce modèle corrélatif à l'aide du modèle mécaniste PHENOFIT qui prédit de base une aire de répartition de l'espèce légèrement supérieur à ce qui est observé. En utilisant une approche bayésienne et en couplant l'ensemble de ces informations, il est probablement encore possible d'améliorer les prédictions de répartition d'espèces actuelles en tenant compte des incertitudes liées à ces différentes approches, et produire des prédictions futures intermédiaires entre « trop pessimistes » et « trop optimistes ».

La prise en compte de la reproduction dans les modèles processus pourrait potentiellement améliorer les prédictions de distribution (Bykova et al., 2012). En effet, pour les arbres, la reproduction influence la fécondité des individus et leurs capacité de migration. De plus, la reproduction, notamment les fortes variations de productions de graines peuvent aussi impacter les interactions entre espèces (Bogdziewicz et al., 2016). La production de graines est par exemple une ressource très prisée des communautés d'oiseaux et des mammifères. Une production de graines importante peut donc impacter les interactions entre espèces ainsi que leurs abondances (Clark et al., 2019). La complémentarité des différentes approches développées et utilisées dans cette thèse ont été intéressantes pour étudier les patrons de reproduction, et pourraient être développées pour étudier les conséquences du *masting* pour la compréhension des patrons biogéographiques.

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Annexes

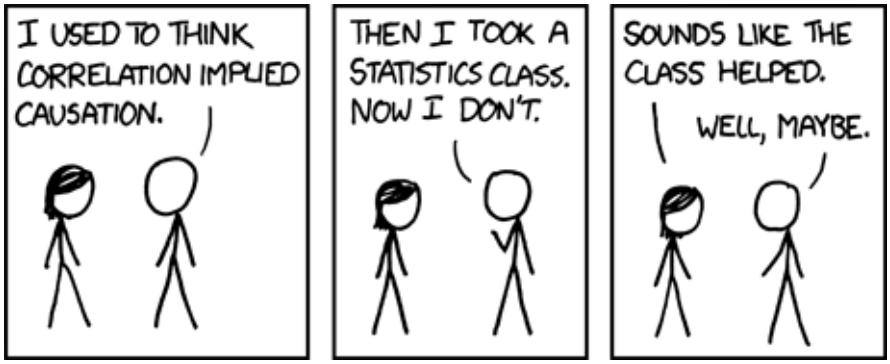

Figure 1: CORRELATION, de xkcd `https://xkcd.com/552/`

1 Cartes issues des modèles de niches corrélatifs pour le climat actuel et futur sur deux espèces forestières européennes

1.1 Zone d'étude et données d'occurrences

La zone d'étude correspond à la zone Europe Ouest (latitudes-10.5°O 40°E ; longitudes 36°S 71°N) représentant environ 11,850,000 km2 (4740 cellules de résolution 0.5*0.5, excluant Mer et Océans) pour les projections actuelles des répartitions d'espèces. A noter que pour les projections avec le climat futur une zone d'étude plus petite a été définie (avec 3784 cellules de résolution 0.5*0.5). Pour les espèces retenues, nous avons travaillé sur le Sapin pectiné (*Abies alba*) et le Hêtre commun (*Fagus sylvatica*), deux essences forestières largement présentes en Europe. Les données de présence sont issues de Mauri et al. (2017). Ces données sont issues d'une compilation des différents inventaires forestiers nationaux, avec des occurrences présentes à l'échelle de 1x1km. Cependant, la résolution des occurrences étant plus fine que la résolution de notre zone d'étude, plusieurs occurrences peuvent être associés à une seule cellule de la zone qui est à une résolution plus grossière. Ainsi, pour chaque cellules présentes dans la zone d'étude et contenant plusieurs présences nous les avons supprimées, de façon à n'avoir qu'une seule et unique présence par cellule. Au final il y a 398 présences sur la zone d'étude pour le sapin et 1195 présences pour le hêtre.

1.2 Données climatiques utilisées

Nous avons utilisé les données climatiques WATCH (*Water and Global Change - WATCH-Forcing-Data-ERA-Interim*) pour le climat actuel. Deux modèles climatiques futures ont été sélectionné issus de la communauté EUR-CORDEX, HADGEM (*EUR-11.SMHI.MOHC-HadGEM2-ES*) et CM5 (*EUR-11.SMHI.CNRM-CERFACS-CNRM-CM5*), avec différents scénario climatiques proposés à savoir RCP4.5 et RCP8.5 (Jacob et al., 2014). Ces modèles climatiques futurs ont été corrigé pour leurs biais potentiels à l'aide du package R "meteoland" (De Cáceres et al., 2018) et en utilisant comme référence le jeu de données climatique WATCH. Pour utiliser les modèles de niches, ces données journalières ont été moyenné pour chaque cellule, et pour les douze mois de l'année. Avec le climat WATCH, les données climatiques ont été moyennée de l'année 1979 à 2008. Pour HADGEM et CM5, les données ont été moyennées sur la période de 2060 à 2099 (Morin & Thuiller, 2009).
Nous avons ensuite retenu les variables climatiques mensuelles, pour chaque scénario climatique (WATCH, HADGEM et CM5), de précipitation, de température maximale et température minimale, convertit ensuite en raster. Ces rasters ont été convertit en variable bioclimatique. Au final il y a 19 variables

bioclimatiques (variables bioclimatiques similaires à celles de WORDCLIM <https://www.worldclim.org/>). Nous avons ensuite utilisé une analyse en composante principale (ACP) pour réduire le nombre de variable et avoir des variables synthétiques. Nous avons pour chaque scenario climatique retenu les cinq premiers axes de l'ACP (voir tableau 3 pour la variance des données pour chaque scénario climatique), et qui ont servi de variables explicatives pour les analyses suivantes. Les cinq axes ACP retenus explique de 93% à 95% de variance. Les variables ont été modifié en raster grâce au package "raster" (Hijmans, 2017), puis les variables bioclimatiques ont été obtenue à l'aide de la fonction *biovars*, du package "dismo" (Hijmans & Phillips, 2017) et l'ACP a été faite à l'aide du package "ade4" (Dray & Dufour, 2007). Toutes les analyses ont été effectuée sous R (version 3.4.4, R Core Team 2018).

	WATCH	**HadGEM**		**CM5**	
	Actuel	RCP4.5	RCP8.5	RCP4.5	RCP8.5
Axe 1 (%)	39.24	39.95	44.14	39.44	41.69
Axe 2 (%)	35.55	35.46	31.99	33.69	31.08
Axe 3 (%)	9.56	7.83	7.93	9.01	9
Axe 4 (%)	6.67	6.5	5.57	6.91	7.13
Axe 5 (%)	4.46	4.63	4.53	5.16	4.73
Total (%)	95.48	94.37	94.16	94.21	93.63

Table 3: Information résumée des axes de l'analyse en composante principale (ACP), utilisée pour la calibration des modèles (seulement à l'aide des données climatiques WATCH) et la projection future pour les différents scénarios climatiques RCP.

1.3 Modèles de niches corrélatifs : méthodes et résultats

Tous les modèles de niches ont été fait à l'aide du package "biomod2" (version 3.1-7.1, Thuiller et al. 2009), et de l'extension MAXENT (version 3.3.3, Phillips et al. 2006). L'algorithme de l'entropie maximale, aussi appelé MAXENT, utilise des point de présences de l'espèces et des "*backgroud points*", similaire à des pseudo-absences générées aléatoirement sur la zone d'étude. Par défaut le nombre de *background points* est défini à 10000, mais ce nombre est trop important pour notre zone d'étude, qui compte 4740 cellules au total. Pour cela nous avons à la place généré 1000 absences sur la zone d'étude (l'échantillonnage se fait dans l'ensemble de la zone et peut sélectionner des points de présence de l'espèce), et répété cette opération 10 fois (Barbet-Massin et al., 2012). Nous avons ainsi 10 jeux de données de présences-*background points*. Pour la calibration, nous avons retenu 75% de l'ensemble de données pour la calibration (i.e. inclusion des *background points* et des présences) et 25% pour la validation du modèle,

et cela pour les 10 échantillonnages des *background points*. De plus, nous avons aussi utilisé une évaluation supplémentaire, où nous avons sélectionné aléatoirement 10 fois le jeu de données de la calibration-validation (75-25). L'étape de calibration-validation a été effectuée sur le climat actuel (i.e. données climatiques WATCH). Au final, pour chaque espèce, il a été fait 100 lancements de modèle de niche pour le climat actuel. Les modèles ont ensuite été évalué avec l'AUC, Are Under the ROC Curve, qui varie de 0.5 pour les mauvaises prédictions de modèles à 1 pour les prédictions parfaites. Les cartes ont finalement été combinées toutes ensemble (i.e. combine les différentes estimations obtenues avec la combinaison des *background points* et des différents sélections aléatoires lors de l'évaluation) à l'aide de la fonction BIOMOD_EnsembleModeling. Une fois le modèle calibré et validé avec les données climatiques actuelles (i.e. données climatiques WATCH), nous avons projeté le modèle calibré sur les différents scénarios climatique future à l'aide de la fonction BIOMOD_Projection. Les cartes sont issues d'un ensemble de modèles pour chaque espèce et pour chaque scénario climatique, à l'aide de la fonction BIOMOD_EnsembleForecasting, et donne la probabilité de présence de l'espèce.
La valeur moyenne de l'AUC pour hêtre est de 0.91 (sd = 0.02) et pour le sapin l'AUC moyen est de 0.87 (sd = 0.03). Dans l'ensemble, les différents modèles de niches ont été assez performants, que ce soit avec une sélection aléatoire de présence-*background points* pour l'étape de calibration (Figure 2, A) ou bien lors de la sélection de *background points* sur la zone d'étude (Figure 2, B). En effet, pour la majorité des modèles de niches, l'AUC a une valeur supérieure à 0.80.

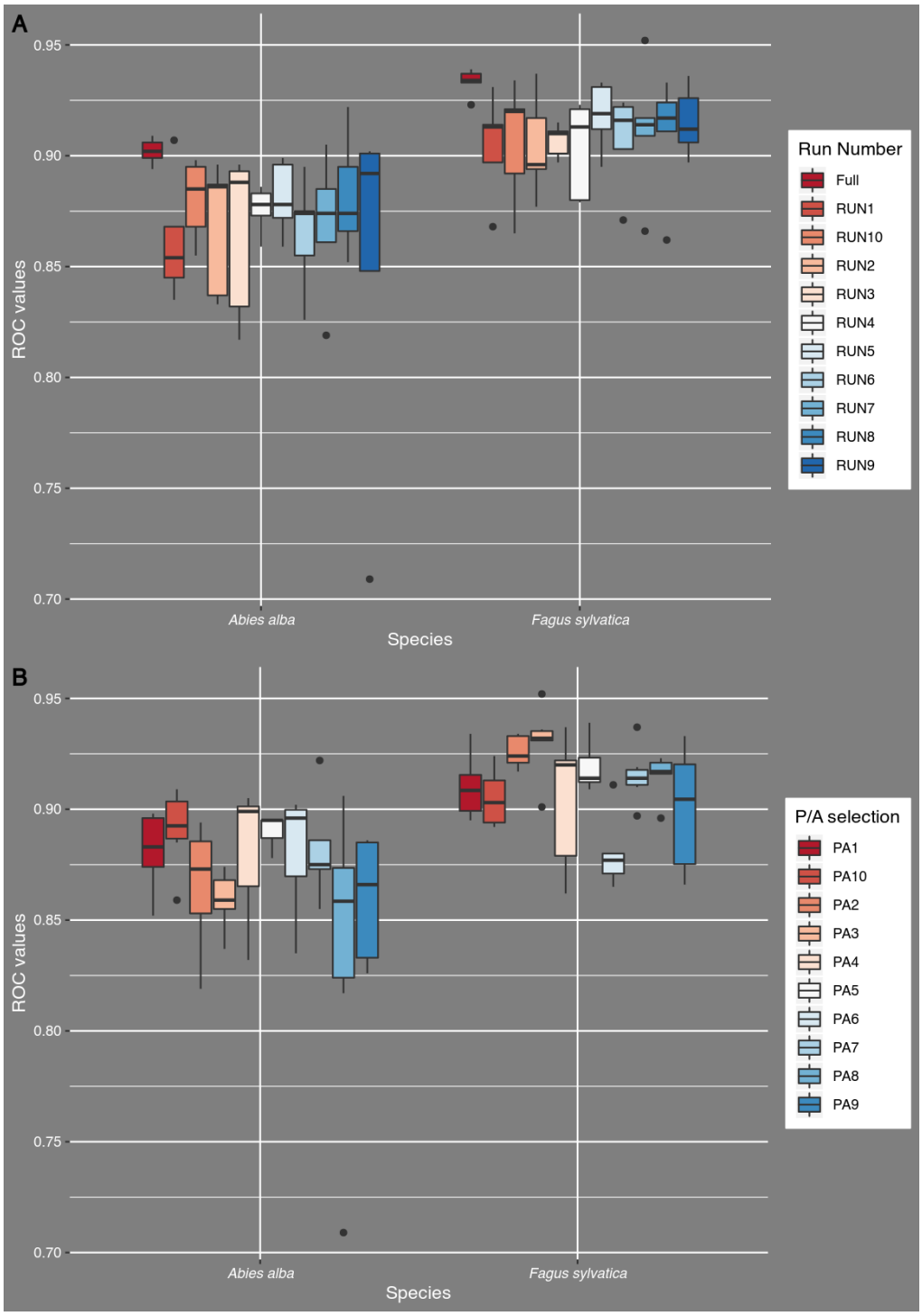

FIGURE 2: Valeurs AUC (ROC values curves) pour le sapin et le hêtre. En A, pour les 10 run d'évaluation et B pour les différents set de sélection de présences-background points retenus.

2 Utilisation de modèle de niche corrélatifs pour prédire les effets du changement climatique sur la biodiversité

Même si l'écologie prédictive n'a rien de nouveau, elle est devenue une approche de plus en plus importante (Mouquet et al., 2015). Par exemple, les modèles corrélatifs font partie des modèles les plus usités en écologie, notamment pour quantifier les facteurs biotiques et abiotiques impliqués dans la répartition géographique des espèces. Ainsi, les modèles de niche corrélatifs, appelés aussi "modèle de distribution d'espèce" ou "modèle de niche écologique", sont couramment utilisés pour prédire l'influence de l'environnement, principalement du climat, sur les répartitions d'espèces (Guisan & Thuiller, 2005; Elith & Leathwick, 2009). Ces modèles sont basés sur des corrélations entre occurrences d'espèces et variables environnementales. Avec cette approche, il a par exemple été montré que le changement climatique peut avoir des effets dévastateurs pour l'ensemble des espèces, et ce quel que soit le groupe taxinomique (Thomas et al., 2004; Thuiller et al., 2011). Plus récemment, des auteurs ont trouvé différentes stratégies pour les espèces d'arbres, où certaines seront beaucoup plus sensibles aux variations climatiques futures et seront vouées à une extinction rapide (Dyderski et al., 2018). Depuis une décennie, cette approche connaît une utilisation importante, avec des centaines d'articles publiés chaque année, liée aussi à une augmentation du facteur d'impact pour certaines revues (Brotons, 2014). En Août 2018, en cherchant sur toute la base de données du Web of Science<http://www.webofknowledge.com/>, avec les termes "species distribution model", "niche model", "habitat suitability model" ou "climate envelope", précisément 3475 articles de recherches y faisaient références (1980-2017) (requête effectuée : TS=("species distribution model" OR "niche model" OR "habitat suitability model" OR "climate envelope") AND PY=(1980-2017)) (Figure 3).

Une alternative à ces modèles peut être d'intégrer des mécanismes entre les traits d'un organisme et son environnement (Kearney & Porter, 2009). Par exemple, des études comparatives sur des essences forestières, entre modèle de niche corrélatif et modèle de niche basé sur les processus ont trouvé des restrictions d'aires de répartition moins importante avec le changement de climat futur (Morin & Thuiller, 2009; Keenan et al., 2011; Cheaib et al., 2012). Un inconvénient de l'approche corrélative est que les paramètres n'ont pas de sens écologique *a priori* et que beaucoup des processus déterminant la niche de l'espèce sont pris en compte implicitement mais ne peuvent pas être distingués entre eux (Dormann et al., 2012). De plus, avec cette approche, le climat est le driver principal des répartitions et les processus dynamiques sont supposés agir à une échelle fine (Araújo & Peterson, 2012). Cependant, peu d'études ont remis en

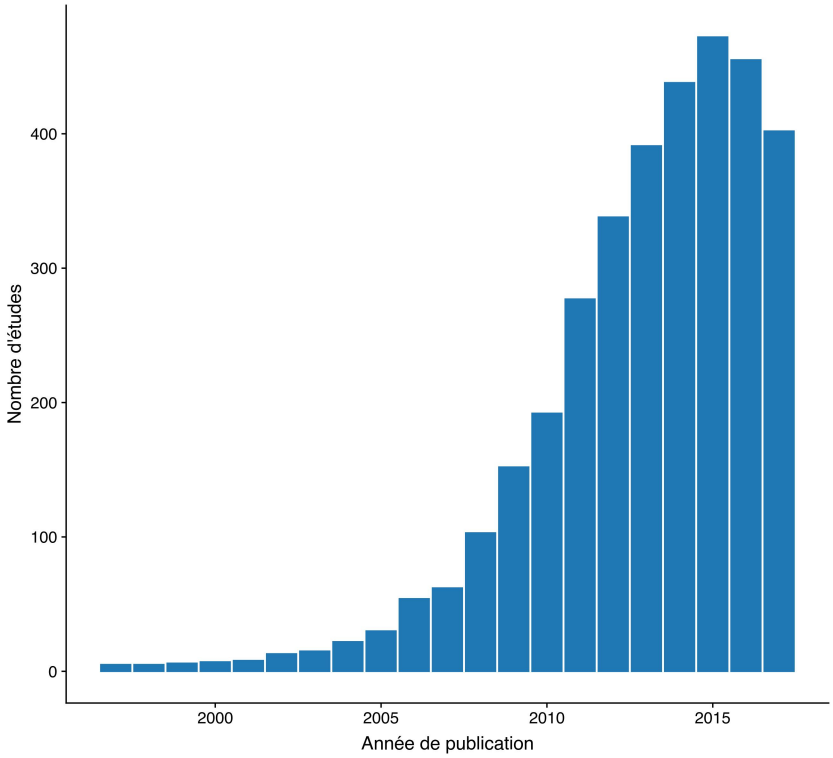

Figure 3: Nombres d'études basées sur les modèles de niche corrélatifs sur la période 2003-2017. Recherche faite sur Web of science `<http://www.webofknowledge.com/>` *(TS=("species distribution model" OR "niche model" OR "habitat suitability model" OR "climate envelope") AND PY=(1980-2017)).*

questions la fiabilité de ces modèles corrélatifs (Bahn & McGill, 2007; Beale et al., 2008; Chapman, 2010; Fourcade et al., 2018).

Dans notre étude, nous voulions savoir si ces modèles de niches corrélatifs sont capables d'identifier le lien entre climat et espèce, et ce pour différents groupes taxinomiques. Ainsi, pour chaque espèce, nous avons créé des espèces virtuelles, qui sont supposées n'avoir aucun lien avec le climat (équivalent à un modèle nul). Nous avons démontré qu'il est possible de prédire la distribution des espèces virtuelles à partir des données climatiques avec une précision égale à celle des espèces réelles. En d'autres termes, les données climatiques peuvent prédire correctement la répartition des espèces même quand le climat n'y joue *a priori* aucun rôle. Il semble donc que le pouvoir prédictif élevé de ces modèles peut être très fortement influencé, voire déterminé, par l'auto-corrélation spatiale dans les données climatiques, sans refléter de relations causales entre climat et répartition des espèces. Ainsi, la performance des modèles de niche corrélatifs ne permet pas d'identifier le lien entre climat et espèce. Les prédictions obtenues

avec cet outil, notamment pour la prédiction future des aires de répartitions des espèces, doivent donc être interprétées avec prudence.

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Correlative climatic niche models predict real and virtual species distributions equally well

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Abstract. Climate is one of the main factors driving species distributions and global biodiversity patterns. Obtaining accurate predictions of species' range shifts in response to ongoing climate change has thus become a key issue in ecology and conservation. Correlative species distribution models (cSDMs) have become a prominent tool to this aim in the last decade and have demonstrated good predictive abilities with current conditions, irrespective of the studied taxon. However, cSDMs rely on statistical association between species' presence and environmental conditions and have rarely been challenged on their actual capacity to reflect causal relationships between species and climate. In this study, we question whether cSDMs can accurately identify if climate and species distributions are causally linked, a prerequisite for accurate prediction of range shift in relation to climate change. We compared the performance of cSDMs in predicting the distributions of 132 European terrestrial species, chosen randomly within five taxonomic groups (three vertebrate groups and two plant groups), and of 1,320 virtual species whose distribution is causally fully independent from climate. We found that (1) for real species, the performance of cSDMs varied principally with range size, rather than with taxonomic groups and (2) cSDMs did not predict the distributions of real species with a greater accuracy than the virtual ones. Our results unambiguously show that the high predictive power of cSDMs can be driven by spatial autocorrelation in climatic and distributional data and does not necessarily reflect causal relationships between climate and species distributions. Thus, high predictive performance of cSDMs does not ensure that they accurately depict the role of climate in shaping species distributions. Our findings therefore call for strong caution when using cSDMs to provide predictions on future range shifts in response to climate change.

Key words: *blocked cross-validation; climate change; model evaluation; null models; range shift; spatial autocorrelation; species distribution models.*

Introduction

Climate is one of the main drivers of global diversity patterns along latitudinal and elevation gradients (von Humboldt 1807, Merriam 1894, Francis and Currie 2003, Willig et al. 2003) and is unquestionably a major determinant of species distributions regardless of taxa (Woodward 1987, Kearney and Porter 2009), as shown by paleoecological data (e.g., Williams et al. 2004), experimental approaches (e.g., Pigott and Huntley 1980, Rehfeldt et al. 2002), or current observations of range shifts in response to climate change (e.g., Walther et al. 2002, Parmesan and Yohe 2003). However, a complex array of factors interacts with climate to shape actual species distributions. Biotic interactions, dispersal, microhabitat availability, and disturbances (including anthropogenic habitat changes or local species extirpation) all contribute to displace boundaries of species ranges away from the limits of their climatic niche (Sexton et al. 2009) and generate differences between the climatic requirements of a species (i.e., its fundamental climatic niche in the sense of Hutchinson 1957) and its geographic realization (Gaston 2003).

Deciphering the links between climate and species distributions is more crucial than ever: Robust predictions of species range shifts in response to climate change is a priority for the conservation of biodiversity and its functions (Coreau et al. 2009, Mouquet et al. 2015), but climate-based predictive models of species distributions rely on crucial assumptions on the role of climate in setting species distribution boundaries (Sexton et al. 2009). These assumptions are straightforward for species whose range limits are known to be affected by climate, but they require a cautious examination in most cases because nonclimatic drivers may be important (Guo

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2003). In fact, disentangling the relative influence of climate and other ecological factors on species distribution, and understanding how these drivers determine species range limits, remains particularly challenging (Coreau et al. 2009).

Various approaches have sought to identify the determinants of range limits in plants and animals (Gaston 2003, Sexton et al. 2009). Among these, frameworks based on correlations between species distributions and climatic variables have a long history (Merriam 1894). Building on this legacy, correlative species distribution models (cSDMs; see Jarnevich et al. 2015) represent the most popular approach by far and have been applied to a wide range of taxa and geographic scales (e.g., Thomas et al. 2004, Pereira et al. 2010, Thuiller et al. 2011). Experiments permit a more direct assessment of the causal role of climatic factors on species distributions (e.g., Breeman 1988, Loehle 1998, Morin et al. 2007*a*), but they are difficult to carry out at large spatial scales and for all organisms. Mechanistic modeling approaches relying on explicit species responses (e.g., growth, survival, reproduction, phenology) to climate variables have also been developed in the last two decades, for plant (e.g., Chuine and Beaubien 2001) and animal species (e.g., Kearney and Porter 2009), emphasizing the role of acclimation to cold temperatures (Leinonen 1996), phenology (Chuine 2000), or metabolic rates (Kearney and Porter 2004). However, these process-based models have been restricted to a small number of species (see, e.g., Morin et al. 2007*b*, Sinervo et al. 2010, Diamond et al. 2012) because the data needed to implement such tools are difficult to collect.

The vast majority of studies aiming at predicting species range shifts in response to climate change have therefore used cSDMs based on climatic variables (Guisan and Thuiller 2005, Pacifici et al. 2015). These "climatic cSDMs" predict local presence probabilities of a species from correlations between distribution data (occurrences in most cases, sometimes abundances) and climatic variables (Elith and Leathwick 2009) and are relatively straightforward to calibrate. Nonclimatic predictors can also be used in cSDMs (e.g., land cover: Thuiller et al. 2004, Ay et al. 2017; dispersal and biotic interactions: Heikkinen et al. 2007, Cabral and Schurr 2010, Boulangeat et al. 2012, Palacio and Girini 2018), but these examples are the exception rather than the rule. However, the ability of climatic cSDMs to identify and quantify the role of climate on species distributions properly is challenged increasingly often. The forecasting abilities of cSDMs can be tested by comparing their predictions of range shifts between past and current distributions—assessed with historical occurrence data—based on observed climate change with actual range shifts. Although there are still few examples (Elith and Leathwick 2009), this approach yielded mixed results so far: Sofaer et al. (2018) reported that modeling was poor at predicting observed range change in North American birds, and Fordham et al. (2018) concluded the opposite in British birds (but with considerable variation in predictive abilities among species; see, e.g., fig. 3 in Fordham et al. 2018). For butterflies, Kharouba et al. (2009) showed that climate-change–,induced range shifts of North American species could be well predicted by SDMs for most of the 160 species tested, but also reported a large variation between species in the abilities of the models to predict observed range shifts correctly, despite high spatial model accuracies during model training. Another widely used approach to evaluate predicting abilities of cSDMs is to compare predicted and observed distribution in invasive areas. Again, this approach produced contrasted conclusions. For instance, Peterson et al. (2003, plants), Petitpierre et al. (2012, plants), or Ramírez-Albores et al. (2016, plants) reported good abilities of cSDMs in predicting invasive ranges, but Broennimann et al. (2007, plants), Beaumont et al. (2009, plants), Gallagher et al. (2010, plants), Early and Sax (2014, plants), Goncalves et al. (2014, plants), or Hill et al. (2017, insects) found opposite conclusions.

One of the main reasons for the success of climatic cSDMs undoubtedly lies in the strong accuracy of their results when compared to observed species distributions. Such high goodness of fit under current climatic conditions is often interpreted as evidence for the ability of cSDMs to represent a causal link between climatic variables and species range (e.g., Pearson and Dawson 2003, 2004, and see review by Elith and Leathwick 2009) or as a way to identify key specific climatic variables driving species range limits (e.g., Bombi et al. 2009, Gogol-Prokurat 2011, Javanbakht et al. 2017). However, several studies have questioned the ability of cSDMs to identify accurately the role of climate in determining species range (Loehle and LeBlanc 1996, Bahn and McGill 2007, Beale et al. 2008, Lozier et al. 2009, Fourcade et al. 2018, Rich and Currie 2018). A key criticism is that cSDMs rely on correlations that do not necessarily have a causal basis, and that they cannot be externally validated because they are typically tested by resampling the data set of available occurrences (Dormann et al. 2012).

Null models represent a more appropriate way to assess the capacity of species distribution models to detect the causal relationship between species and climate (Gotelli and Graves 1996). Only a handful of studies have used null models to assess the robustness of climatic cSDMs in the past, either by comparing the output of cSDMs obtained on actual species distributions and on virtual species distributions (Bahn and McGill 2007, Beale et al. 2008, Jiménez-Valverde et al. 2011) or by using randomized environmental predictors (Boucher-Lalonde and Currie 2016, Fourcade et al. 2018). These null model approaches have yielded mixed results. For instance, Beale et al. (2008) concluded that species–climate associations found by cSDMs were no better than chance in a majority of European bird species, while Jiménez-Valverde et al. (2011) found the

opposite conclusion for North American birds. However, most of these studies questioning the actual robustness of cSDMs have focused on bird species, and no study that we know of has used null models to assess the goodness of fit of cSDMs across several taxonomic groups, i.e., to test whether the robustness of cSDMs may depend on the group of taxa considered.

In this study, we used real species from five taxonomic groups and virtual species distributions of the same range size to test whether or not the accuracy of cSDMs calibrated with climatic variables reflect the role of climate in shaping species distribution. By doing so, we assessed the extent to which cSDMs can actually capture the processes linking climate and species distributions. A key requirement of our approach is the design of appropriate null models. We used random diffusion models, unconstrained by climatic gradients, to build virtual species distributions that have no causal link to climate, then compared the performance of climatic cSDMs when predicting real and virtual species distributions. We selected real species in five groups differing in their ecology and dispersal abilities, which excludes that our findings are explained by biological traits specific to a given group of organisms. Our aim was to answer the following question: can the distribution of virtual species be predicted with a similar accuracy as real species? Doing so, we do not question the role of climate as a major driver of species distributions (see Merriam 1894, Walther et al. 2005, Chen et al. 2011), or that cSDMs can be useful for assessing climate change impacts whenever climate is the main factor limiting a species range. Instead, what we precisely question is the use of cSDMs to assess the importance of climate on species distributions and consequently their use in predicting range shifts in response to climate change in species where the link between climate and range limits has not been clearly established.

We focus this study on the Western Palearctic region (Europe, North Africa, and the Middle East) because species distributions there are known with greater accuracy than in most other areas and can be associated with reliable climatic data. We selected two plant functional groups (herbaceous plants and trees), and three vertebrate groups, two ectotherms (reptiles and amphibians), and an endotherm (birds). We randomly picked 25 species (hereafter "real species") of widely variable range size (i.e., prevalence) in each of these five groups. For each real species, we generated 10 virtual species distributions with spatial cohesion. We hypothesized that the predictive power of cSDMs varies across each taxonomic group because of their contrasted ecologies. For example, one may expect that plants, amphibians, and reptiles could be more influenced by the variation in climate variables than warm-blooded species such as birds (Gaston 2003). We also expect that the predictive accuracy of cSDMs decreases with increasing species range size, because larger distributions tend to sample broader arrays of climatic conditions than restricted-range species. Furthermore, we used a newly proposed rigorous evaluation of models' outcomes (Roberts et al. 2017) to strengthen the scope of our findings. We therefore (1) assessed the sensitivity of our analysis to range size and (2) compared accuracy of cSDM results on real species distributions between the five species groups, then (3) compared the accuracy of climatic cSDM suitability maps obtained for these virtual species distributions to those obtained for the real species, across the five groups of taxa.

Methods

Study area and climatic variables

The study area corresponds to the Western Palearctic ecozone, including the European region of Eurasia together with North Africa (north of the Sahara) and the Middle East (Fig. 1). It is located roughly between the latitudes of 30° to 72° N and the longitudes of 12° W to 68° E and covers an area of 33,152,400 km² (i.e., 331,524 pixels of 5-arcmin resolution) when excluding oceans and large water bodies. Using a finer resolution would have been relevant regarding the resolution of species distribution. Because pixels are different around the shores to the Caspian Sea, we redefined the Caspian Sea with a specific mask.[5] We downloaded 19 climatic variables from the WORLDCLIM database[6] (Appendix S1: Table S1; see Hijmans et al. 2005 for more details) and added elevation[7] because it strongly correlates with local climatic conditions in the study area. We used a principal-component analysis (PCA) to reduce the number of predictors to a smaller number of uncorrelated synthetic variables. The first six axes of a PCA on all 20 original variables explained ca. 97% of the variance of the data set (Appendix S1: Table S1) and were retained as predictors in all subsequent modeling analyses. This was sufficient for our purpose, as we did not aim to identify the most relevant climatic variables influencing the range of a given species.

Real species distribution data

We first built a species list for birds, amphibians, reptiles, and herbaceous plants occurring in Europe, retaining only species native to Europe that have most of their breeding range within Europe. We further excluded seabirds and other strictly coastal or insular bird species. Once the lists were completed, we randomly selected 25 species for each of these taxa (100 species in total). For these four taxonomic groups, species distributions were downloaded from the International Union for Conservation of Nature (IUCN) Red List website (IUCN 2017).

[5] http://www.naturalearthdata.com/downloads/50m-physical-vectors/

[6] www.worldclim.org, version 1.4

[7] https://lta.cr.usgs.gov/SRTM

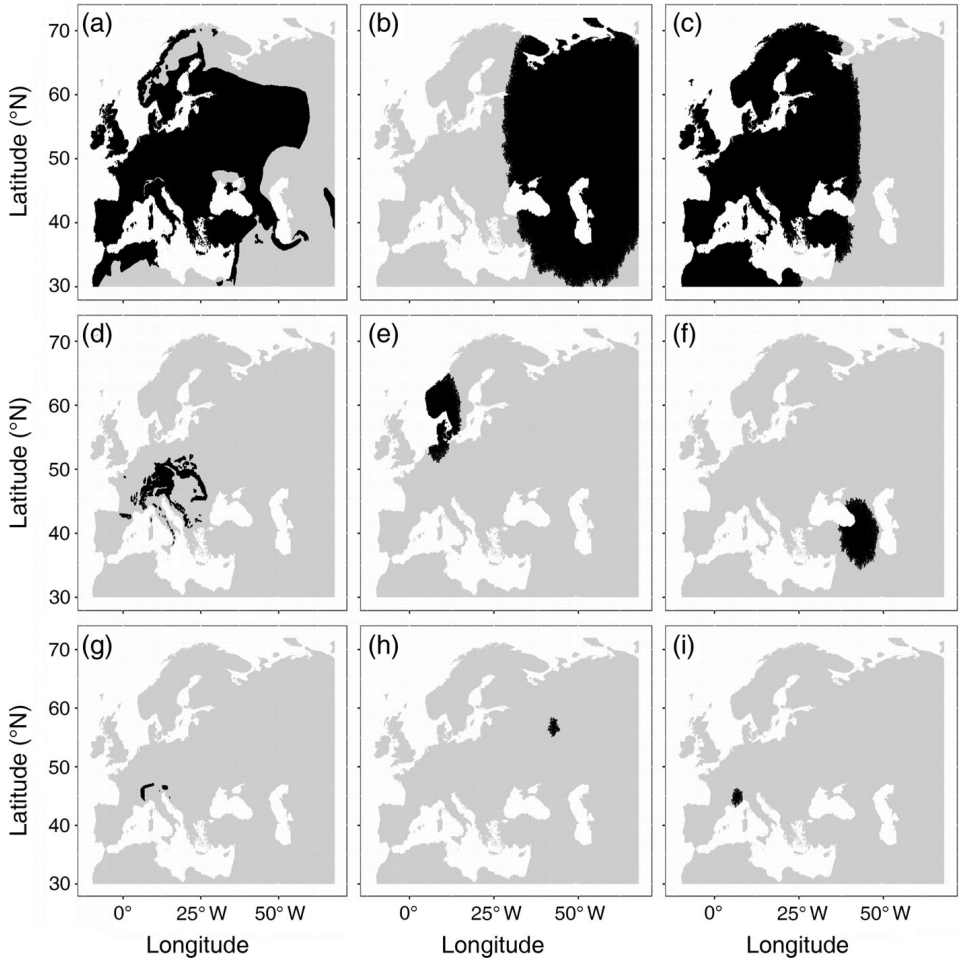

FIG. 1. Distribution of (a) *Chloris chloris* (bird), (d) *Abies alba* (tree) and (g) *Eryngium alpinum* (herbaceous plant), and two examples of virtual distributions for each of these three species [(b) and (c) for *C. chloris*; (e) and (f) for *A. alba*; (h) and (i) for *E. alpinum*].

If a distribution was not available for a given species, we randomly picked another species of the same group in our list. For trees, we downloaded the distributions of all 26 available species (at the time of the study in 2016) from EUFORGEN[8] (San-Miguel-Ayanz et al. 2016). We removed areas of nonnative presence (if any) and nonbreeding range for birds, as well as parts of the range located outside the study area. We then rasterized species distribution maps into presence–absence data at a 5-min resolution to match climatic data. Because some of the selected species had small ranges (i.e., less than 100 pixels), we anticipated difficulties to fit accurately a distribution model (as illustrated in other studies, e.g., Stockwell and Peterson 2002). We therefore added three supplementary species of amphibians and herbaceous plants to circumvent this issue. In total, we gathered data for 132 species distributions of five taxonomic groups. The distributions of 88 species were entirely included within our study zone. The distributions retained for the final analyses vary from local endemics (minimum of six pixels) to continent-wide presence (maximum of 244,492 pixels on 331,524 land pixels; see Data S1 and Metadata S1).

[8] http://www.euforgen.org

Null models

For each real species, we generated 10 virtual species distributions with the same range size (prevalence) as the real species (Fig. 1; Appendix S1: Fig. S1). We chose to generate spatially cohesive distributions for virtual species, that is, the virtual distributions were formed of a single block rather than multiple isolated pixels with occurrence data (see Discussion). We developed an algorithm under the R environment (R Development Core Team 2016) to generate these virtual species distributions using a diffusion model approach (Data S2 and Metadata S2). We started by randomly selecting one pixel in the study area. The virtual distribution was then extended gradually by colonizing adjacent pixels in a direction chosen randomly at each step, until the final range size was reached (i.e., the same range size as the corresponding real species). Whenever a pixel was

selected within a large water body, it was exchanged with the closest unoccupied pixel in land. This procedure guaranteed that sea basins were not a barrier to "colonization" and avoided the middomain effect (Colwell and Lees 2000), where most distributions would be located in the center of the study area.

Distribution modeling

All cSDMs were fitted with the R package BIOMOD2 (Thuiller et al. 2009). We used the same modeling workflow for real and virtual distributions (Appendix S1: Fig. S1). We used two kinds of algorithms to fit the cSDMs. First we built generalized additive models (GAMs; Wood 2006) to describe the relationships between presence–absence data and the six climatic predictors. GAMs are commonly used in species distribution modeling because they handle complex responses and are robust to data quality as well as to the number of absence data (Barbet-Massin et al. 2012).

As our main aim was to compare real with virtual species, we did not need to split the data set of observed presences as commonly done to test for the validity of the fitted model. Thus we first fitted GAMs by including all the pixels in our study area (331,524 pixels, from 6 to 244,492 presences depending on the species), considering all pixels outside species' distributions as absences.

However, considering all pixels may inflate goodness-of-fit values and thus level differences between real and virtual species. In most cSDMs-based studies, model validation is assessed on a random subsample of the data set of observed presences or presences–absences different from the subsample of data used for model calibration. Calibration and validation based on random samples of presence–absence data can underestimate the errors when dependence structures are present in the data (Roberts et al. 2017), as is the case with climatic data. In fact, defining separate blocks for training and testing model represents a new opportunity to limit effect of spatial structure for climate and species distribution (Roberts et al. 2017). Block cross-validation can address these issues. As recommended by Roberts et al. (2017), we defined two nonrandomly chosen blocks of data, one for cSDM calibration and another one for cSDM validation. To do so, we split the study area in two according to the mean latitude of species distribution. We then sampled 5,000 absences in each block to ensure a minimal value of 10,000 absences in total for the study site (Barbet-Massin et al. 2012). When it was impossible to split the study area according to latitude, we used longitude. We present results for both methods, that is, with and without cross-validation, for GAM algorithm. Our general methodology is summarized in Appendix S1: Fig. S1.

As GAMs are prone to overfitting and may produce response functions that are difficult to interpret biologically (Wood 2006), we also used MAXENT (v3.3.3, Phillips et al. 2006, using only presence data) to assess the robustness of our findings to changes in algorithm. The results obtained with MAXENT were qualitatively similar to those obtained with GAMs and are not detailed here (see Appendix S1: Section S1). Note that overfitting can also affect machine learning methods or MAXENT (Elith et al. 2006, Elith and Graham 2009).

Model evaluation and statistical analysis

We used the two most common evaluation methods (Fourcade et al. 2018) to calibrate and validate GAMs, the area under the receiver operating curve (AUC) criterion and true skill statistics (TSS). AUC is independent from the threshold value used to convert probabilities of presence per pixel into presence—absence data (Elith and Leathwick 2009) and is one of the most popular criteria to evaluate cSDMs. An AUC value of 1 means a perfect fit, and a value of 0.5 corresponds to random prediction of a species presence in a given cell.

To check whether our conclusions are sensitive to the evaluation metrics used, we also used a threshold-dependent metric with the GAM algorithm, the TSS (Allouche et al. 2006). The TSS is an alternative metric used in cSDMs studies that is not influenced by the distribution size. It is based on presence–absence data and varies between −1 (poor fit) and 1 (perfect fit). To convert the probabilities of presence into presence–absence data for TSS, we used a threshold value maximizing sensibility and specificity as recommended by Liu et al. (2013). Two real species and 49 virtual species were not predicted because of the low number of presences used to calibrate the model, but the results yielded the same conclusions than the AUC (see Fig. 3).

To compare the accuracy of cSDMs results for virtual and real species distributions, we assigned a rank to each real species based on its AUC (or TSS) value compared with the AUC (or TSS) values of its 10 corresponding virtual species: if the real species was found to have the highest AUC (or TSS) it was assigned the first rank, that is, rank 1, whereas if it was found to have the lowest AUC (or TSS) it was assigned the last rank, that is, rank 11. We then compared the rank distribution of the real species to the expected distribution under the null hypothesis that AUC (or TSS) values did not differ between real and virtual species. We also used a *t*-test to test whether AUC (or TSS) values of cSDMs differed between real and virtual species and an *F*-test of equality of variances I to test if real and virtual species had AUC (or TSS) of equal variance (Stats package in R).

Last, we ran a general linear model in Statistica version 10 (StatSoft 2011) to examine the effects of group and prevalence on AUC (or TSS) for real species only. Prevalence was log-transformed prior to analysis to reduce nonnormality and group was defined as random. We started with the complete model AUC (or TSS) = log (prevalence) + group + group * prevalence.

Results

Comparison between real and virtual species

The distributions of the real species were generally accurately predicted without cross-validation (hereafter CV), with AUC values ranging from 0.899 to 1.00 ($\mu_{AUC} = 0.972$, $\sigma_{AUC} = 0.02$), and AUC values with blocked CV ranged from 0.308 to 0.99 ($\mu_{AUC-CV} = 0.675$, $\sigma_{AUC-CV} = 0.179$, Appendix S1: Fig. S3). The TSS values ranged from 0 to 0.99 without CV ($\mu_{TSS} = 0.844$, $\sigma_{TSS} = 0.129$) and from 0 to 0.98 with blocked CV ($\mu_{TSS\text{-}CV} = 0.323$, $\sigma_{TSS\text{-}CV} = 0.278$, Appendix S1: Fig. S3). The AUC and TSS values of cSDMs for virtual species distribution were also higher without CV ($\mu_{AUC} = 0.975$, $\sigma_{AUC} = 0.05$; $\mu_{TSS} = 0.848$, $\sigma_{TSS} = 0.20$), than with blocked CV ($\mu_{AUC\text{-}CV} = 0.741$, $\sigma_{AUC\text{-}CV} = 0.16$; $\mu_{TSS\text{-}CV} = 0.432$, $\sigma_{TSS\text{-}CV} = 0.28$). The goodness-of-fit values of models fitted without CV were similar between virtual and real species (GAM AUC, *t*-test, $t = -1.27$, df = 283.62, $P = 0.206$; GAM TSS, *t*-test, $t = -0.39$, df = 200.16, $P = 0.691$). However, mean values were different between real and virtual species distribution fitted with blocked CV (GAM AUC-CV, *t*-test, $t = -4.36$, df = 1,450, $P < 0.0001$; GAM TSS-CV, *t*-test, $t = -4.20$, df = 1,450, $P < 0.0001$), with virtual species showing higher AUC and TSS values on average.

The AUC and TSS values of cSDMs for virtual species distribution were more variable than for real species (AUC: *F*-test of equality of variances; $F_{131,1,319} = 4.88$, $P < 0.00001$; TSS: *F*-test of equality of variances; $F_{131,1,319} = 2.39$, $P < 0.00001$). However, these differences disappeared with blocked CV (AUC-CV: *F*-test of equality of variances; $F_{131,1,319} = 0.832$, $P = 0.14$; TSS-CV, *F*-test of equality of variances; $F_{131,1,319} = 1.04$, $P = 0.75$).

Most real species distributions had a lower rank than virtual species distributions, and only 8 of the 132 real species were ranked first in comparison to their virtual species. The majority of virtual species distributions were thus predicted with a stronger accuracy than real species distributions (Figs. 2 and 3a; Data S1 and Metadata S1). The proportion of real species ranked first is very similar to the expected proportion if species rank was randomly assigned, regardless of their "status" (i.e., real or virtual): under random expectations, 1 out of 11 real species should show a better fit than its 10 associated virtual species, that is, a total of 12 (132/11) real species ranked first by chance. The results were similar regardless the metric and the methodology used (Fig. 3b–d, Data S1 and Metadata S1) or the algorithm (Appendix S1: Fig. S2; Data S1 and Metadata S1). We can thus conclude that real and virtual species' distribution were predicted with the same accuracy.

Effect of prevalence and taxon on the fit of the cSDMs for the real species

Prevalence strongly and negatively affected the cSDMs accuracy (AUC and TSS, without CV and with blocked CV) for real species (Table 1). The group did not have a significant effect on AUC and on TSS with blocked CV, but it significantly affected TSS without CV (Table 1). In this last case, the interaction between prevalence and group was also significant. In all cases, AUC or TSS seemed to decrease more for birds than for the other groups when prevalence increased (Fig. 4).

Discussion

Our main result is that SDMs based on climatic variables (cSDMs) predict equally well the distribution of real species and of virtual species whose distribution is independent of climate, regardless of the method used to fit cSDMs. Using a blocked cross-validation showed that virtual distributions may be even better predicted with cSDMs than real species distributions. Our findings therefore demonstrate that a strong predictive power of cSDMs should not necessarily be interpreted as an accurate depiction of the link between climate and species distribution, and thus calls for a greater caution when using cSDMs to make predictions about future changes in species distributions in response to climate change.

Prevalence and taxonomic groups did not affect our conclusions

We expected the increased size of the distribution (or prevalence; see Stockwell and Peterson 2002, van Proosdij et al. 2016) to increase the accuracy of cSDMs, as previously found in invertebrates (Aguirre-Gutiérrez et al. 2013) and tetrapods (mammals, reptiles, amphibians, and birds; Morán-Ordóñez et al. 2017). In agreement with these studies, we found that predictive accuracy of cSDMs decreased with increasing range size in real species. Contrary to our expectations, we did not find a significant variation of predictive performance of cSDMs between taxonomic groups, despite a tendency for weaker accuracies for birds (different slope of the AUC–prevalence relationships; Fig. 4). We might speculate that this tendency for a lower accuracy of climatic cSDMs in birds would become significant with a larger sample size per taxonomic group (approximately 25 real species per group in our study), as expected if birds, being endotherms, are less constrained by climate than ectotherms and plants (Gaston 2003). The main objective of including several taxonomic groups in our study was not to test for differences in accuracy among groups, however, but to ensure that our main conclusion was not dependent on the taxonomic group used. Therefore, virtual species distributions can be predicted as accurately as real species distributions, and this pattern does not depend on the size of the distribution group and also appears consistent regardless the ecological characteristics of the real species investigated.

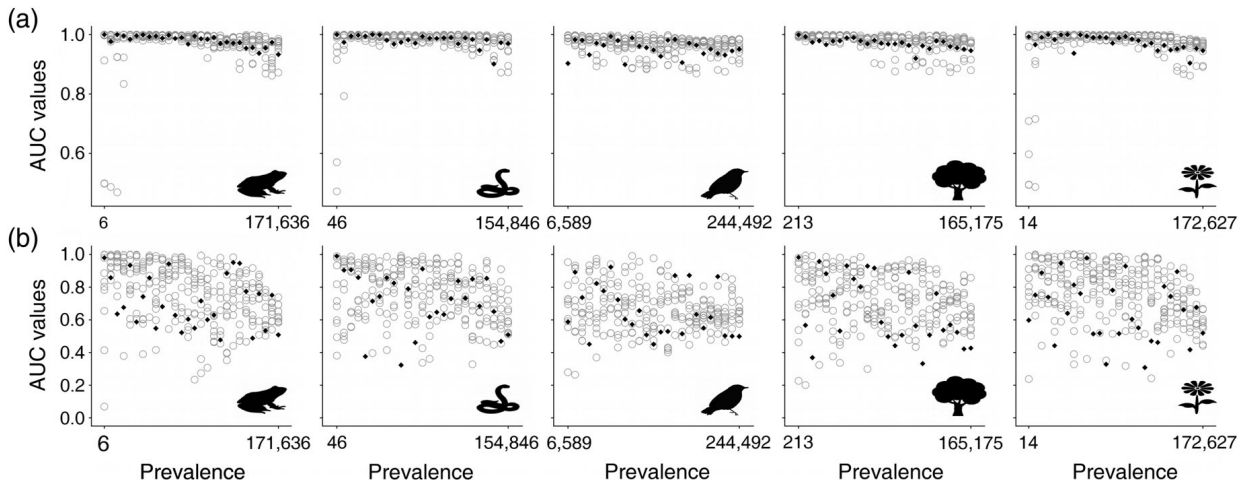

FIG. 2. Comparison of the AUC values (a) without cross-validation and (b) with blocked cross-validation for real species distributions and virtual species distributions, for each taxonomic group. Gray circles correspond to the area under the receiver operating curve (AUC) for virtual species, and black dots to the AUC for real species (amphibians, reptiles, birds, trees, herbaceous). Note that *y*-axis scale is different between (a) and (b).

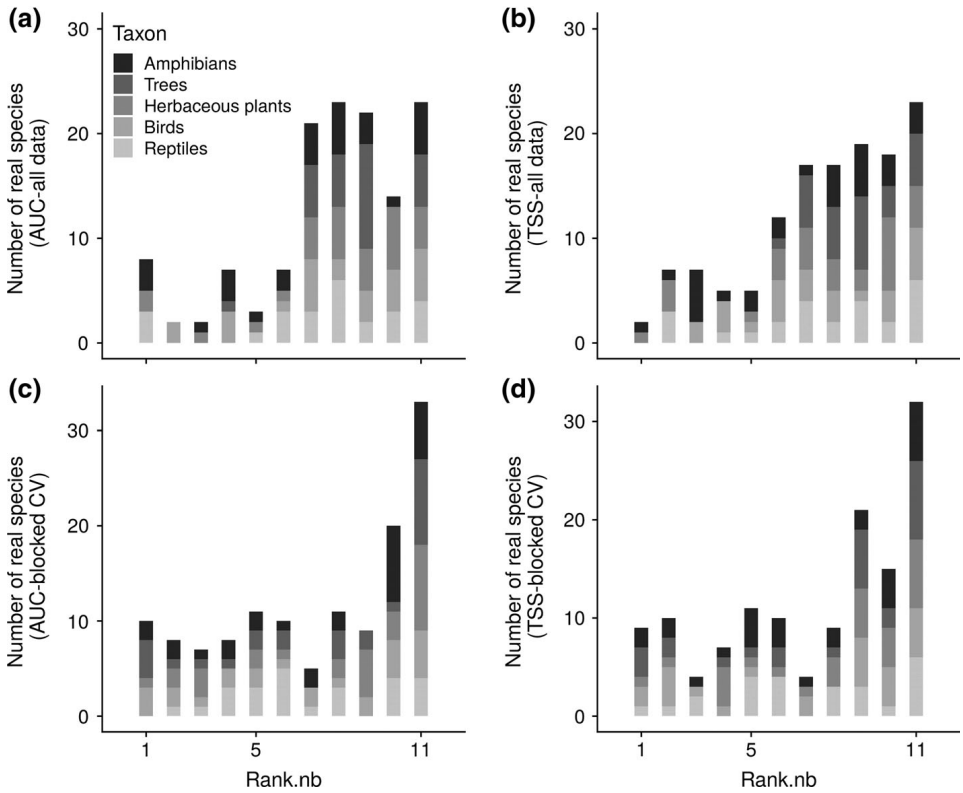

FIG. 3. Ranks of metrics values [area under the receiver operating curve (AUC) and true skill statistics (TSS)] of all real species distributions modeled with a generalized additive model (GAM) algorithm with (a), (b) all data and (c), (d) with block cross validation. Metrics values of real species are compared with the 10 corresponding virtual species. (a) Ranks of AUC values of all real species distributions modeled with GAM algorithm. (b) Ranks of TSS values of all real species distributions modeled with GAM algorithm. Note that two real species and 49 virtual species were not modeled because of the low number of presences used to calibrate the model. (c) Ranks of AUC values of all real species distributions modeled with GAM algorithm and a blocked cross-validation. (d) Ranks of TSS values of all real species distributions modeled with GAM algorithm and a blocked cross-validation. Results presented for (c) and (d) correspond to the validation block (AUC or TSS values of real species compared with the 10 corresponding virtual species).

TABLE 1. Linear mixed model for the effects of group (random) and prevalence on evaluation metrics for generalized additive models (GAM) with and without blocked cross-validation. The interaction term was removed from the final model when it was nonsignificant (*P* values between 0.25 and 0.82 for the three models with nonsignificant interaction term). See text for details.

	AUC–no CV			TSS–no CV			AUC–blocked CV			TSS–blocked CV		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Group	4.126	1.98	0.101	4.122	5.69	<0.001	4.126	0.91	0.46	4.126	0.73	0.57
log (Prevalence)	1.126	46.69	$<10^{-5}$	1.122	0.33	0.59	1.126	13.26	<0.001	1.126	23.35	<0.001
Group * log (Prev)	–			4.122	4.44	0.002	–			–		

Note. AUC = area under the receiver operating curve; TSS = true skill statistics; CV = cross-validation.

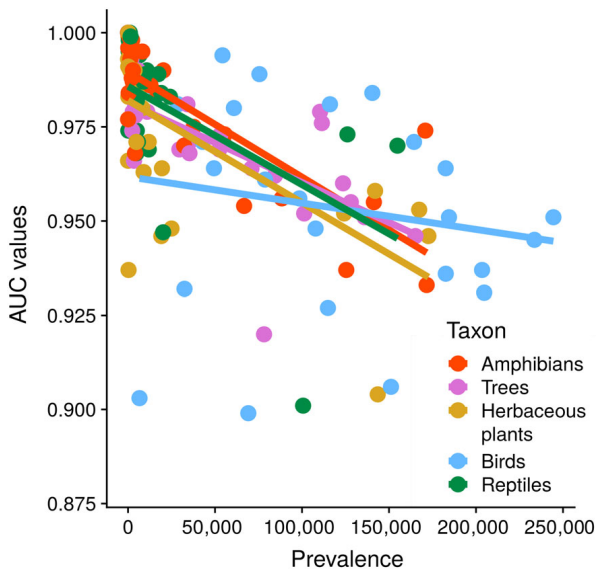

FIG. 4. Effect of taxonomic group and prevalence on the area under the receiver operating curve (AUC) values.

Spatial autocorrelation of climatic variables is the most likely culprit to explain our finding

How to explain that climatic variables can accurately predict a distribution range even when it is not linked to climate? Bahn and McGill (2007) already suggested that the spatial structure and autocorrelation of environmental variables could generate spurious relationships with species distributions, while Chapman (2010) simulated climatic gradients to demonstrate that the spatial structure of climate data drove the fit and the accuracy of cSDMs. Boucher-Lalonde and Currie (2016) removed all causal links between species distributions (here birds and mammals) and climate but retained the spatial autocorrelation structure of environmental variables. They found that the relation between climatic niche breadth and species range size could be adequately explained by the spatial autocorrelation of species ranges and climatic predictors. By using pseudo-predictors based on art paintings, Fourcade et al. (2018) recently demonstrated that any variable with a strong geographic structure (spatial autocorrelation) can accurately predict the distribution of a species.

In this study, we retained actual climatic variables (in contrast to Chapman 2010, Boucher-Lalonde and Currie 2016, Fourcade et al. 2018) but we generated virtual species distributions of the same size as real species but built without any causal relationships with climate (as done by Bahn and McGill 2007 or Beale et al. 2008 for birds). Our approach for generating virtual species distributions, using a random diffusion method, generated virtual distributions that had a more biologically realistic outline than previous studies based on simpler approaches (e.g., Bahn and McGill 2007) and retained the autocorrelation of species distributions necessary to build an appropriate null model, as rightfully advocated by Beale et al. (2008). With an approach similar to Beale et al. (2008) but (1) using a novel and more rigorous evaluation of models (i.e., blocked cross-validation) and (2) attaining more generality by incorporating species with more contrasted range sizes and ecologies, we confirmed that the spatial structure of climatic predictors allows the accurate modeling of almost any spatially coherent distribution with a cSDM. In fact, there seems always to be a combination of climatic variables that can describe a climatic envelope of a given distribution with a good accuracy, because of the strong latitudinal and longitudinal gradients of most climatic variables in Europe. A proper empirical test of this hypothesis would require altering the degree of spatial autocorrelation of climatic variables and examine how it affects accuracy of cSDMs.

Deciphering the role of climate on species distributions

Most studies that used null models to assess the ability of cSDMS to identify causal links between climate and species distributions concluded that climatic cSDMs did not perform generally better than alternative null models (Bahn and McGill 2007, Beale et al. 2008, Boucher-Lalonde and Currie 2016, Fourcade et al. 2018, Rich and Currie 2018; but see Jiménez-Valverde et al. 2011). Among these studies, some have argued that, because cSDMs based on climatic variables can predict null distributions with no relationship to climate as accurately as real species distributions, or because environmental variables added no predictive power beyond what spatial interpolation could provide, climate might not be the main

factor driving species distribution (e.g., Beale et al. 2008, Rich and Currie 2018). We do not share this view.

In our opinion, the ability of climatic cSDMs to model virtual species' distributions with the same accuracy as real species distribution tells nothing about the role of climate in shaping species distributions. These results simply demonstrate that fitting climatic cSDMs is not necessarily an appropriate tool to test for the role of climate in shaping species distributions. Because climatic cSDMs can and will accurately predict distributions that have no link to climate (Bahn and McGill 2007, Beale et al. 2008, our results), we need other approaches to investigate which species distributions are limited by climate or by other biotic or abiotic factors.

Testing the role of climate on species distributions is more crucial than ever. If fitting cSDMs cannot inform us on the causal link between climate and species occurrence, which possibilities can be envisaged? Possible alternative approaches include mechanistic models linking ecophysiological and/or demographic components to climatic variables on the basis of empirical and/or experimental data (Chuine and Beaubien 2001, Sinervo et al. 2010, Gutiérrez et al. 2016). Although some of the processes embedded in these mechanistic approaches may sometimes be modeled partly through correlations (for instance, if a process relies on bioclimatic thresholds inferred from presence–absence observed in distribution maps), the bias is certainly much weaker than for cSDMs that fundamentally depend on the species range size to be calibrated. Therefore, because they mostly rely on response functions that are a priori defined in experimental settings, they are not biased by spatial autocorrelation, and the effect of climate is directly tested. Another promising approach is the experimental manipulation of range limits (reviewed in Hargreaves et al. 2014). Last, the current level of climate change offers pseudo-experimental settings to test the impact of climate on species distribution directly (Kerr et al. 2007). Whenever actual changes in range limits as a response to climate change match the predictions of climatic cSDMs, the causal role of climate in determining distribution becomes well supported. As mentioned in the introduction, such approaches have yielded mixed responses within a general pattern of poleward and upward range shifts and it is likely that the direct contribution of climate to range limits varies between taxonomic groups and/or biogeographic regions (see Lenoir and Svenning 2015). Unfortunately, none of these alternative approaches is as easy to use or as general as correlative SDMs.

Comparisons with previous studies and the need for repeatability in ecology

Our work is not the first one to use virtual species distributions to assess the power of cSDMs to capture actual links between climate and species distributions (see references in the introduction). However, we wish to point out here the novel aspects of our study.

First, the most original aspect of this work is clearly the comparison of several taxonomic groups of real species. Most previous papers using similar approaches focused on only one group of species (in most cases avian species), and it could be argued that their results were driven by a possible lack of response of birds to climate (in comparison with other kinds of organisms with physiological requirements more directly related to climate, like plants or ectotherms). In fact, one of the previous similar studies (Beale et al. 2008) concluded that "the distributions of most birds in our study are not strongly associated with the climate variables currently available," rather than questioning the bases of correlative climatic niche modeling. We are not aware of any study comparing the performance of cSDMs on virtual and real species for such a wide range of taxa (i.e., the four main groups of terrestrial vertebrates and two functional groups of plants), thus comparing species strongly differing in dispersal abilities (from birds and trees to salamanders) and ecophysiology (endotherms vs. ectotherms and plants). We detected some differences between groups (consistent with the ecology of the groups), yet our conclusions draw a strong general trend. Therefore, with studies such as ours, it will be difficult to argue that the lack of power of cSDMs is restricted to the group(s) investigated.

Second, validation practices rapidly evolve in niche modeling, and low performance of cSDMs compared to null models has also been linked to failure of validation tools. The study by Fourcade et al. (2018) concluded on "the inability of current evaluation metrics to assess the biological significance of distribution models." Here, we used the most stringent and recent validation tools—in addition to the commonly used AUC—and we showed that our conclusions did not change with the validation tools.

Last, we also wish to point out that in spite of the previous studies mentioned above, common practice has not changed much in the field, and cSDMs are still widely used for forecasting without much caution: cSDMs are more widely used than ever, and the limits of this modeling technique and philosophy are almost never acknowledged. Like in many other fields, it will take at least a series of independent studies by several teams (see Palmer 2000, Kelly 2006, Nagakawa and Parker 2015 on the need to repeat studies in ecology and evolution) before the cautionary message is heard. We thus think that it is important to publish independent studies reinforcing previous conclusions with different approaches and independent data sets. In that sense, we believe that our study, based on several groups of species, relying on spatially explicit virtual distributions (instead of randomizations) across Europe and using the most recent methods in cSDM validation represents a significant step in this direction.

Methodological issues and perspectives of our study

The methods used in this study differ from the classical way of fitting cSDMs in several aspects. First, we used polygons of distribution range as presence data, resulting in the spatial segregation of presence and pseudo-absence pixels. Many studies using cSDMs used actual occurrence data instead, resulting in a mixture of presence and pseudo-absence data inside the distribution range of species. Such an approach assumes that (a) pseudo-absence data inside the distribution range of species are more likely to correspond to real absences than to pixels where the species is actually present but has not been detected and (b) that the environmental factors used to model species occurrence differ between presence and pseudo-absence pixels. The first assumption might be realized in some species with high detectability in well-prospected areas, but is certainly not verified in most empirical studies that we know of. The second assumption seems unrealistic in climatic cSDMs based on broad-scale climatic variables (such as the WORLDCLIM data base), as most of the variables used for modeling certainly do not vary at the spatial scale corresponding to the spatial resolution of the presence and pseudo-absence data. In other words, it is highly unrealistic to use climatic variables varying over regional or continental scales to explain whether a species is present or absent in particular pixels of a local region. We are therefore confident that using polygons of distribution range as presence data does not undermine our work. We nevertheless checked the sensitivity of our results to this methodological choice by modeling real and virtual species distribution after removing 20, 40, 60, and 80% of the presence data and selecting pseudo-absence randomly inside and outside the species range, as done in many empirical studies (e.g., Araújo et al. 2005, Elith and Graham 2009, Barbet-Massin et al. 2012). Using various proportions of presence data did not alter our results, and our conclusion that real species distributions are not predicted with stronger accuracy than virtual species distributions therefore remains valid (Appendix S1: Section S1).

Secondly, the size of the study area is known to affect the accuracy of modeling results of cSDMs (Thuiller et al. 2005). If the study area is too large relative to the species distribution, there is a risk of overfitting (i.e., increased AUC values), leading to less realistic estimates of niche characteristics (Anderson and Raza 2010, Barve et al. 2011). This is simply because increasing the range of climate conditions spanned in a study area increases the ability of cSDMs to discriminate the range of conditions suitable for a given species, but at the cost of decreasing the accuracy. In this work, we did not adjust the size of the study area to be proportional to each distribution (Fig. 1; Data S1 and Metadata S1) because defining a specific study area for every real and virtual species distribution would distort the modeling procedure and would not allow a fair comparison for all species. However, the key point was that real and associated virtual species always had the same range size. Furthermore, many real species selected had a large prevalence, so the effect of large study area relative to species range cannot be responsible for our main conclusion.

Third, we chose to assess the performance of the model through a blocked cross-validation (Roberts et al. 2017, Fourcade et al. 2018). This method provides a better spatial independence between calibration and validation data sets than usually done in cSDMs-based studies with random cross-validation. Doing so also strengthened the robustness of our results.

Lastly, the generated virtual distributions were on average less fragmented than the real species distributions (Fig. 1). This pattern arose because our null models relied on continuous distributions obtained through a diffusion model, whereas real species may have disjointed distributions, especially those located in mountains and/or at high latitude. It has been shown that the aggregation level may influence the goodness-of-fit of cSDMs, with species distribution with a high level of aggregation usually showing higher AUC values (Beale et al. 2009). Although this approach is likely to have a weak impact on our results, a relevant perspective to this work would be to create a diffusion model allowing the design of fragmented distributions, in order to compare real and virtual species' distributions with a similar level of spatial fragmentation and/or convolutions of distribution limits. However, we do not expect this to affect our main conclusion, because our set of real species also includes distributions that have simple shapes and they were not better predicted than virtual species distributions (for examples see Appendix S1: Fig. S4), and because, alternatively, some of the virtual distributions with a convoluted outline were adequately predicted by cSDMs. We are thus confident that the main finding of the present study is robust to this limitation about the level of fragmentation of the virtual distributions.

Combining various approaches to better predict the impact of climate change

Forecasting distributions (e.g., projecting climate change impact on species distribution) is conditioned by two assumptions: that current distributions are mainly limited by climatic variables and that climatic niches remain stable through time (this is called the "climatically constrained hypothesis" by Rich and Currie 2018). It is probably sensible to assume that evolutionary changes in climatic niche will be rare enough (i.e., be expressed in few species) or small enough (i.e., be of low magnitude) at contemporary time scales to have a limited effect on most forecasting attempts, even if contemporary adaptation to new climate has been documented before (e.g., Colautti and Barrett 2013, Geerts et al. 2015, While et al. 2015). However, assuming that all current species distributions are mainly limited by climatic

variables is highly questionable, as explained in the introduction and earlier in the discussion. Our results further emphasize that forecasting distributions with cSDMs should be done with caution: correlative species distribution models may be useful to predict changes in species distribution due to climate change whenever climate is the main factor determining range limits (Lee-Yaw et al. 2016). For instance, Kharouba et al. (2009) constructed cSDMs under historical conditions for butterfly species and predicted range shifts reasonably well when climate changed for many (but not all) species. This is consistent with the fact that the physiology of many insect species (phenology, survival rates) is strongly dependent on climate (Chuine and Régnière 2017). Because current distributions are not necessarily limited by climatic factors, recent developments of cSDMs have tried to incorporate nonclimatic factors such as land use, interspecific interactions, or dispersal abilities to improve the modeling tools (Thuiller et al. 2004, Cabral and Schurr 2010, Boulangeat et al. 2012). Such efforts have improved the fit of the models to current distributions and shed light on the role of nonclimatic drivers of species distributions, so they certainly represent a promising venue for forecasting the impact of climate change. The climatic part of these hybrid SDMs remain the same as in classic cSDMs in most cases, however, and their forecasting abilities should be rigorously evaluated, for example, using historical distribution data or out-of-range introductions, as has been done with classical cSDMs.

Given these limitations, how can we obtain robust predictions of the impact of climate change on species distributions? As mentioned previously, although the use of process-based or experimental approaches is currently expanding, these are not straightforward to develop. A first attempt to solve this issue may be to limit forecasting with cSDMs to species for which range shifts have been shown to be predicted with strong accuracy through calibration on historical distributions and validation with current distributions (Kerr et al. 2007) or to invasive species whose invasive areas have been well predicted—although these approaches had contrasting results, as reviewed in the introduction. Other possibilities may be to focus on species where the link between climate and the probability of presence is grounded on solid biological bases, such as experiments in controlled conditions (Rehfeldt et al. 2002, Chuine and Régnière 2017) or using measures of the effects of climate on life-history traits (Pigott and Huntley 1980, Sinervo et al. 2010), and to select those climatic variables that are biologically meaningful prior to the modeling steps of cSDMs. Lee-Yaw et al. (2016) nicely illustrates how climatic cSDMs can provide accurate information on niche limits and suitability in a given location when experimental data demonstrate a causal link between climate and fitness; this was the case for 31 of the 40 plant species investigated, so for nearly a quarter (9 out of 40) of the species investigated a link between suitability as predicted by cSDMs and actual local persistence as assessed by transplant experiments was not supported. An even more mixed pattern emerges from studies using human-mediated species translocations as quasi-experiments (see Introduction), so a direct link between climate and current range limits cannot always be taken for granted.

Conclusion

Disentangling the role of climate and other factors in shaping species ranges overreaches fundamental ecology and has far-reaching consequences when trying to predict biodiversity responses to climate change. Fitting cSDMs using climatic variables and using them to predict range change in response to climate change rests on the untested hypothesis that climate determines where a species is found. Our study highlights that fitting correlative SDMs based on climatic variables to current species distributions is not enough to assess the effect of climate on species distribution. This especially calls for caution when forecasting the impact of climate change on species range. Although cSDMs remain an important tool in the emergence of predictive ecology (Mouquet et al. 2015), a better understanding of the drivers of species distribution is crucial for conservation and climate change impact issues. It will allow the development of more realistic forecasting models incorporating dispersal, biotic interactions, actual relationships between climate and fitness, and nonclimatic environmental factors.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2912/suppinfo

Supporting Information. Valentin Journé, Jean-Yves Barnagaud, Cyril Bernard, Pierre-André Crochet, and Xavier Morin. 2019. Correlative climatic niche models predict real and virtual species distribution equally well. *Ecology*.

Appendix S1

Section S1: Other methods to calibrate and validate cSDMs for real and virtual species distributions.

1) MAXENT

The MAXENT algorithm uses only presence data and background points. These background points correspond to a random sample of points selected in the study area and give information about the environmental conditions for the modelling procedure (the default number is set at 10,000, see Phillips et al. 2006 for more information; Elith et al. 2011 for statistical explanations).

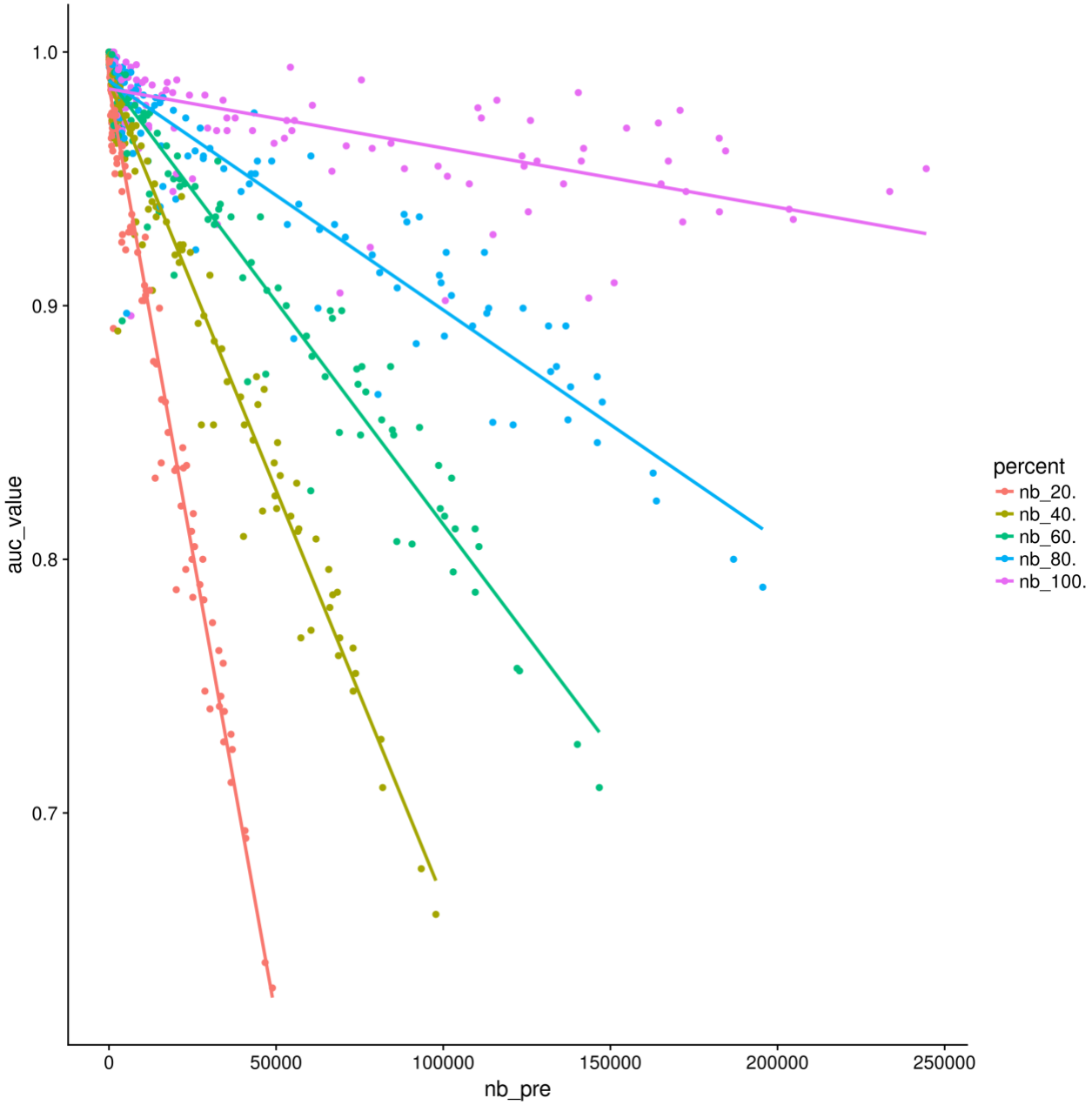
For each species distribution, real or virtual, we used a random cross-validation procedure with MAXENT, selecting 75% of the presence-background data for model calibration and the rest of presences for validation. Ten evaluation runs were done to obtain a robust estimation of the model's performance, and we calculated a mean AUC value for each distribution. In total, we fitted 13,200 cSDMs with MAXENT. Results are presented in Figure S3 in Supporting Information.

2) GAM with varying proportion of species occurrences

Many empirical studies of species distribution modelling use actual occurrence data, resulting in a mix of presences and background or pseudo-absences (depending on the method) data inside the distribution range of species (Barbet-Massin et al. 2012). We decided to test whether the number of presence used to calibrate and validate a cSDM can influence the quality of our models. For each species distributions (real and virtual) we randomly selected 20%, 40%, 60%, 80% and 100% of presences. Once we selected presences in the distribution, we fitted cSDMs with GAM algorithm from the package BIOMOD2 (Thuiller et al. 2009) and our 6 PCA axis, and defined 10,000 pseudo-absences in the study site. We then used a cross-validation procedure, where 75% of the presence-pseudo-absences data were used for model calibration and the remaining part for validation to obtain the AUC value (Araújo et al. 2005).

Some distribution were too small (ie. included too few pixels) to fit a cSDM. The goodness-of-fit of the models increased with the proportion of presence data used (Figure S1-1). Comparisons between real and virtual distribution are the same as in the main text and are presented in the Figure S1-2 (132

real species * 5 values of the proportion of presence selected). For all distributions obtained, less than 10% were better predicted than virtual species distributions, in accordance with our conclusions.



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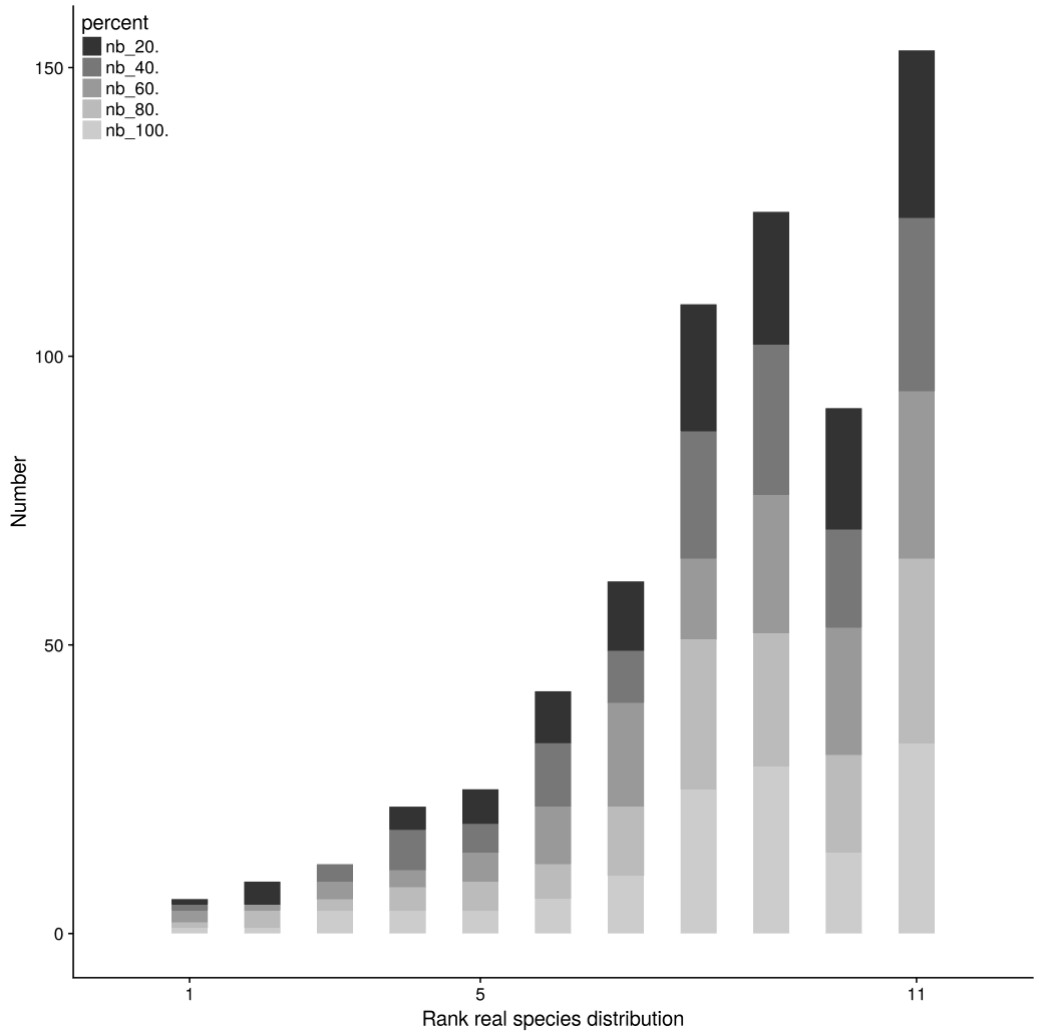

Figure S1-1: Relationships between prevalence (*nb_pre*) and model performance (AUC, *auc_value*) for real species distributions, with various proportions of presence data to fit the models (from 20 % to 100%).

Figure S1-2: Rank of AUC values of real species relative to their 10 corresponding virtual species for varying proportion of presence data used on the models (from 20% to 100%).

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Table S1: Summary of the PCA of the 20 climatic and topographic variables (current conditions, interpolations of observed data, representative of 1960-1990) used for fitting the cSDMs. PC1 to PC6 correspond to the first 6 principal components, with the contribution of each variables (in percentage).

Variables	PC1	PC2	PC3	PC4	PC5	PC6
Alt -altitude (elevation above sea level) (m)	0.58	1.17	30.71	2.02	19.74	18.87
BIO1 - Annual Mean Temperature (°C)	6.74	4.70	3.22	1.36	0.29	0.92
BIO2 - Mean Diurnal Range (Mean of monthly (max temp - min temp)) (°C)	8.11	0.05	4.75	1.46	1.21	9.70
BIO3 - Isothermality (BIO2/BIO7) (* 100) (°C)	4.03	8.50	0.28	1.80	3.12	0.79
BIO4 - Temperature Seasonality (standard deviation *100) (°C)	0.00	14.65	0.53	9.50	4.02	2.57
BIO5 - Max Temperature of Warmest Month (°C)	9.12	0.03	0.54	7.40	2.20	4.76
BIO6 - Min Temperature of Coldest Month (°C)	2.87	11.09	4.29	0.20	0.00	0.03
BIO7 - Temperature Annual Range (BIO5-BIO6) (°C)	0.64	13.13	2.84	8.74	1.62	4.59
BIO8 - Mean Temperature of Wettest Quarter (°C)	0.05	1.29	28.44	13.20	37.19	0.81
BIO9 - Mean Temperature of Driest Quarter (°C)	6.58	4.66	0.07	0.00	4.51	0.41
BIO10 - Mean Temperature of Warmest Quarter (°C)	8.56	0.28	2.60	7.68	2.96	2.98
BIO11 - Mean Temperature of Coldest Quarter (°C)	4.05	9.68	2.76	0.10	0.04	0.00
BIO12 - Annual Precipitation (mm)	6.89	4.96	0.37	3.81	0.30	0.89
BIO13 - Precipitation of Wettest Month (mm)	5.21	5.08	2.75	14.21	0.39	1.67
BIO14 - Precipitation of Driest Month (mm)	7.39	2.32	1.12	0.34	1.00	14.69
BIO15 - Precipitation Seasonality (Coefficient of Variation) (mm)	5.56	0.31	7.20	6.72	7.84	17.58
BIO16 - Precipitation of Wettest Quarter (mm)	5.42	5.31	2.44	12.23	0.16	1.35
BIO17 - Precipitation of Driest Quarter (mm)	7.37	2.69	1.07	0.15	1.24	14.14
BIO18 - Precipitation of Warmest Quarter (mm)	8.99	0.05	1.02	0.53	4.99	2.57
BIO19 - Precipitation of Coldest Quarter (mm)	1.82	10.06	3.01	8.54	7.18	0.66
Explained variance	47.57	28.96	8.81	4.73	3.48	3.22

The last line corresponds to the variance explained by each axe.

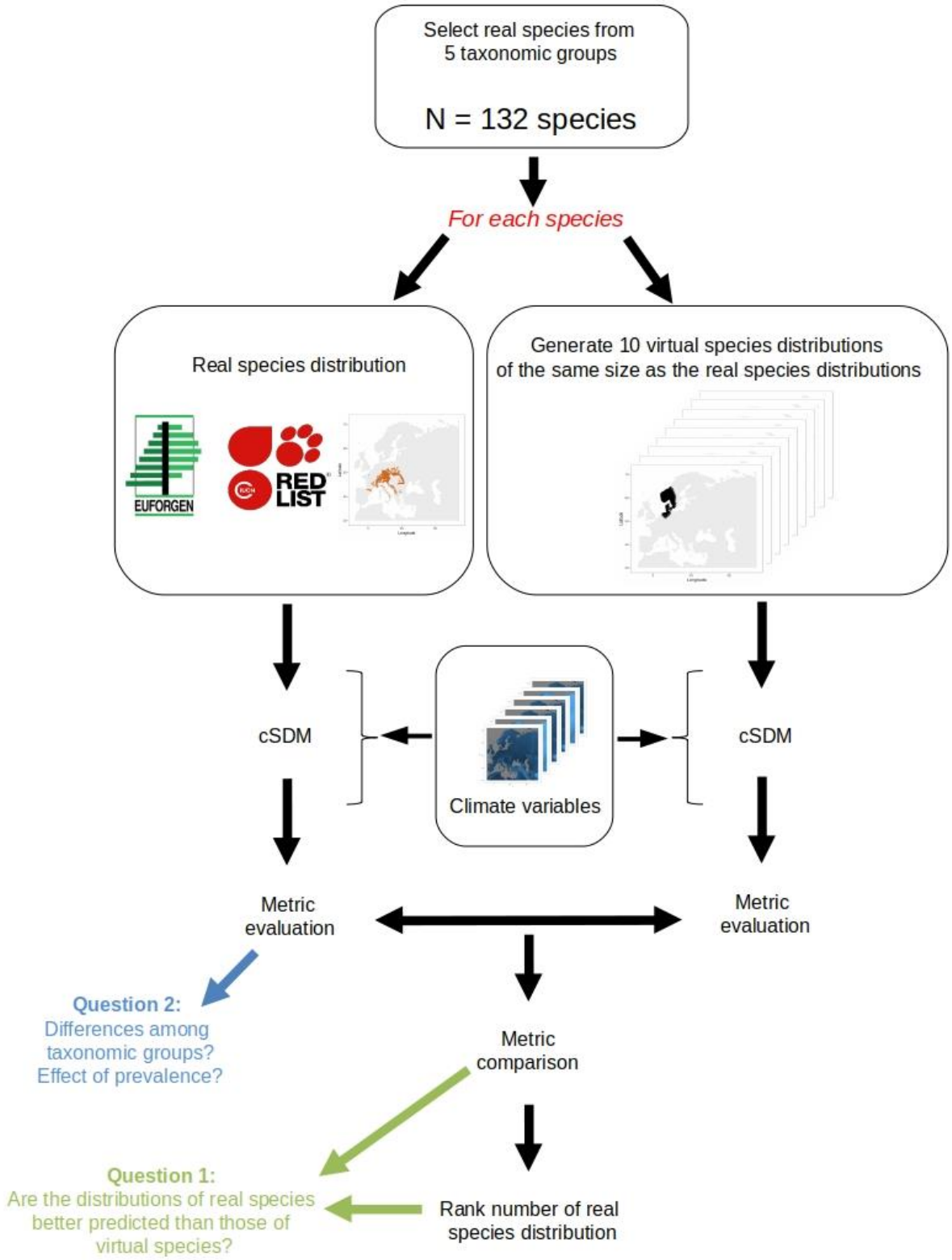

Figure S1: Workflow of the methodology used in our study.

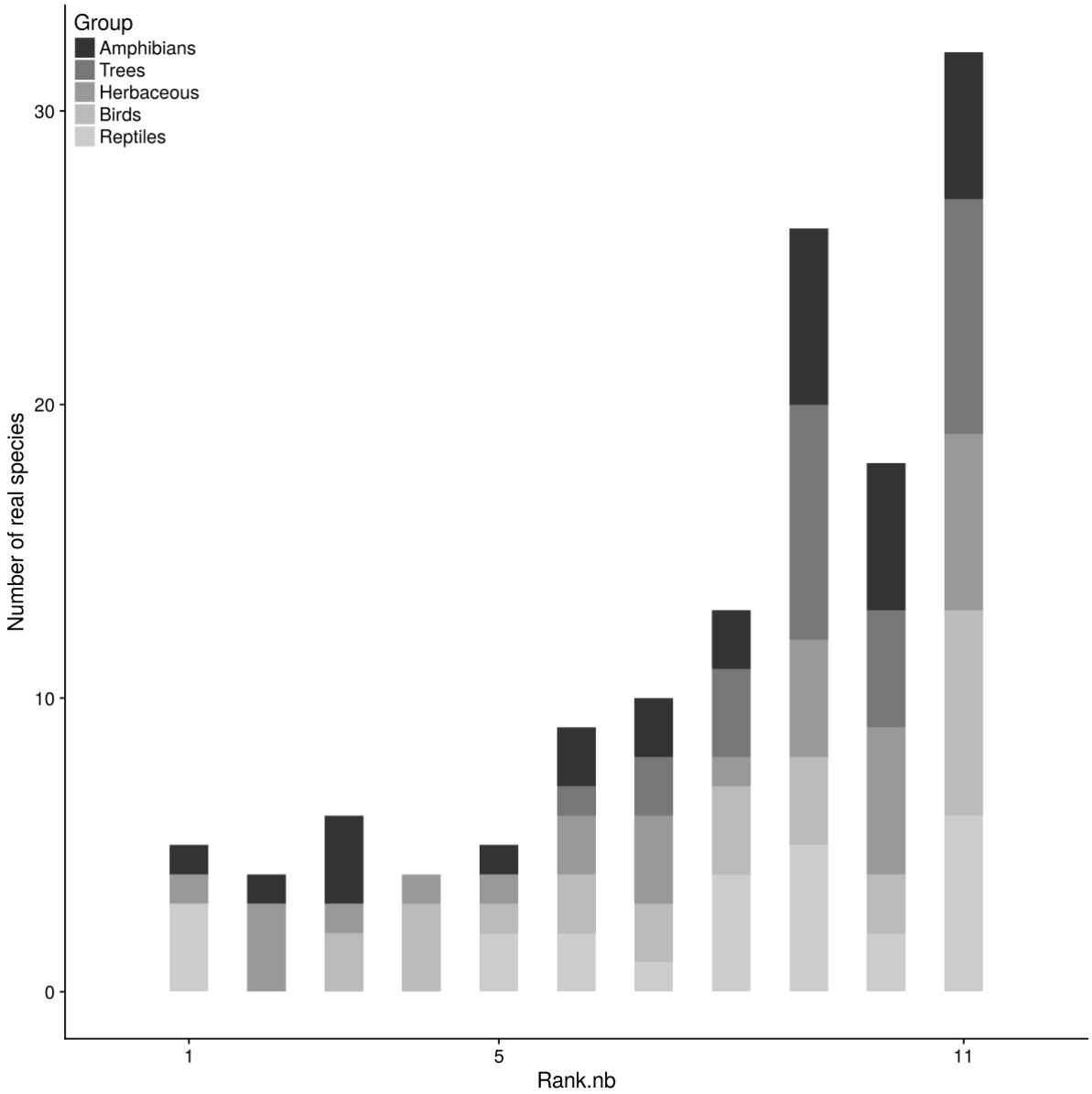

Figure S2: Ranks of AUC values of all real species distributions modelled with MAXENT algorithm (AUC values of real species compared with the 10 corresponding virtual species).

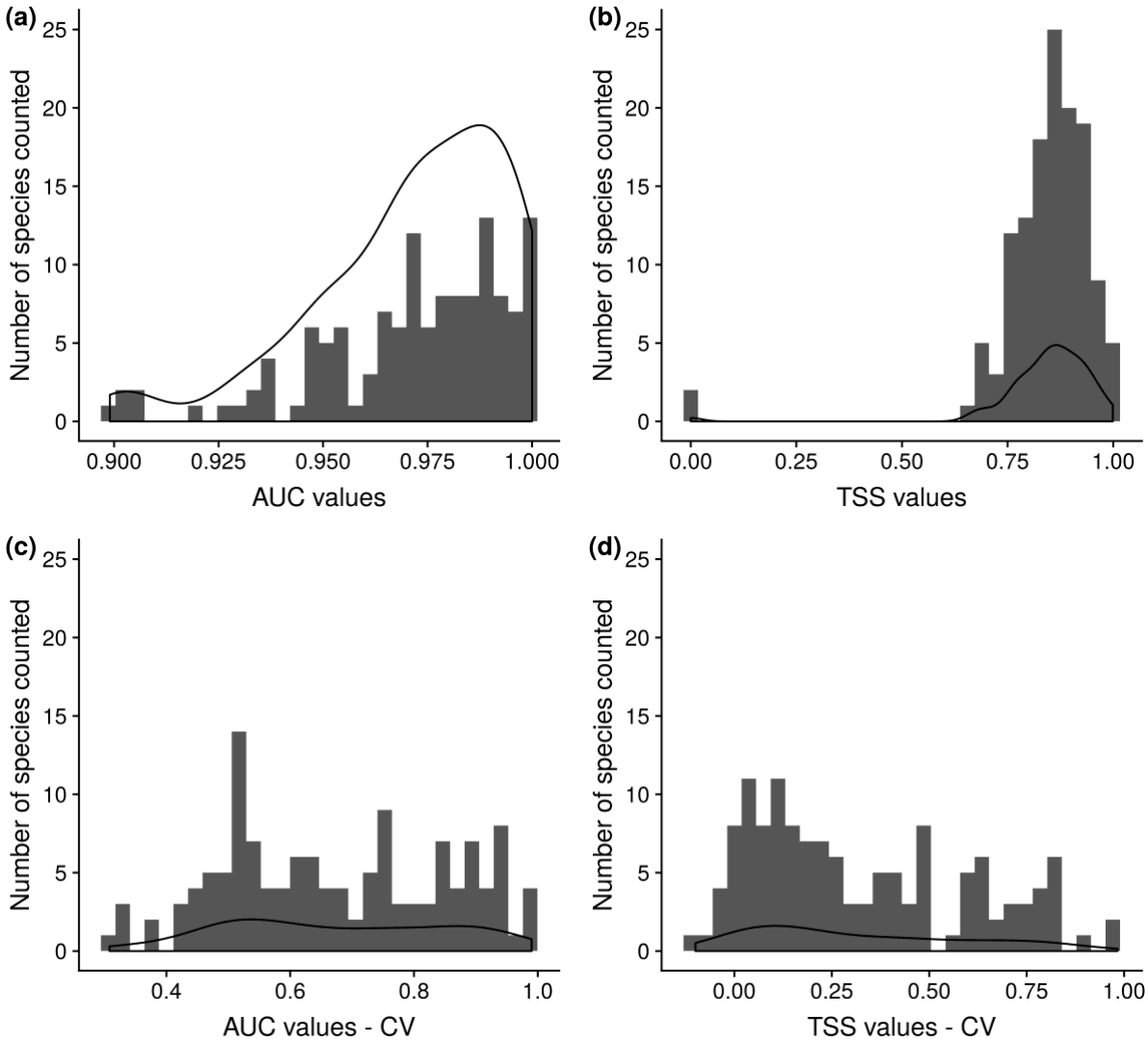

Figure S3: Histogram and density of metric values. (a) Histogram of AUC values for real species distribution with GAM with all data. (b) Histogram of TSS values for real species distribution with GAM with all data. Note that species with low prevalence where not predicted. (c) Histogram of AUC values for real species distribution with GAM with a bloc cross validation approach. (d) Histogram of TSS values for real species distribution with GAM with a bloc cross validation approach.

Figure S4: Examples of real species distributions with simple shape. Distribution of the herbaceous species *Lythrum portula* (a, left, ranked 9th), amphibian *Rana graeca* (b, middle, ranked 11th) and reptile *Podarcis siculus* (c, right, ranked 9th).

8

3 Impact de la défoliation des arbres sur la croissance et la reproduction

Dans cette étude, les auteurs se sont intéressés à l'effet de la défoliation foliaire sur la croissance et la reproduction pour une population marginale Sud du Hêtre commun. La fécondité mâle et femelle ont été estimées pour chaque individus grâce à des analyses de parentés. La fécondité femelle diminue et la croissance des arbres diminue avec le niveau de défoliation et la compétition. La fécondité mâle diminue lorsque la compétition augmente. De plus il a été observé que pour des arbres défoliés, certains individus ont une fécondité femelle plus élevé au détriment de leurs croissance, et d'autres individus avec une croissance plus élevée et une fécondité femelle plus faible. Dans ce projet, j'ai contribué à la partie sur la phénologie de la reproduction dans l'introduction et sur l'allocation des ressources entre croissance et reproduction dans la discussion.

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Crown defoliation decreases reproduction and wood growth in a marginal European beech population

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Keywords: Mediterranean forest, dieback, drought, female fecundity, male fecundity, radial growth, *Fagus sylvatica*, Mixed Effect Mating Model, parentage analyses, microsatellite, margin of species distribution

Abstract

1. Abiotic and biotic stresses related to climate change have been associated to increased crown defoliation, decreased growth and a higher risk of mortality in many forest tree species, but the impact of stresses on tree reproduction and forest regeneration remains understudied. At dry, warm margin of species distributions, flowering, pollination and seed maturation processes are expected to be affected by drought, late frost and other stresses, eventually resulting in reproduction failure. Moreover, inter-individual variations in reproductive performances versus other performances (growth, survival) could have important consequences on population's dynamics.

2. We investigated the relationships between individual crown defoliation, growth and reproduction in a drought-prone population of European beech, *Fagus sylvatica*. We used a spatially explicit mating model and marker-based parentage analyses to estimate effective female and male fecundities of 432 reproductive trees, which were also monitored for basal area increment and crown defoliation over nine years.

3. Female and male fecundities markedly varied among individuals, more than did growth. Both female fecundity and growth decreased with increasing crown defoliation and competition and increased with size. Male fecundity only responded to competition, and decreased with increasing competition. Moreover, the negative effect of defoliation on female fecundity was size-dependent, with a slower decline in female fecundity with increasing defoliation for the large individuals. Finally, a trade-off between growth and female fecundity was observed in response to defoliation: some large trees maintained significant female fecundity at the expense of reduced growth in response to defoliation, while some other defoliated trees rather maintained high growth at the expense of reduced female fecundity.

4. *Synthesis*. Our results suggest that while decreasing their growth, some large defoliated trees still contribute to reproduction through seed production and pollination. This non-coordinated decline of growth and fecundity at individual-level in response to stress may compromise the evolution of stress-resistance traits at population level, and increase forest tree vulnerability.

Introduction

The increasing impact of stresses associated with climate and global change are likely to cause widespread forest decline, eventually leading to massive tree mortality due to inability to recover from stresses (Allen et al., 2010; McDowell et al., 2011). Depending on their frequency, duration, or intensity, abiotic stresses (e.g. drought, wind throw, flood, heavy snow, late frosts, fire) and biotic stresses (predation, competition) have the potential to alter tree structure (e.g. branch breakage, leaf fall), physiological processes (e.g. hydraulic failure, reduced photosynthesis) and overall vigour (e.g., crown defoliation) and performances (e.g. reduced growth, reproduction and survival). Moreover, as stresses often co-occur and interact, it is notoriously difficult to disentangle the drivers of tree decline observed in a given environment. Hence, the diversity of both stresses and decline components needs to be accounted for in order to better predict forest decline in response to environmental change.

The warm and dry margins of tree species distributions are expected and already observed to suffer massive forest decline, driven by increasing temperatures, drought, late frost and other stresses. Most importantly, prolonged droughts and high temperatures have been extensively associated to decreasing tree growth and forest productivity (Zhao & Running, 2010; Zimmermann, Hauck, Dulamsuren, & Leuschner, 2015), increasing crown defoliation and leaf fall (Dobbertin, 2005; Galiano, Martínez-Vilalta, & Lloret, 2011) and higher risks of tree mortality (Adams et al., 2017; Allen et al., 2010; Anderegg, Kane, & Anderegg, 2013). There is also an increasing concern that the advance in spring phenology currently observed in many species expose them to a higher risk of late frost, with damaging effects on crown development (Bigler & Bugmann, 2018; Charrier, Ngao,

Saudreau, & Améglio, 2015). Overall, the response of tree sexual reproduction and forest regeneration to abiotic and biotic stresses remain largely under-documented, despite the critical importance of reproduction for the maintenance, demography and adaptation of populations at the rear-edge of species distribution (Hampe & Petit, 2005). Here, we consider sexual reproduction globally, including all the stages from floral initiation to the production of mature seeds.

Based on species physiology, abiotic stresses such as droughts or late frosts are expected to directly reduce plant sexual reproduction through altered reproductive phenology (i.e. the timing of flowering and fruiting), a higher risk of pollen abortion or pollination failure, a shorter seed maturation cycle and/or a higher risk of seed abortion (Bykova, Chuine, Morin, & Higgins, 2012; Hedhly, Hormaza, & Herrero, 2009; Zinn, Tunc-Ozdemir, & Harper, 2010). Moreover, indirect negative effects are also expected: for instance, by decreasing photosynthetic activity, leaf fall may reduce the amount of stored resources to invest in reproduction of the next year (Obeso, 1988). The few results available so far from experiments manipulating stresses *in situ* overall support these expectation of negative impacts of stresses on reproduction and growth. By manipulating temperature during pollen dispersal and germination, Flores-Rentería *et al.* (2018) demonstrated negative impacts of high temperatures on male reproduction, particularly on pollen viability of *Pinus edulis*. Bykova *et al.* (2018) also showed that water deficit increases pollen abortion and thus decreases pollen production in *Quercus ilex*. In *Quercus ilex*, Pérez-Ramos *et al.* (2010) showed that reduced water availability increased the rate of acorn abortion, while Sanchez-Humanes & Espelta (2011) showed that increased drought reduces acorn production in coppice. In parallel, these drought-manipulation experiments demonstrated that growth generally decreases (e.g. Delaporte, Bazot, & Damesin, 2016; Lempereur et al., 2015) and crown defoliation increases (e.g. Galiano et al., 2011) in response to increasing water stress.

On the other hand, stresses have been hypothesised to shift patterns of resource allocation and act like a cue stimulating higher reproductive effort and reduced growth (Bréda, Huc, Granier, & Dreyer, 2006; Lee, 1988; Pulido et al., 2014; Wiley, Casper, & Helliker, 2017). However, results from experiments manipulating stresses *in situ* hardy support this expectation, even though they highlight flexible allocation rules to reproduction and growth in response to stress. Using experimental warming, Sherry *et al.* (2007) demonstrated divergent responses of reproductive phenology to water stress for grass species: some species advanced their flowering and fruiting phenology before the peak of summer heat while other species started flowering after the peak temperature and delayed their reproduction. In *Quercus ilex*, Pulido et al. (2014) did not find evidence that drought enhances resource allocation to reproduction but suggested that the negative individual correlation between growth and female reproduction observed in controlled conditions disappears under limited resources (including water stress). The clearest experimental evidence of the positive impact of biotic and abiotic stresses on reproduction can be found in the literature on (fruit) tree orchards. Among the cultural practices allowing early and abundant flowering, water stress is used to enhance flower initiation in conifers, while hot, dry summers are reported to induce abundant seed crops in both conifers and broadleaved species (Meilan, 1997). Another practice relies on circumferential girdles (the removal of a swath of the bark, down to the phloem, around the entire stem), which are associated to reduced vegetative growth and increased fruiting (Bonnet-Masimbert & Webber, 2012). Finally, pruning (the reduction of crown leaf area) is also recommended to favour reproductive development while reducing vegetative growth in fruit trees (Karimi et al., 2017).

Taken together, these results suggest that stress impacts on reproduction and the relationship between reproduction and growth in response to stress both need further investigations (Figure 1). Environment-manipulation experiments typically use a limited number of individuals in controlled conditions to characterize the fine impacts of stresses on the physiological mechanisms driving plant performances (eventually testing for

individual effects, e.g. Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015). Besides these ecophysiological approaches, we also need population ecology approaches to investigate the among-individual variations in reproductive and vegetative performances in response to stress, and their consequences on population dynamics. Here, we propose to use crown defoliation taken as an indicator of stress, and to analyse the relationship between crown defoliation, reproduction and growth in order to test two hypotheses. First (H1), crown defoliation is associated to a proportional decrease in growth and reproduction through the impact of stresses on the resources allocated to these performances, so that the relationship between reproduction and growth does not change with increasing crown defoliation. Alternatively (H2), if defoliation or stresses act like a cue stimulating reproductive performances at the expense of reduced growth, then the relationship between reproduction and growth should change with increasing crown defoliation.

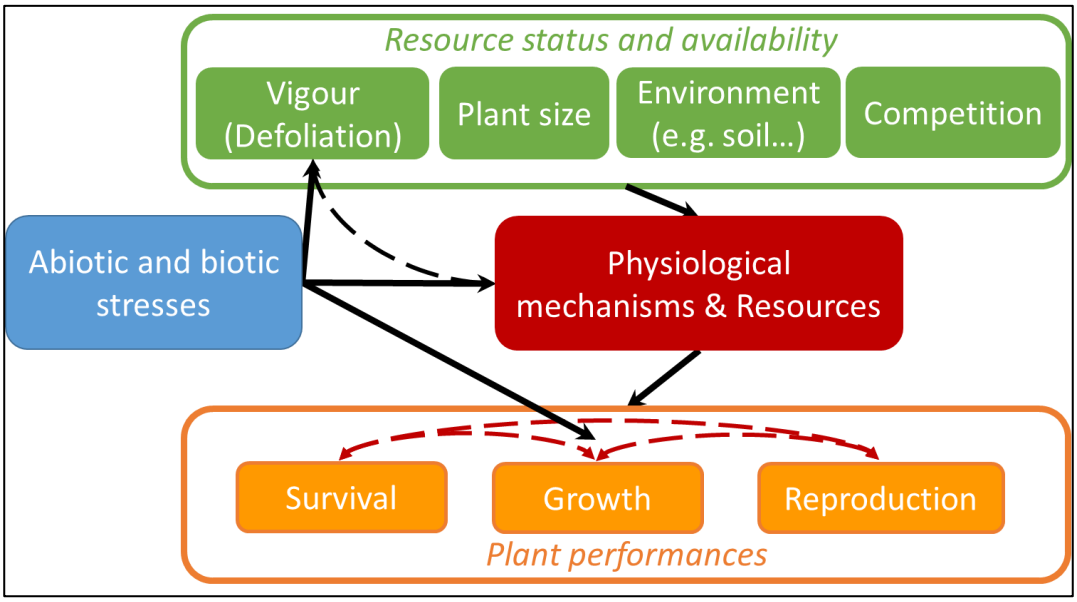

Figure 1: Conceptual framework for the impacts of abiotic and biotic stresses on individual plant performances (survival, growth, and reproduction). Stresses are expected to affect performances through their effect on the physiological mechanisms and the level of resources of the plant. Usually not easily measurable in natural populations, this level of resources also varies among individuals as a function of (i) plant resource status, a combination of plant size and vigour, and (ii) resource availability, which depend on the quality of the local environment and on competition. Vigour (eg crown defoliation) can in turn rapidly change in response to stress or to the level of resources (i.e. potential feedback loops, dashed arrows), and therefore it is itself an indicator of stress. Finally, stresses can act like cues changing resources allocation to survival, growth and reproduction, thereby affecting their correlations at individual level (eg., tradeoffs, dashed red arrows).

We focus here on the European beech (*Fagus sylvatica* L.), a major broadleaf tree species considered to be vulnerable to summer drought. Beech is a monoecious, wind-dispersed species, and shows an intermittent production of large seed crops synchronized across a population (i.e., masting), triggered both by weather and plant resource status (Vacchiano et al., 2017). Hacket-Pain, Lageard, & Thomas (2017) showed that drought years were associated to both reduced reproduction and growth, while during non-drought years, both masting and high growth could be observed. By contrast, Bréda *et al.* (2006) reported increased seed production associated to leaf fall in high drought years, even though this relationship between crown defoliation and fruit production may not be directly causal. This study investigates the relationships between tree defoliation, growth

and fecundity in 432 individuals within a single, rear-edge natural population of *F. sylvatica* in Southern France, where crown defoliation and mortality are being surveyed since 2003 (Petit-Cailleux et al., submitted). We used molecular markers and parentage analyses to estimate effective, relative female and male fecundities, which integrate the success of pollination and germination processes cumulated from 2002 to 2012. Growth over the same period was assessed through inventory data, completed by ring-width measurements. We analysed the relationships between crown defoliation, growth and fecundity at the among-individual scale in order to (i) characterize the decline in fecundity and growth associated with defoliation and (ii) investigate the correlation between growth and fecundity in response to defoliation.

Our study is based on the well-accepted hypothesis that recurrent defoliation is related to physiological stresses and symptomatic of a declining health in beech (Bréda et al., 2006; Peñuelas & Boada, 2003). Using statistical models and 4327 trees individually surveyed, a companion study in the same population showed that crown defoliation increases the risk of mortality (Petit-Cailleux et al., submitted). Moreover, simulations with a process-based physiological model indicated that the mortality rate in this population is driven by a combination of drought-related processes (conductance loss, carbon reserve depletion) and late frost damages (Petit-Cailleux et al., submitted). Crown defoliation thus appears as an appropriate indicator of a higher intrinsic sensitivity to these stresses, and/or a higher impact of these stresses due to a lower availability of resources in a heterogeneous environment.

Material and methods

Study site

Located in southern France and bordering Spanish Cataluña, the Massane forest is situated on the foothills of Eastern Pyrenees (Figure 2B). This coastal range, called Albera massif, covers about 19,000 ha on the French territory. The Massane forest National Nature Reserve (42° 28' 41" N, 3° 1' 26" E) was created in 1973. It covers 336 ha on the highest part of the Massane valley, from 600 to 1,127 m a.s.l., and is only around 5 km far from the Mediterranean Sea. The site is under a meso Mediterranean climate influence (Quézel & Médail, 2003: mean annual temperature = 11.95°C; annual precipitations = 1164.9 mm, monitored on site since respectively 1976 and 1960; Figure S1A). This site is one of the French beech location the most prone to water stress (Figure S1B).

More than half of the Reserve is constituted of an old grown forest, where no logging operation has been performed since at least 1886. The canopy is dominated by European beech in mixture with downy oak (*Quercus pubescens* Willd.), maples (*Acer opalus* Mill., *Acer campestris* L., *Acer monspessulanum* L.) and holly (*Ilex aquifolium* L.). A 10 ha fenced plot was remote from any cow grazing since 1956. All trees from this protected plot are monitored since 2002.

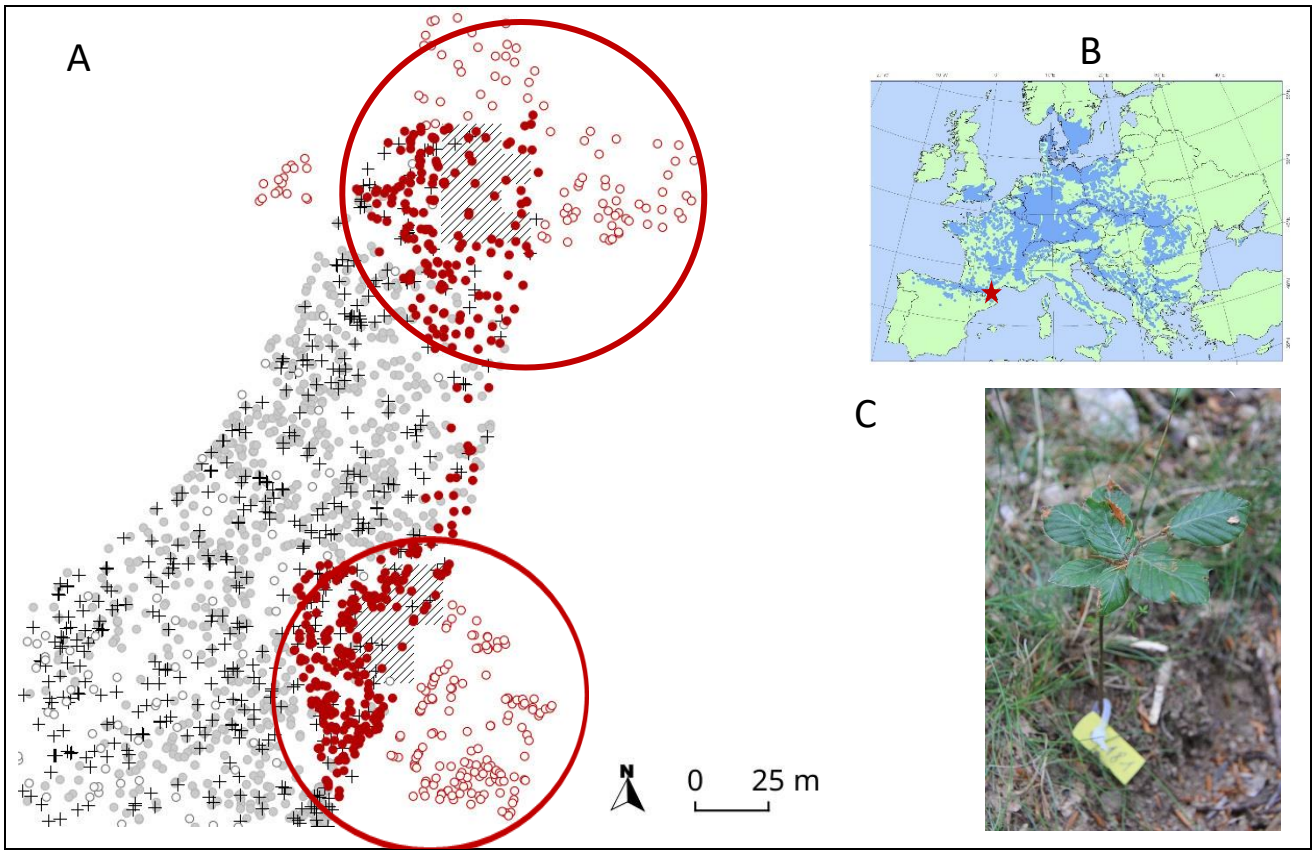

Figure 2: Study site and (A) sampling design: red filled dots (●) represent the 432 beech trees for which individual fecundity, growth and defoliation were assessed. Hatched squares represent the seedlings patches used to estimate fecundity through parentage analyses and mixed-effect mating models (MEMM). The two red circles encompass all the individuals (seedlings and adult) used for MEMM analyses. Red empty dots (○) represent the 244 beech trees outside of the protected area and included in the fecundity analyses (but not phenotyped for growth and defoliation). Grey dots (●) and crosses (+) represent other beeches within the protected area not included in the fecundity analyses either because they were far from sampled seedlings (●) or because they were dead in 2012 (+). Empty dots (○) represent other species within the protected area. (B) Study site location (red star) on European Beech distribution map (source Euforgen). (C) Picture of a sampled seedlings.

Adult seed-tree inventory and phenotyping

This study was conducted on two circular-shaped plots (as classically used in parentage analyses) covering 0.17 ha in total, where all the 683 alive adult beeches were mapped and collected for genetic analyses in 2012 (red dots on Figure 2). Although beech reproduction is mostly sexual, vegetative reproduction may occasionally occur, with the production of stump shoots resulting in multiple stems (i.e. several ramets for a single genet). In obvious cases of vegetative reproduction (ie root-connected stems), we sampled only the biggest ramet of each genet for genetic analyses.

Only 439 among the 683 collected beeches were included within the protected plot and monitored since 2002 (filled dots on Figure 2). The monitoring consisted first in measuring tree size as the diameter at breast height (DBH) in 2002 and 2012, which allowed us to derive the basal area ($BA=\pi*DBH^2/4$). Individual growth was

measured by the basal area increment (herein BAI) between 2002 and 2012, as estimated by: $BAI=\pi(DBH^2_{2012}-DBH^2_{2002})/4$.

The presence of dead branches and leaves was recorded each year between 2004 and 2012 as a qualitative measure (1=presence; 0=absence). We used the sum of these nine annual defoliation scores (herein DEF) as an integrative, qualitative ordered measure, combining the recurrence of defoliation and the ability to recover from defoliation.

The conspecific local density (herein $Dens_{dmax}$) was estimated as the number of beech neighbors found within a radius of *dmax* around each mother-tree. We also used the Martin-Ek index (Martin & Ek, 1984) to quantify the intensity of competition on a focal individual *i*. This index (herein $Compet_{dmax}$) accounts simultaneously for the diameter and the distance of each beech competitor *j* to the competed individual *i*:

$$\text{Compet}_{i,d_{\max}} = \frac{1}{\text{DBH}_i}\sum_{\text{j=1}}^{n_{dmax}} \text{dbh}_j e^{\frac{-16d_{\text{ij}}}{DBH_i+DBH_j}} \quad \text{(equation 1)}$$

where DBH_i and DBH_j are the diameter at breast height (in cm) of the competed individual *i* and of competitor *j* (any adult tree of any species with $DBH_j>DBH_i$), n_{dmax} the total number of competitors in a given radius d_{max} (in m) around each individual *i*, and d_{ij} the distance between individuals i and j. We computed a total of 20 $Dens_{dmax}$ variables and 20 $Compet_{dmax}$ variables, by considering d_{max} values between 1 and 20 m with a 1m-step. The $Dens_{dmax}$ variables were strongly and positively correlated with each other's, and so were the $Compet_{dmax}$ variables, but $Dens_{dmax}$ variables were not correlated with $Compet_{dmax}$ variables (Figure S2).

Offspring sampling and genotyping

To estimate adult fecundity, we sampled 365 seedlings established amidst the 683 genotyped adult beeches (shaded quadrats on Figure 2). Two cohorts of seedlings were sampled exhaustively within a selected number of quadrats at the center of each circular plot: 165 "young" seedlings germinated in spring 2012 (masting year 2011), and 200 "old seedlings" germinated from spring 2011 back to spring 2001 (age was estimated using annual bud scars). Qualitative surveys indicated that masting occurred in years 2002, 2004, 2006 and 2009. In this study, the two seedlings cohorts were mixed, in order to estimate cumulated reproduction from 2001 to 2012.

The genotypes of the 683 alive adult beeches and 365 seedlings were scored at a combination of 18 microsatellite loci (Table S1). DNA extraction, PCR amplifications and genotype scoring with a MegaBACE 1000 sequencer were performed using the conditions described by Oddou-Muratorio, *et al.* (2018). The total number of alleles observed in each cohort was greater than 95 (Table S1). Adult genotypes revealed seven pairs of clones among the adult beeches. We checked that these clones were always spatially clustered, and kept only one ramet for each genet in the MEMM analyses (i.e. 676 adult beeches).

Inference of male and female relative fecundities: MEMM analyses

Male and female fecundities were jointly estimated with the pollen and seed dispersal kernels in a Bayesian framework implemented in the MEMM program (Oddou-Muratorio et al., 2018). MEMM is one of the recently developed spatially explicit mating models based on naturally established seedlings (see also Burczyk, Adams, Birkes, & Chybicki, 2006; Goto, Shimatani, Yoshimaru, & Takahashi, 2006; Moran & Clark, 2011; Oddou-Muratorio & Klein, 2008). These models provide joint estimates of individual male and female fecundities together with the pollen and seed dispersal kernels and mating system parameters, so that estimates of fecundity are not biased by the confounding effects of spatial and sampling designs (the arrangement of male/female parents and sampled seedlings).

Briefly, the Mixed-Effect Mating Model (MEMM) considers that each sampled seedling originates either (i) from a mother tree located outside the study site (implying seed immigration) or (ii) from a mother tree located within the study site. The latter case includes three possible origins of the fertilizing pollen: (i) pollen immigration, (ii) selfing, or (iii) pollination by a male tree located within the study site. The approach bypasses parentage assignation and focuses instead on the fractional contribution of all adults, either as female or as male parent, to each seedling (see Appendix A1 for details). For instance, the probability π_{Sij} of each sampled female tree *j* to contribute to the seedling pool at the spatial location of seedling *i* is modeled as:

$$\pi_{S_{\mathrm{ij}}} = \frac{F_{\mathrm{Fj}}\theta_S(d_{\mathrm{ij}})}{\sum_{l:\mathrm{mother}} F_{\mathrm{Fl}}\theta_S(d_{\mathrm{il}})} \quad \text{(equation 2)}$$

where F_{Fj} and F_{Fl} are the female fecundities of mother *j* and *l*, respectively; d_{ij} and d_{il} are the distances between seedling *i* and mother *j* and *l*, respectively; and ϑ_s is the seed dispersal kernel. Both the seed and pollen dispersal kernels (ϑ_s and ϑ_p) are modelled using a power-exponential function. All the parameters of the model are estimated in a Bayesian framework (Appendix A1). Note that F_F (and F_M) estimates are relative, with the average F_F-value (and F_M-) over the entire parent population fixed to 1.

Note that the fecundity estimates provided by MEMMs are related but not equivalent to the traditional resource-based estimates of female (i.e. the biomass/number of ovules, seeds, ovuliferous flowers or fruits) and male fecundity (i.e. the biomass/number of pollen grains or staminate flowers). First the latter estimate the resources allocated by each plant to reproduction while the former can only estimate a relative amount of pollen or seeds produced by each plant as compared to other plants. Second, the resource-based estimate is a pre-dispersal evaluation of seed and pollen production while MEMM estimates an effective amount of pollen achieving successful fertilization, and of seeds achieving successful germination. In consequence, MEMM-based estimates of fecundities account for individual effects (either maternal or genetic) that act independently on location to modify the success of mating, seed maturation or germination, or early survival during the post-dispersal processes preceding the sampling stage (Oddou-Muratorio et al., 2018).

For the estimation, we accounted for typing errors at microsatellite loci, with two possible types of mistyping: in the first type, the allele read differs only by one motif repeat from the true allele with a probability P_{err1}, while in the second type, the allele read can be any allele observed at this locus with a probability P_{err2}. We considered a mixture of the two error types, with $P_{err1} = 0.01$ and $P_{err2} = 0.01$. We ran 10 Markov chain Monte Carlo (MCMC) of 10,000 steps, each with additional 500 first MCMC steps as burn-in, checked that the different chains converged to the same value visually, and then combined the 10 chains together. Individual female (F♀) and male (F♂) fecundities were summarized by their median value across the 100,000 iterations.

Adult subsampling for dendrochronological analyses

We selected 90 trees within the protected plot for which we sampled cores to measure ring-width. These 90 trees were chosen to represent contrast in terms of defoliation and female fecundity (Figure S3). Cores were extracted in February 2016 at 1.30 m above ground. After sanding, cores were scanned at high resolution (1200 dpi). Boundary rings were read using CooRecorder v 9.0. Ring width were transcribed, individual series were checked for missing rings and dating errors and mean chronologies were calculated using Cdendro 9.0 (CDendro 9.0 & CooRecorder 9.0; Cybis Elektronik & Data AB. Sweden). Using the sum of ring width increments between 2002 and 2012 (Σrw), the growth of the 90 individuals between 2002 and 2012 was estimated as: $BAI_{wood}=\pi((DBH_{2002}/2+\Sigma rw)^2-DBH^2_{2002}/4)$.

Statistical analyses of the ecological drivers of growth and fecundities

Our objective herein was to test whether defoliation significantly affected individual growth and female/male fecundity. For each response variable independently (i.e., growth as measured by BAI, and fecundities as estimated with MEMM), we considered the following initial linear model:

$$\text{BAI or F♀ or F♂} = \text{DEF} + \text{DBH}_{2002} + \text{DBH}_{2002}^2 + \text{Compet}_{dmax} + \text{Dens}_{dmax}$$

$$+\text{DEF:DBH}_{2002} + \text{DEF:Compet}_{dmax} + \text{DEF: Dens}_{dmax} \text{ (equation 3)}$$

where all the predictors are quantitative variables (Table S2). Besides the target defoliation factor (DEF), this model includes one size-related factor (DBH_{2002}), and two competition-related factors ($Compet_{dmax}$ and $Dens_{dmax}$). Size and competition are considered here as "nuisance" parameters, susceptible to blur the signal between defoliation, growth and reproduction. A quadratic effect of DBH_{2002} was also included, as growth and sometimes fecundity are known to be proportional to basal area. Density and competition index can both be relevant to capture competition effect on growth or fecundity, and moreover, their influence may vary with the distance up to which competitors are accounted for. Therefore, we first selected the best $Compet_{dmax}$ and the best $Dens_{dmax}$ terms for each response variable independently using the model described by equation 3 without interaction terms, and retaining the d_{max} values leading to the highest R^2. Then, we included interactions terms (the three last terms in equation 3) to investigate specific effects of defoliation depending on individual size or on the level of competition.

The model was fitted on 432 focal adult beech trees within the protected plot (Figure 2) for which BAI was estimated from inventory data. All response variables were log-transformed to approach Gaussian distribution and to account for the higher variance associated to higher fecundity or higher growth. We visually inspected the relationship between each predictor and each response variable (Figure S4). For each response variable, we selected the most parsimonious model based on the AIC using the functions 'lm' and 'step' in R 3.3 (R Core Team 2018). The residuals were visually inspected through a plot of residuals vs predicted. Interaction effects were visualized with the package 'jtools' (Long, 2018).

Collinearity resulting from correlations between predictor variables is expected to affect statistical significance of correlated variables by increasing type II errors (Schielzeth, 2010). To evaluate this risk, we computed variance inflation factors (VIF) associated to each term retained in the best model with R package 'car' (Fox & Weisberg 2011).

Statistical analyses of the joint defoliation effects on female fecundity and growth

Our objective herein was to focus on the two variables (growth and female fecundity) responding to defoliation (see results), and to investigate how the relationship between these two variables varied with defoliation. We first compared the effects of defoliation on female fecundity vs growth after centring and normalizing fecundity and growth, and by using the best models fitted with equation 3 to estimate the effect of defoliation on these transformed variables.

Then, we investigated the individual correlation between raw relative female fecundity and growth for non-defoliated trees (DEF=0) versus defoliated trees (DEF>0). Note that a part of these correlations may be due to variation in size and/or competition among individuals. Moreover, they do not account for the quantitative nature of DEF. To overcome these limitations, we further investigated the trade-off between growth and female fecundity using the following linear model:

$$\text{F♀} = \text{BAI} + \text{DEF} + \text{DBH}_{2002} + \text{DBH}_{2002}^2 + \text{Compet}_{dmax} + \text{Dens}_{dmax}$$

$$+\text{DEF:BAI} + \text{DEF:DBH}_{2002} + \text{DEF:Compet}_{dmax} + \text{DEF: Dens}_{dmax} \text{ (equation 4)}$$

where BAI and the interaction between BAI and DEF are added to the model described by equation (3) above. A quadratic effect of DBH_{2002} was also included.

Results

Patterns of covariation of defoliation, tree size and competition

Recurrent crown defoliation was overall limited in the 432 individuals, with 95 trees with a non-null DEF-value (mean=0.36, Table S2). Defoliation increased with tree size; the significant interaction between DBH_{2002} and competition (mediated by Comp19) or density (mediated by Dens20) reflected a stronger effect of size on defoliation as competition increased (Figure S5).

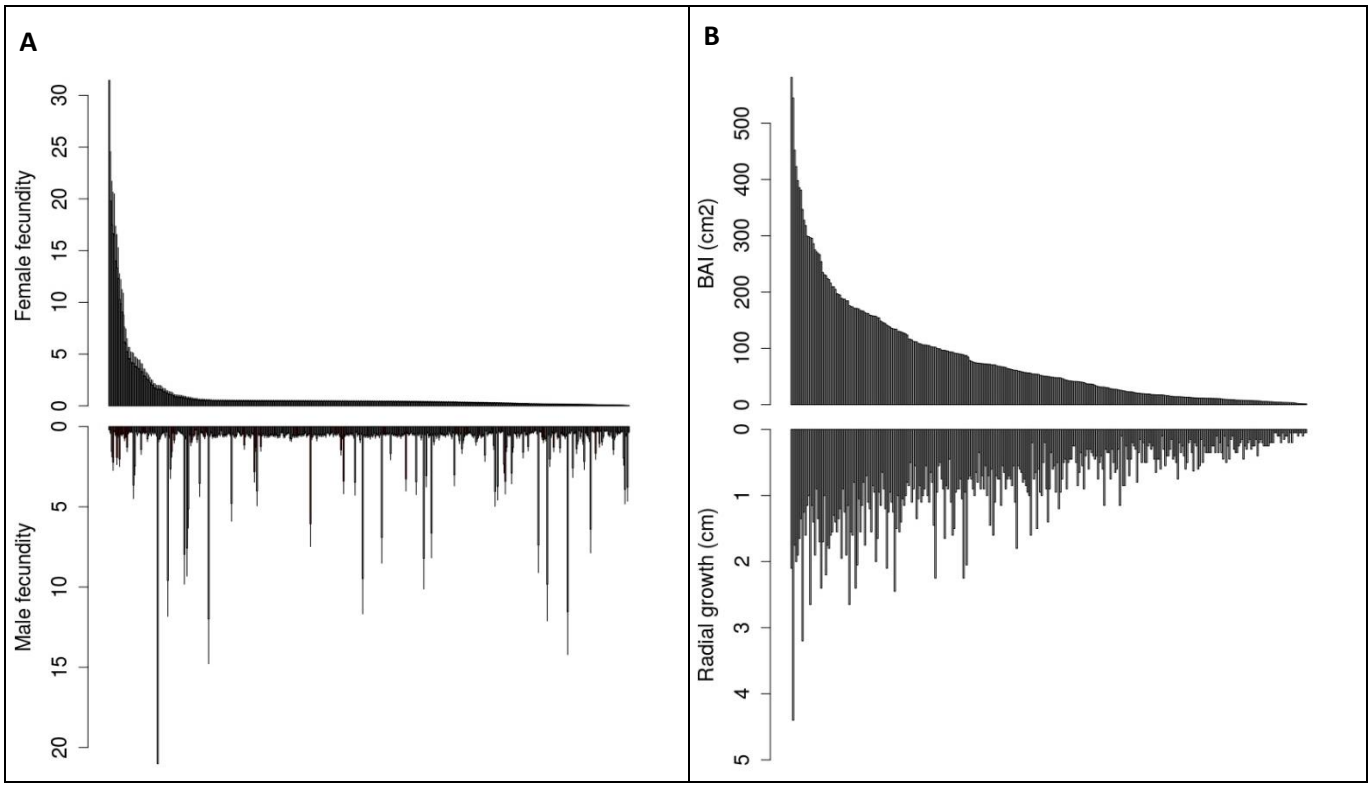

Figure 3: Distribution of individual (A) relative female (top) and male (bottom) fecundities estimated with MEMM, and (B) absolute growth estimated by BAI (top) or radial growth (bottom) for the 432 adult trees. Parents on the x-axis are ranked in decreasing order of female fecundity (A) or BAI (B).

Inter-individual variations in relative fecundities and growth

The distributions of relative female and male individual fecundities (F♀ and F♂) estimated by MEMM were strongly L-shaped (Figure 3A). Female fecundities varied from 0.03 to 32.44 (median=0.42, mean= 1, sd= 2.78), while male fecundities varied from 0.17 to 21.16 (median= 0.48, mean =1, sd= 1.86). By comparison, the distribution of growth values was less L-shaped than those of fecundity (Figure 3B). In the data set of 432 adult

trees, where cumulated growth from 2002 to 2012 was estimated through inventory data, radial growth varied from 0 to 4.4 cm (median=0.45, mean= 0.60, sd= 0.62), while BAI varied from 0 to 581.22 cm^2 (median=23.98, mean= 61.58, sd= 86.87).

In the subset of 90 cored trees, where cumulated growth from 2002 to 2012 was estimated through ring width data, radial growth varied from 0.17 to 2.70 cm (median=0.97, mean= 1.03, sd= 0.57), while BAI varied from 7.8 to 805.89 cm^2 (median=126.30, mean= 180.07, sd=172.7). Moreover, for these 90 cored trees, the correlation between inventory-based and ring-width-based radial growth was 0.84 (p-value<0.001), while the correlation between inventory-based and ring-width-based BAI was 0.68 (p-value<0.001). The lower correlation for BAI values was due to the largest trees, for which inventory data generally underestimated growth (Figure S6).

Ecological drivers of fecundities and growth

Defoliation, size and competition overall explained a significant part of the variation in growth (57%) and female fecundity (12%), while competition alone was found to marginally explain a small part of the variation in male fecundity (<1%). In the whole data set of 432 individuals, the most parsimonious model showed that female fecundity (F♀) significantly decreased with defoliation and competition (mediated by Compet10), while it increased with DBH_{2002} and density (mediated by Dens10; Table 1A). Moreover, the interaction between DEF and DBH_{2002} was significant, reflecting a weaker negative effect of defoliation on female fecundity as tree size increased (Figure 4A). By contrast, male fecundity (F♂) was only marginally (and negatively) affected by competition (mediated by Dens5, Table 1B). Finally, growth (as measured by BAI) significantly decreased with defoliation and competition (mediated by Compet7), and increased with DBH_{2002} and density (mediated by Dens10; Table 1C). By contrast with female fecundity, no interactions between defoliation and size were detected on growth. For all fitted models, variance inflation factors (VIF in Table 1) were all below 10, ruling out any serious multicollinearity issue. Diagnostic plots confirmed the quality of the fitted models (Figure S7).

To compare the effect of defoliation on fecundity and growth, we centred and normalized F♀ and BAI, and ran the best models for each response variable. The average decline in response to a one-unit increase in DEF was -0.06 for F♀ (S.E.= 0.10; measured in standard unit of trait) versus -0.10 for BAI (S.E.=0.04).

Table 1. Analysis of variance table for (A) *F♀*: female fecundity (B) *F♂*: male fecundity and (C) BAI: basal area increment, in response to ecological determinants included in equation (3). We show the results of the most parsimonious model: its adjusted R^2, the type III sum of squares (SSQ) and degree of freedom (df) associated to each term. For each predictor, we give the estimate of its effect, the standard error (S.E.) and associated t and p-value. Variance inflation factors (VIF) were computed with R package CAR. All the response variables were log-transformed. Results are based on the whole data set of 432 individuals for *F♀* and *F♂*, and on the 341 with non-null BAI for BAI.

Predictor	R^2	SSQ	df	Estimate	S.E.	t	p-value	VIF
(A) log(F♀)	*0.12*						*<0.001*	
DEF		9.33	1	-0.349	0.111	-3.148	0.002	4.13
DBH_2002		11.97	1	0.013	0.004	3.564	<0.001	2.19
Compet10		7.9	1	-0.033	0.011	-2.896	0.004	1.43
Dens10		7.46	1	0.010	0.003	2.815	0.005	1.35
DEF:DBH_2002		7.28	1	0.006	0.002	2.780	0.006	4.61
residuals		401.29	426					
(B) log(F♂)	*0.004*						*0.097*	
Dens5		1.695	1	-0.01	0.01	-1.662	0.10	-
residuals		263.854	430					
(C) log(BAI)	*0.61*						*<0.001*	
DEF		4.89	1	-0.153	0.058	-2.646	0.00853	1.05
DBH_2002		139.39	2	15.494	1.167	13.275	<0.001	1.21
DBH_2002²				-5.539	0.886	-6.251	<0.001	
Compet7		20.92	1	-0.090	0.016	-5.473	<0.001	1.27
Dens14		4.78	1	0.005	0.002	2.617	0.00927	1.16
residuals		234.02	335					

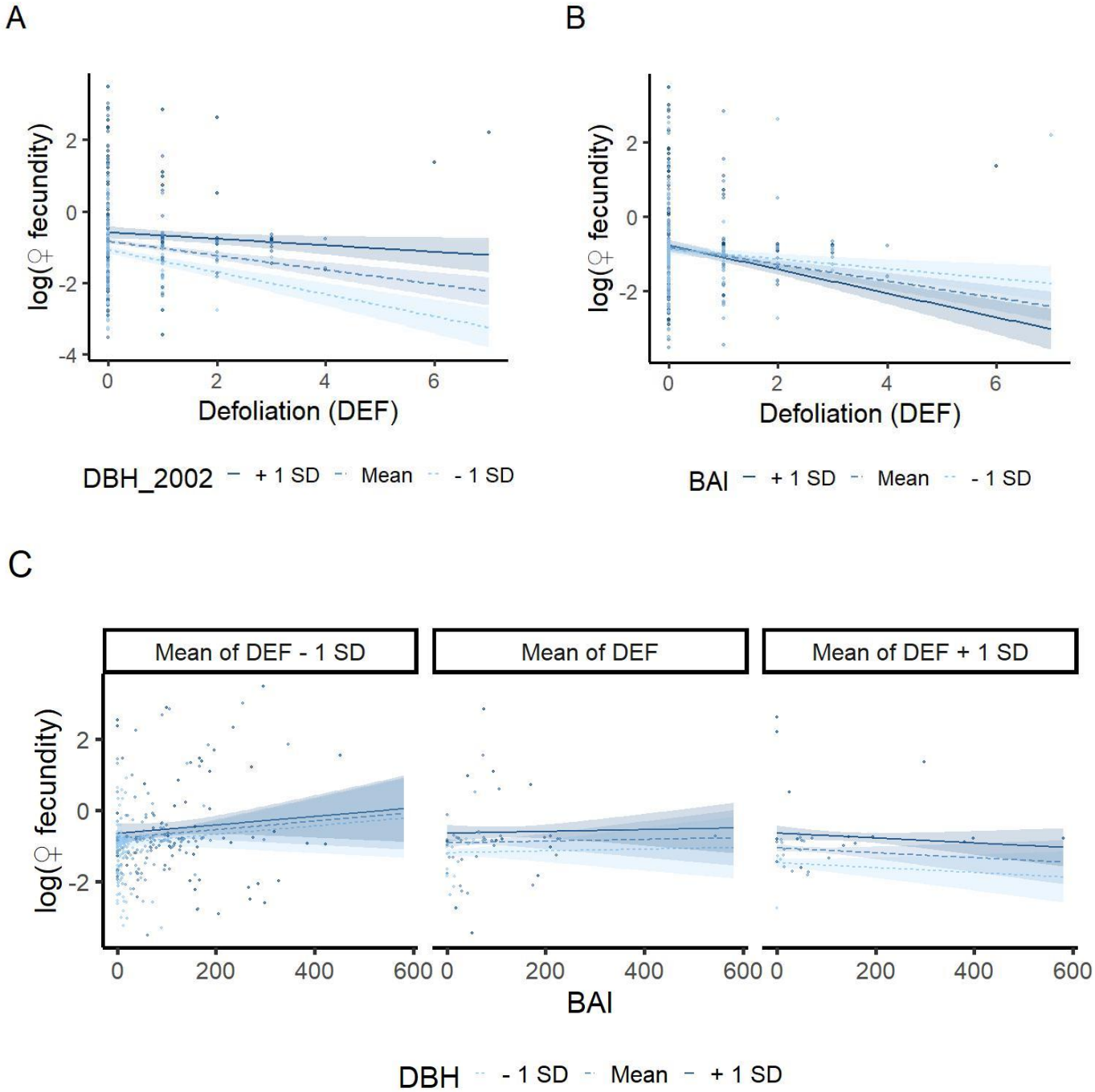

Figure 4: Interaction plots for (A) DEF and DBH_{2002} effects on female fecundity (B) DEF and BAI effects on female fecundity, (C) BAI, DBH_{2002} and DEF effects on female fecundity. Regression lines are plotted for three values of each moderator variable, corresponding to +/- 1 standard deviation from the mean. Confidence interval at 80% are shown around each regression line. Points are the observations.

Joint defoliation effects on female fecundity and growth

The raw F♀s and BAIs were significantly and positively correlated in the 337 non-defoliated trees ($cor_{F♀\text{-}BAI\text{-}nondef}$ = 0.31, p-value<0.001), but not in the 95 defoliated trees ($cor_{F♀\text{-}BAI\text{-}def}$=0.13, pval=0.2; Figure 5).

The linear model for F♀ including BAI as a predictor (equation 4) allowed us to disentangle the respective effects of defoliation, size and competition on the relationship between female fecundity and growth. In addition to the previous effects, a significant interaction between BAI and defoliation was detected (Table 2): F♀ overall decreased with increasing defoliation, but this decrease was faster and stronger for trees with a higher BAI (Figure 3B). The complex interaction between BAI, DEF and DBH_{2002} on F♀ resulted in a defoliation-dependent trade-off between growth and female fecundity: F♀ of the non-defoliated trees (Figure 3C, left panel) increased with BAI (no trade-off), whereas F♀ of the most defoliated trees (Figure 3C, right panel) decreased with increasing BAI (trade-off). Moreover, F♀ of small trees (Figure S8, left panel) always decreased in response to increasing defoliation, whatever their BAI, whereas the female F♀ of large trees (Figure S8, right panel) could increase in response to increasing DEF, at the expense of reduced BAI. Diagnostic plots confirmed the quality of the fitted models (Figure S9).

Table 2. Analysis of variance table for female fecundity, in response to ecological determinants included in equation (4). Results are based on the whole data set of 432 individuals. See Table 1 for legends.

Predictor	R^2	SSQ	df	Estimate	S.E.	t	P-value	VIF
	0.13						*<0.001*	
BAI		0.56	1	0.001	0.001	0.773	0.440	2.468
DEF		11.04	1	-0.384	0.112	-3.433	0.001	4.231
DBH		6.24	1	0.011	0.004	2.582	0.010	3.171
Compet10		7.49	1	-0.032	0.011	-2.828	0.005	1.444
Dens10		6.85	1	0.009	0.003	2.704	0.007	1.354
BAI:DEF		4.09	1	-0.001	0.001	-2.091	0.037	2.857
DEF:DBH		11.39	1	0.009	0.003	3.488	0.001	6.750
Residuals		397.03	424					

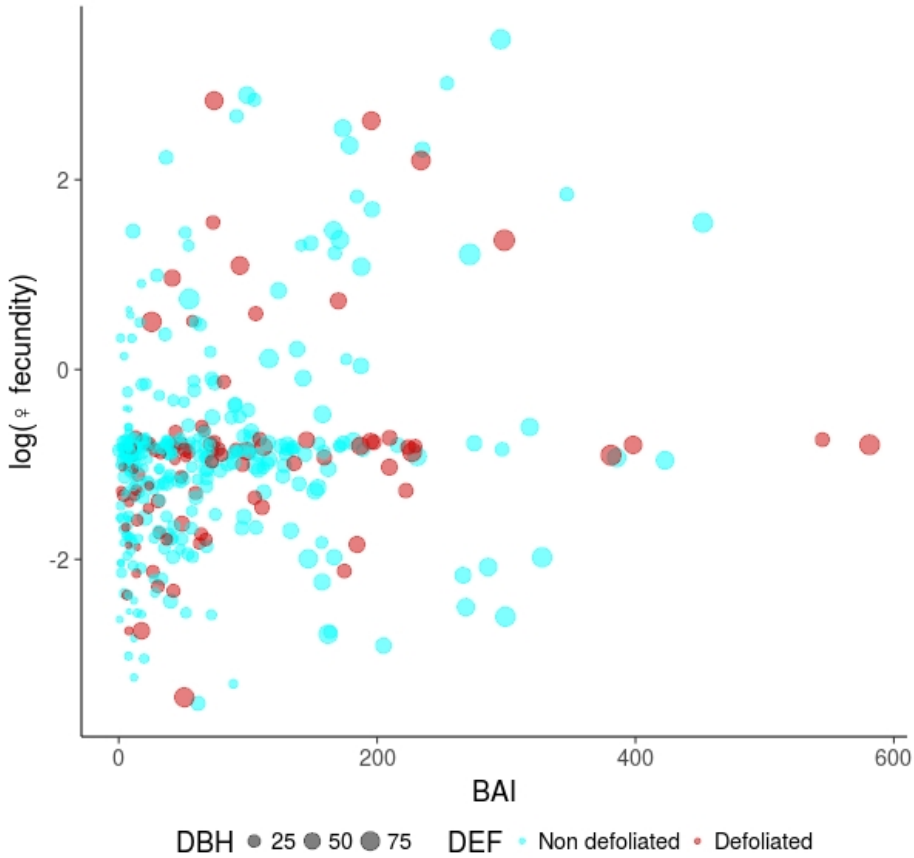

Figure 5: Correlation between growth, measured by the Basal Area Increment (BAI) and female fecundity (F♀), plotted on a log scale. The size of the dots is proportional to tree diameter (DBH_{2002}). This is a scatter plot of raw data, and not of model predictions.

Discussion

By investigating the among-individual variation in the impact of stress-induced defoliation on female/male fecundity and wood growth within a beech natural population at the warm, dry margin of the species distribution, this study brings new insights on the response to stress of a major European tree species. We show that crown defoliation was significantly associated to a decrease in wood growth and female fecundity, but not in male fecundity. A trade-off between growth and female fecundity was observed in response to defoliation, suggesting that some large defoliated individuals can maintain significant female fecundity at the expense of reduced growth. The consequences of these results on short-term evolutionary dynamics of the studied population are discussed.

The response of wood growth and reproduction to stress-induced crown defoliation.

The coordination between increasing crown defoliation and decreasing wood growth observed in this study is consistent with the temporal sequence of ecophysiological processes involved in tree

response to water stress and late frosts. During summer, low precipitation and high evaporative demand due to high temperatures and vapor-pressure increase water stress, which leads trees to close stomata, in order to reduce transpiration and protect the integrity of the hydraulic system by maintaining water potentials above irreversible embolism thresholds. Drought also directly impacts wood growth by limiting cell division and elongation of wood cells due to carbon limitation (Lempereur et al., 2015). Post-drought stomatal closure can prolong the decrease in photosynthesis and potentially affect carbon storage (Bréda et al., 2006), which may lead to a decrease in radial growth in subsequent years. Under severe drought, some branches can experience hydraulic failure or undergo carbon starvation, which leads to leaf fall. Leaf fall can then in turn have a negative effect on radial growth, first by decreasing photosynthesis and thus carbon availability in the years following defoliation. Secondly, leaf fall can induce allocation shifts that reduce the priority of growth relative to other sinks such as reserves storage, as observed in black oak (Wiley et al., 2017). On the other hand, when late frosts damage young leaves, beech trees can reflush, i.e. produce another cohort of leaves (Menzel, Helm, & Zang, 2015), at least for some parts of the crown. However, the time required to reflush leads to a shorter growing season, which directly reduces wood growth. For these non-mutually exclusive reasons, related to either carbon-, sink-, or temporal limitation of growth, a negative effect of crown defoliation on growth is often observed, especially on beech (Delaporte et al., 2016, this study).

Although seed production is recognized as being resource-limited in plants (Lloyd & Bawa, 1984), the ecophysiological processes involved in the response of tree sexual reproduction to physiological stresses are less well characterized than those involved in wood growth response. The negative effect of crown defoliation on female fecundity observed in this study is consistent with the expected decrease in photosynthesis and thus in carbon availability induced by leaf fall. Moreover, this result combined with the absence of crown defoliation effect on male fecundity is also consistent with the expected higher resource-limitation of female fecundity (costly nut-seeds) as compared to male fecundity in beech (Lloyd & Bawa, 1984; Obeso, 1988). This second expectation is also supported by the marked increase in female fecundity with increasing tree size and decreasing competition while male fecundity was only marginally (and negatively) affected by competition. Moreover, recent studies showed that many tree species use mainly current photosynthates to maturate their fruits, while flowers are produced from old carbon storage (Hoch, Siegwolf, Keel, Körner, & Han, 2013; Ichie et al., 2013). Altogether, our results suggest that beech reproduction is more limited by the carbon resources needed for maturating seeds than for those required for producing flowers. Although nitrogen storage and remobilization is usually a limiting resource for seed production, and particularly masting (Han & Kabeya, 2017), this may not be the case in our study site, where cow grazing could favour nitrogen enrichment.

Defoliation induced a trade-off between growth and reproduction

Several studies tested the existence of a negative correlation between growth and reproduction at the individual level, as a signature of the possible trade-off between these functions. The key assumption underlying this trade-off is that reproduction is costly and competes with growth for resources (Koenig & Knops, 1998; Obeso, 2002; Thomas, 2011). By contrast, the absence of correlation is usually interpreted as independence between these functions in terms of resource pool (Knops, Koenig, & Carmen, 2007; Obeso, 2002; Pulido et al., 2014). A trade-off between growth and

reproduction was already found for beech (Hacket-Pain, Friend, Lageard, & Thomas, 2015; Lebourgeois et al., 2018; Hacket-Pain et al., 2018). More precisely, Hacket-Pain et al. (2017) found for beech that masting years (i.e. high seed production) are negatively correlated with growth and this trade-off is more pronounced during drought years due to resource scarcity.

We found here a negative (respectively positive) correlation between growth and reproduction for defoliated (respectively non-defoliated) trees. Hence, among the defoliated trees, some individuals maintained significant female fecundity at the expense of reduced growth, and reciprocally. These results support the general idea that the correlation between reproduction and growth depends on the level of resource (Obeso, 2002; van Noordwijk & de Jong, 1986), a trade-off being present only under limiting resources, i.e. crown defoliation in our case. By contrast, the higher resource level of non-defoliated individuals could allow them to insure reproduction and growth with independent resource pool, as it was found also for *Fagus* genus (Yasumura, Hikosaka, & Hirose, 2006). Moreover, the detailed analysis of the interactions between defoliation, size and growth on female fecundity showed that those defoliated trees maintaining high female fecundity were the largest ones, suggesting that crown defoliation could shift the allocation of carbon to reproduction above a given tree size. Besides the literature on forest seed orchards and fruit trees orchards, one of the rare studies supporting such hypothesis is that of Wiley, Casper & Helliker (2017), who experimentally defoliated black oak, a tree species which maturates its acorns over two years. Recovery following defoliation was shown to involve substantial allocation shifts, with carbohydrate storage and already initiated reproduction cycles (i.e. maturation of 2-year acorn) being favored relative to growth and new reproductive cycles (i.e. flowering and production of new 1-year acorn).

The positive correlation between growth and reproduction for non-defoliated trees may also indicate an effect of the unobserved level of resource, which probably varies among individuals. More generally, elucidating the causal relationships between defoliation as an impact of stress, the (non-observed) level of resource, growth and reproduction would deserve further investigations, accounting for the complex multivariate relationships among the interrelated variables mapped on Figure 1. This could be achieved using for instance path analyses (Shipley, 2016) or other Bayesian tools introducing the level of resource as a latent variable (e.g., Journé et al., submitted). The use of such approaches in this study was however hampered by two main limitations. First, resource allocation between two compartments are difficult to handle in path analyses, and a reciprocal relationship between growth and reproduction such as depicted by the red double arrow on Figure 1 cannot be specified (Shipley, 2016). The solution to this problem usually consists in accounting for the time dimension, focusing on among-year lagged effects between annual variables (e.g. Hacket-Pain et al., 2018, Journé et al., submitted). However, this solution was intractable in this study, where growth and reproduction were measured as integrated values over the period 2002-2012. The second limitation stems from the weak ability of variance-covariance based methods such as path analyses to deal with non-normality. Whereas deviations from a Gaussian distribution are not necessarily crucial for predictor variables in a linear model, they cannot be handled in path analyses simultaneously with latent variable to our knowledge (Lefcheck, 2016).

Long-term consequences for population adaptive response to stress

In the studied population, some large, defoliated individuals maintained a high female fecundity under stressful conditions, at the expense of reduced growth. Moreover, as male fecundity was insensitive to crown defoliation, the less competed defoliated trees also contribute to reproduction through male function. Hence, we can reject the hypothesis H1 that the relationship between reproduction and growth does not change with increasing crown defoliation. Note however that the alternative hypothesis H2 (defoliation or stresses act like a cue stimulating reproductive performances at the expense of reduced growth) was only supported for some individuals. This response to stress could have major consequences for the short-term evolutionary dynamics of the population. Indeed, assuming that at least some of the traits underlying vulnerability to stresses are under genetic control, we showed here that the most vulnerable individuals (those that are the most impacted by stress) still contribute to regeneration, which could lead the population to evolve traits compromising its adaptation to stress. By contrast, if the defoliated individuals would decrease simultaneously their growth and reproduction (hypothesis H1), their potentially non-adapted genotypes could be purged more efficiently.

Deriving demo-genetic scenarios for the population adaptive response to stress and testing for a reproduction load would however require further investigations. First, the observed inter-individual variation in the level of defoliation is probably shaped in part by genetic variation but also by microenvironment variation and ontogeny, since the largest and most competed individuals were more susceptible to defoliation. Hence, the importance of genetic factors driving the level of defoliation remains to be characterised, in order to better decipher the intra-individual variation in the vulnerability to stress from that of the stress exposure, and to investigate possible evolutionary changes (Hamanishi & Campbell, 2011). Second, our MEMM-based estimates of fecundity have the advantage to integrate the whole regeneration processes and not just seed/pollen production. This is important as post-dispersal processes and recruitment patterns may compensate the decline in seed production in populations under stressful conditions, as suggested for drought by Barbeta et al. (2011). However, they also have the drawbacks to be relative, and to convey no information on the absolute contribution of defoliated or non-defoliated individuals to the regeneration, and thus on the demographic impact of defoliation.

Finally, investigating the population adaptive response to stress would ideally require accounting for the physiological mechanisms involved. For instance, when dealing with drought-induced defoliation, we would need to consider the two main ecological strategies widely acknowledged in plants for drought response: 1) the water economy strategy, where plants maintain low growth rates and low rates of gas exchange during droughts, and 2) the water uptake strategy, where plants have a more rapid instant growth through higher rates of gas exchange when water is available, typically spring in Mediterranean climate, allowing them to complete important biological functions before drought onset (Arntz & Delph, 2001). These two strategies rely on different combinations of physiological, morphological or phenological trait values (in particular those related to hydraulics and carbon-storage). Bontemps et al. (2017) demonstrated the co-existence of these two strategies in a drought-prone population of beech and showed a higher reproductive output of the water uptake strategy. In this context, defoliation could be one of the traits involved in the water uptake strategy,

allowing the maintenance of the water balance after drought onset. Indeed, if defoliated trees are characterized by higher xylem vulnerability but also higher hydraulic conductivity, the more a tree is efficient for transpiration and photosynthesis, the more it is vulnerable to drought (Cochard, Lemoine, & Dreyer, 1999).

Data accessibility

The data set analysed in this preprint is available online under the zenodo platform (DOI: 10.5281/zenodo.3516305). More detailed data (genotypes) and R scripts for statistical analyses are available from the corresponding author.

Supplementary material

The MEMM software for estimating female and male fecundities is available at: https://informatique-mia.inra.fr/biosp/memm.
Supplementary materials (Figures and Tables) for this preprint are available on bioRxiv (doi: https://doi.org/10.1101/474874).

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Conflict of interest disclosure

The authors of this preprint declare that they have no financial conflict of interest with the content of this article. SOM is a recommender for PCIEcology.

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4 Contributions scientifiques de la thèse

Congrès nationaux et internationaux

— Octobre 2017, **Les 20 ans du réseau RENECOFOR**, Beaune (Fr). Poster intitulé “Modéliser les réponses des écosystèmes forestiers au changement climatique pour bien anticiper les conséquences”. Résumé page 293.

— Août 2018, **Evolution Montpellier 2018**, Montpellier (Fr). Présentation orale intitulée “Trade-off between growth and reproduction in a long-lived plant”, dans la session Evolutionary physiology. Résumé page 294.

— Avril 2019, **European Geosciences Union (EGU) 2019**, Vienne (Au). Présentation orale intitulée “Risk of fruit production failure caused by the interaction of phenology changes and extremes events occurrence detected with a process-based model”, dans la session Phenology and seasonality in climate change. Résumé page 295.

Vulgarisation

— Fête de la science : Speed dating jeunes chercheurs, Rencontres avec des jeunes étudiants de l’Université d’Avignon, de l’Inra et du CEA (2018), animation de stand sur la phénologie et changement climatique (avec F. Jean en 2017, INRA URFM), sur le changement climatique et la reproduction (avec F. Jean en 2018, INRA URFM).

— Un chercheur à ma table, café des sciences spécial doctorant (2018).

— Conférence grand public Midiscience, intitulée *Comment le climat influence la reproduction chez les arbres forestiers ?* (2019).

— Participation à la rédaction d’articles de vulgarisation et communication scientifique (liens, <"Mieux comprendre comment les plantes survivent aux sécheresses">, <"On a lu, on a vu pour vous, échos de conférences">, <"Prédire la répartition future des espèces avec des modèles corrélatifs est hasardeux">).

Autres missions scientifiques

— Co-encadrement, avec Hendrik Davi. Mousny Esther (2017). Variation spatiale des dynamiques d’émission de pollen des arbres forestiers. Stage de deuxième année d’école d’agronomie. Bordeaux Sciences Agro

— Participation à la rédaction d’un manuel d’utilisation de CASTANEA, avec Hendrik Davi et Cathleen Petit.
`https://www.overleaf.com/read/nmyvszjkfxxh`

— groupe de travail sur le masting (TG20 COST Profound, G. Vacchiano), groupe de travail sur la phénologie (SOERE Tempo).

Modélisation mécaniste de la reproduction chez les arbres forestiers pour mieux prédire l'impact du changement climatique sur l'évolution des forêts

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Les peuplements forestiers sont menacés par le réchauffement climatique, en particulier dans la marge sud de leur aire de distribution. Face à ces changements et compte tenu des temps de générations longs chez les arbres forestiers, les réponses possibles sont limitées : (1) le déplacement des populations vers des aires plus favorables par le mécanisme de migration des graines et du pollen ou (2) l'adaptation au nouveau milieu que ce soit de façon immédiate (plasticité phénotypique) ou au cours des générations, par le biais de la sélection naturelle (évolution naturelle). Le sapin, espèce emblématique de nos montagnes, est actuellement présent jusque dans les montagnes du sud de l'Europe, mais son avenir y est très incertain. C'est pourquoi, à l'INRA d'Avignon, l'URFM (Unité de Recherche « Écologie des Forêts Méditerranéennes ») développe des modèles empiriques et mécanistes afin de quantifier les réponses du fonctionnement écophysiologiques et des dynamiques évolutives du sapin aux changements environnementaux à l'échelle locale. Pour ce faire, des expérimentations sont conduites le long d'un gradient environnemental naturel localisé sur le versant Nord du Mont-Ventoux. On observe, sur la zone d'étude s'étendant de 900 à 1500m d'altitude, un gradient thermique de l'ordre de 3.66°C (Gillmann, 2007), soit 0.64°C pour 100m et un gradient de précipitation de l'ordre de 14mm pour 100m (2008-2009 ; Cailleret, 2011). Après avoir modélisé la dispersion des graines en fonction de critères environnementaux (Amm, 2011), ma thèse intègre une dimension mécaniste de la modélisation de la reproduction qui tienne compte du fonctionnement écophysiologique des arbres. L'objectif principal de ma thèse est de développer un modèle générique d'allocation du carbone à la reproduction, couplé au modèle à base écophysiologique CASTANEA (Dufrêne et al, 2005). Ainsi, en modélisant la variabilité spatiale et temporelle de l'allocation du carbone à la reproduction, des simulations réalisées suivant divers scénarios climatiques permettront de déterminer l'impact de la variation de l'allocation du carbone à la reproduction sur les dynamiques forestières et sur l'évolution génétique.

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Trade-off between growth and reproduction in a long-lived plant

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Abstract

The assumption of a trade-off between growth and fecundity, reflecting the constraint of simultaneously investing in different traits due to the allocation of limited resources, is a common feature of life history models. However, it is often difficult to demonstrate this trade-off in natural populations due to the difficulty to account for the amount of available resources and their allocation scheme, which can be influenced by several factors, acting at individual level or in its ecological neighborhood. Moreover, the temporal timing of resource acquisition and allocation may induce hierarchical constraints on the traits related to growth or reproduction over a period of time. The main objective of this study is to explore the trade-off between growth and reproduction in tree using a resource-based, physiological framework. We developed a Bayesian hierarchical model to directly estimate the correlation between growth and fecundity on the one hand, and male and female fecundity on the other hand, based on measurement of growth, and male and female reproduction over several years. The model considers unobserved latent variables such as resource status or the number of initialized male and female flowers. Climatic conditions are accounted for to model the level of resources dispatched between growth and reproductive functions, using two approaches (i) a statistical model obtained from the literature and (ii) an ecophysiolocal process-based model. The model was applied on a Mediterranean coniferous *Cedrus atlantica*, which display a synchronous and highly variable seed production among years and individuals, which is referred as masting. Our results suggest that early season process of allocation is responsible for the trade-off between growth and reproduction, with a negative correlation between the number of initialized flower and tree growth. This approach opens new possibilities for the exploration of ecophysiological process and species trade-offs.

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Risk of fruit production failure caused by the interaction of phenology changes and extremes events occurrence detected with a process-based model

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Many perennial species, such as trees, show large variations of fruit production between years (the so-called masting) which can have major consequences on forest dynamic and species interactions. Among other drivers of fruit production failure, years of reduced fruit production can be due to the increase of temperature and the resulting advance in vegetative and reproductive phenology and timing of extreme events, such as drought or late frost. Indeed, flowers may fail to complete their maturation due to a 'veto' effect, i.e. variation of climatic conditions, promoting pollen limitation, fruit abscission, or more generally inducing reproductive failure. This veto effect may alter reproductive cycle which in turn impacts forest ecosystem functioning. Our hypothesis is that interactions between shifts in phenology and "veto" effects have major consequences on reproductive tree cycle at species range scale, considering the increasing number of extreme climatic events associated to ongoing and predicted climate change. To investigate this hypothesis, we used a process-based model (CASTANEA) previously calibrated and validated on European beech, a major European temperate tree. The model simulates stocks and fluxes between forest and atmosphere, from physiological characteristics of tree species. We simulated fruit production across Europe with a scenario accounting for veto (frost or drought) and a scenario without veto in order to detect the species margins associated to reproduction failure for that species. The detailed comparison of the two scenarios allowed us to assess when and where the different "vetos" explain the reproductive failure and how they interact with phenology changes. This study highlight how extreme climatic events can disrupt phenology of reproduction and thus change species distribution.