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Range-wide demographic patterns in European forests along climatic marginality gradients: An approach using national forest inventories

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À Jacqueline, Roger, Edouard et Renée, mes grands parents

Patrons démographiques à large échelle des forêts européennes le long des gradients de marginalité climatique: une approche utilisant les Inventaires Forestiers Nationaux.

Résumé : Le changement climatique contemporain modifie la répartition des espèces, en particulier celle des organismes aux lentes capacités de migration comme les arbres. La composition des forêts devrait être affectée dans les prochaines décennies, modifiant en même temps les fonctions et la biodiversité de ces écosystèmes, avec de fortes conséquences écologiques et sociétales. La distribution des arbres dépend de traits démographiques tels que le recrutement, la croissance et la mortalité qui interagissent le long des gradients climatiques. Les taux de mortalité forestière augmentent dans tous les biomes du monde. En Europe, par exemple, la mortalité augmente en marge chaude des aires de répartition des espèces en réponse à la sécheresse. Ces taux de mortalité élevés s'accompagnent de faible taux de recrutement, induisant des changements de végétation et rendant de nouveaux espaces disponibles, qui sont une opportunité pour les espèces exotiques envahissantes. Néanmoins, ces réponses démographiques au climat sont espèces et traits dépendantes. Comprendre comment s'articulent ces traits démographiques le long des gradients climatiques est donc un enjeux important pour prédire l'impact du changement climatique sur la dynamique forestière. Dans ce travail, je me suis intéressé aux patrons et aux déterminants de la mortalité et du recrutement de vingt espèces d'arbres indigènes et deux espèces exotiques dans les forêts européennes. Dans ce but, j'ai utilisé les données de 2 millions d'arbres provenant de 153892 parcelles mesurées dans les inventaires forestiers nationaux Français, Espagnol, Allemand, Wallon, Suédois et Finlandais.Je me suis d'abord intéressé à la mortalité des arbres. J'ai montré que l'occurrence de la mortalité est plus élevée en marge chaude et liée à des taux de sécheresse élevés alors que les évènements intenses de mortalité sont eux expliqués par différents facteurs incluant la compétition, la sécheresse et des températures élevées et peuvent se manifester sur l'ensemble de l'aire de répartition. En outre, l'occurrence de la mortalité est plus élevée en marge chaude des espèces tempérées et plus faible en marge froide pour la moitié des espèces méditerranéennes. J'ai ensuite analysé le recrutement de ces mêmes espèces et montré que pour la majorité, les taux de recrutement varient peu le long de leur aire de répartition. Le recrutement était fortement limité par la compétition et dépendait souvent de l'âge ou du taux de croissance du peuplement. De plus, le rôle de la sécheresse sur le recrutement des arbres n'est significatif qu'en interaction avec la compétition. Enfin, j'ai évalué le caractère envahissant de deux espèces exotiques, *Quercus rubra* et *Robinia pseudoacacia.* Mes résultats montrent que les deux espèces sont capables de recruter de nouveaux individus sous le couvert d'autres espèces et même de devenir dominantes au détriment de celles-ci. Mes résultats montrent également une expansion de leur aire de répartition au nord comme au sud. Ces résultats s'expliquent en partie par une sensibilité à la sécheresse relativement plus faible que les espèces indigènes. Dans l'ensemble, mes résultats soulignent que la sensibilité des arbres au changement climatique est trait-dépendent et varie le long des aires de répartition. Alors que la mortalité en marge chaude semble largement induite par la sécheresse, le recrutement y est beaucoup moins sensible. Cette différence de réponse suggère qu'un recrutement élevé pourrait compenser les effets négatifs du changement climatique. Néanmoins, les espèces exotiques, moins affectées par les facteurs environnementaux que les espèces méditerranéennes et tempérées, pourraient bénéficier du réchauffement climatique. Il reste donc à explorer dans quelle mesure le recrutement peut aider des espèces à persister in situ et quelles stratégies de gestion pourraient aider les forêts à atténuer le changement climatique futur.

Mots-clés : Changements globaux, répartition des espèces, Inventaires Forestiers Nationaux, démographie, modélisation, espèces invasives

Range-wide demographic patterns in European forests along climatic marginality gradients: an approach using National Forest Inventories.

Abstract: Modern climate change is reshaping species distributions, particularly on slow shifting organisms such as trees. Forests composition is therefore expected to change in the coming decades, which will alter ecosystem functions and biodiversity, with negative ecological and societal consequences for the planet. Tree distribution depends on several demographic traits such as recruitment, growth and mortality that interact across large climatic gradients. Yet, mortality is rising in all forested biomes in the world. In Europe for instance, forest mortality increases towards the climatic trailing edge of the species ranges as a response to drought. These high mortality rates are usually related to a lack of recruitment, which may induce vegetation shifts, but also opening new opportunities for the establishment of exotic invasive species. As demographic trait responses to climate vary across and within species, understanding trait interactions along large climatic gradients is crucial to better predict the impact of climate change on forest productivity, composition and range-shift dynamics. In this work I analyzed tree mortality and recruitment patterns of twenty of the most common native species and two exotic species in European forests and their triggered drivers. To this aim, I used data of 2 million trees from 153 892 plots measured in the National Forest Inventories from France, Spain, Germany, Belgium (Wallonia), Sweden and Finland. In the first chapter, I analyzed tree mortality and showed that the highest mortality occurrence happens in the climatic trailing edge, driven by drought, whereas the intensity of mortality is triggered by competition, drought and high temperatures and was uniformly scattered across species ranges. In addition, the occurrence of mortality was the highest in the trailing edge of temperate species and the lowest in the leading edge for half of the Mediterranean species. In the second chapter I analyzed tree recruitment, showing that for most species, there are no differences in recruitment across species ranges. Recruitment was strongly limited by competition and often depended on age, or growth rate of the plot. Surprisingly, the role of drought in tree recruitment only was evident in interaction with tree competition. In the third chapter, I assessed the invasiveness of two exotic invasive species, *Quercus rubra* and *Robinia pseudoacacia*. My results showed that both species are able to recruit new individuals under all other species canopies, to become dominant at the expanse of many trees species and suggested that they are both expanding their ranges northwards and southwards, in part because they are relatively less sensitive to drought than the other species. All together, my results highlight that trees sensitivity to current climate change is trait-dependent and differs across species ranges. The southern part of the species ranges can be shaped by drought-induced mortality, while recruitment is much less affected by drought. This different sensitivity to climate of tree mortality and recruitment suggests that recruitment could counteract the negative effects of climate change to a certain extent and that forests might be more resilient than what was previously thought. Yet, the exotic species expansion is less affected by the surrounding environment than Mediterranean and temperate species and could benefit from climate warming. Hence, the potential help of recruitment for in-situ species range persistence, and the management strategies which could help forests to mitigate future climate change remains to be explored.

Keywords: Global change, species distribution, National Forest Inventory, demography, modelling, invasive species

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Avant-propos

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Résumé substantiel

Introduction

Le changement climatique contemporain modifie la répartition des espèces, en particulier celle des organismes aux lentes capacités de migration comme les arbres. La composition des forêts devrait être affectée dans les prochaines décennies, modifiant en même temps les fonctions et la biodiversité de ces écosystèmes, avec de fortes conséquences écologiques et sociétales.

Les forêts européennes représentent plus de 25% de la totalité forestière terrestre et représente plus d'un million d'hectares de surface. La valeur estimée du seul secteur forestier en Europe est d'environ 103 millions d'euros et il fournit un emploi et un mode de vie durable à 3 millions de personnes. Les principales perturbations des forêts européennes proviennent des incendies, des ravageurs, des événements climatiques extrêmes, et de ceux liés à la gestion des forêts et à l'abandon des terres. Les facteurs anthropiques tels que l'utilisation et la gestion des terres peuvent également affecter les services et fonctions écosystémiques des forêts. Au total, 3,7 millions d'hectares de forêts sont touchés par des dommages forestiers.

Le changement climatique en cours devrait augmenter la fréquence et l'intensité de toutes ces perturbations dans les décennies à venir, avec des conséquences désastreuses sur les forêts. Les taux de mortalité forestière augmentent déjà dans tous les biomes du monde. En Europe, par exemple, la mortalité augmente en marge chaude des aires de répartition des espèces en réponse à la sécheresse. En plus de ces évènements de mortalité extrêmes ou «die-off», la mortalité dite «de fond», non catastrophique, augmente elle aussi en réponse au climat. Ces taux de mortalité élevés peuvent s'accompagner de faibles taux de recrutement, une composante démographique essentielle pour la persistance des populations d'arbres, répondant également fortement au climat.

Ces changement de mortalité et de recrutement peuvent induire des changements de végétation, qui sont particulièrement évident aux «ecotones», la zone de transition à laquelle deux biomes convergent. Ces écotones sont d'une importance particulière car ils rassemblent à leur marge nord («leading edge») des espèces qui pourraient potentiellement bénéficier du changement climatique, et à leur marge sud («trailing edge») des espèces qui pourraient être plus affectées par le changement climatique et présenter par exemple des taux de mortalité élevés.

De nombreux exemples de remontées altitudinales et latitudinales ont été mis en évidence

aux écotones. C'est le cas par exemple du Chêne vert (*Quercus ilex*) qui remonte au nord de son aire de répartition au sud de l'Europe limitant en même temps la recrutement de nombreuses espèces de Pins (*Pinus spp.*). De manière générale, un certain nombre d'études suggèrent que les espèces Méditerranéennes remontent au nord en réponse aux changements climatiques, au détriment des espèces plus tempérées. Par ailleurs, d'autres études mettent en évidence les remontées en altitude des arbres de multiples espèces en zone montagneuse. Bien que les changements climatiques en cours semblent favoriser les espèces Méditerranéennes a leur marge nord, ces déplacements d'espèce rendent également de nouveaux espaces disponibles, ce qui pourrait être une opportunité pour les espèces exotiques envahissantes pouvant ainsi s'établir au détriment d'autres espèces.
Néanmoins, la question de savoir si les espèces invasives vont bénéficier du climat ou non reste ouverte. Par ailleurs, ces réponses démographiques au climat sont espèces et traits dépendantes. Ainsi, comprendre comment s'articulent ces traits démographiques le long des gradients climatiques est un enjeux important pour prédire l'impact du changement climatique sur la dynamique forestière.

L'objectif principal de ce travail de thèse est d'identifier les principaux déterminants de la mortalité et du recrutement des arbres européens à travers de larges gradients climatiques afin d'évaluer la vulnérabilité des forêts, y compris la probabilité que les espèces exotiques se répandent au détriment des espèces indigènes. Dans ce but, j'ai analysé les principaux facteurs de mortalité et de recrutement des arbres de vingt espèces indigènes et de deux espèces exotiques dans les forêts européennes, de l'Espagne à la Finlande. Le large gradient latitudinal et le choix des espèces font que les habitats méditerranéens, tempérés et boréaux ainsi que les espèces exotiques sont représentés. J'ai utilisé environ 2 millions d'arbres provenant de 153 892 parcelles, mesurés dans les inventaires forestiers nationaux (IFN) Français, Espagnol, Allemand, Belge (Wallonie), Suèdois et Finlandais pour identifier les patrons de recrutement et de mortalité des arbres ainsi que leurs facteurs déclenchants le long de larges gradients géographiques, avec une emphase particulière dans les zones dites de "marginalité climatique". Afin d'identifier les marges climatiques de chaque espèce, j'ai développé une méthode permettant de classer les placettes des IFNs en fonction de leurs caractéristiques climatiques. Sur la base de 21 variables climatiques dont la moyenne a été calculée sur la période 2000-2014, j'ai d'abord appliqué une analyse en composantes principales pondérées (Weighted PCA), puis une analyse en composantes principales discriminantes (DPCA) afin de classer les placettes en trois catégories : cœur climatique (Core), bord d'attaque climatique (marge froide, leading edge) et bord de fuite climatique (marge chaude, trailing edge).

Chapitre 3: Mortalité des arbres dans les forêts européennes

Dans le premier chapitre, j'ai analysé la mortalité des arbres. La mortalité dite "de fond" (background) des arbres est définie comme l'occurrence de la mortalité en l'absence d'événements catastrophiques tels que les incendies, le vent, les vagues de chaleur, la sécheresse et les épidémies de pathogènes, tandis que la mortalité dite "catastrophique" (die-off) est un phénomène local où de nombreux arbres meurent ensemble en réponse à des événements exceptionnels tels qu'une sécheresse intense, des vagues de chaleur, des tempêtes ou des incendies. Dans ce chapitre, j'ai supposé que l'occurrence de la mortalité (l'occurrence d'au moins un événement de mortalité dans une période donnée) trouvée dans une placette reflète la mortalité de fond tandis que l'intensité de la mortalité des arbres (la quantité d'arbres qui sont morts dans la même période étant donné qu'un événement s'est produit) trouvée dans une placette reflète la mortalité catastrophique pour les événements les plus intenses.

En utilisant des modèles de Hurdle (modèle négatif binomial tronqué en zéro) pour distinguer l'occurrence et l'intensité de la mortalité des arbres, j'ai cherché à i) identifier les facteurs sous-jacents de l'occurrence et de l'intensité de la mortalité et la façon dont ils sont influencés par la marginalité climatique de la population et ii) décrire les patrons d'occurrence et d'intensité de la mortalité des arbres à l'échelle de l'aire de distribution des espèces. J'ai émis l'hypothèse que les populations marginales (Leading edge et trailing edge) présenteront une occurrence de mortalité plus élevée que les populations centrales, et que l'intensité de la mortalité présentera une distribution plus disparate le long des aires de distribution des espèces, reflétant la nature stochastique des événements de mortalité catastrophique.

D'une part, mes résultats confirment l'importance majeure de la compétition tant dans la mortalité de fond que dans la mortalité catastrophique, avec des taux de mortalité plus élevés chez la plupart des espèces en conditions de compétition plus élevées. Par ailleurs, mes résultats montrent que les plus fortes probabilités de mortalité se trouvent en marge chaude et sont induites par de la sécheresse, alors que les evènenements de mortalité catastrophiques sont déclenchés par la compétition, la sécheresse, des températures élevées et ne présentent pas de patrons spatiaux particulier le long des aires de répartition des espèces. En outre, l'occurrence de la mortalité était la plus élevée en marge chaude des espèces tempérées et la plus faible aux marges froides pour la moitié des espèces Méditerranéennes.

L'ensemble de mes résultats suggèrent l'effet bénéfique potentiel de pratiques de gestion telles que la réduction de la surface terrière afin de diminuer la compétition et *in fine*, atténuer les taux de mortalité élevés. D'autre part, mes résultats suggèrent que l'écotone méditerranéen-tempéré pourrait être un hotspot des changements dans la composition des forêts et quelques parties sud des aires de répartition des espèces pourraient être en partie façonnées par la mortalité induite par la sécheresse.

Chapitre 4: Recrutement dans les forêts européennes

Dans le deuxième chapitre, j'ai analysé le recrutement des arbres, défini comme les nouveaux individus ajoutés à une parcelle forestière sur une période de temps donné. Dans ce but, j'ai développé des modèles de recrutement espèce-spécifiques à l'échelle de la parcelle en distinguant l'occurrence et la quantité de recrutement afin de déterminer d'une part les principaux facteurs déclenchant du recrutement, et d'autre part ses patrons au travers de larges gradients biotiques et abiotiques.

Mes objectifs étaient de : i) décrire les patrons spatiaux de l'occurrence et de la quantité de recrutement au cœur, et en marges (chaude et froide) des aires de répartition des espèces ; ii) identifier les principaux facteurs de recrutement des arbres et leurs interactions avec la marginalité climatique et iii) identifier les effets d'interaction de la compétition et de la sécheresse avec les caractéristiques des parcelles. J'ai émis les hypothèses suivantes: i) le recrutement est plus important au cœur de l'aire de répartition des espèces que dans les marges, avec des zones de faible recrutement dans les parties les plus méridionales, suivant les patrons de mortalité ; ii) la compétition interspécifique et intraspécifique sont les déterminants les plus importants du recrutement dans le cœur écologique, alors que la sécheresse est le principal déterminant chez les populations écologiquement marginales ; et iii) l'effet de la compétition change en fonction de la sécheresse et des caractéristiques des parcelles.

Mes résultats montrent que la compétition est le facteur le plus limitant du recrutement chez l'ensemble des espèces étudiées, indépendamment des conditions climatiques. De plus la compétition intraspécifique était le facteur le plus important, suggérant que la densité dépendance négative conspécifique est un phénomène majeur du recrutement et donc de la dynamique forestière, comme cela a largement été démontré en forêt tropicale et plus récemment en forêt tempérée. Par ailleurs je montre que chez un certain nombre d'espèces (*P. sylvestris*, F. *sylvatica*, *P. abies*, *Q. ilex*, *P. pinea*) le recrutement bénéficie de la présence d'individus d'autres espèces, suggérant des processus de facilitation ou de complémentarité de niche.

Par ailleurs, mes résultats indiquent que le climat et plus particulièrement la sécheresse jouent un rôle secondaire sur le recrutement, et que son influence varie peu entre le coeur et les marges des aires de répartition. Néanmoins, plusieurs espèces sensibles à la sécheresse, telles que *F. sylvatica*, *P. sylvestris*, *A. glutinosa* et *B. pendula*, ont montré un recrutement plus faible en marge chaude tandis que *P. pinea* et *Q. ilex* ont montré un recrutement plus élevé en marge froide. Mes résultats sont cohérents avec d'autres étud tandis que les chênes méditerranéens tels que *Q.ilex* étendent leur aire de répartition et remplacent *Pinus sp.* dans la région méditerranéenne, favorisé par une combinaison de changements climatiques et d'incendies.

Dans l'ensemble, ces résultats suggèrent un déplacement potentiel vers des altitudes et des latitudes plus élevées d'un certains nombre d'espèces, tant dans les Alpes que dans les Pyrénées, en réponse à des événements climatiques extrêmes en interaction avec la compétition. En outre, étant donné que la compétition détermine fortement l'interaction négative du recrutement avec le climat, ces résultats suggèrent qu'une stratégie de gestion telle que l'éclaircie sélective pourrait être un moyen efficace d'atténuer le changement climatique.

Chapitre 5: espèces exotiques envahissante dans les forêts européennes

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Les espèces exotiques sont des espèces introduites accidentellement ou intentionnellement dans une zone donnée en raison de l'activité humaine. Elles deviennent envahissantes lorsqu'elles se reproduisent en grand nombre au fil du temps et sont capables de se répandre sur une zone géographique considérable.

Quercus rubra et *Robinia pseudoacacia* ont été introduits en Europe à partir de l'Amérique du Nord à la fin du XVIIe siècle comme arbres ornementaux et forestiers. Depuis la fin du 20ème siècle, les gestionnaires forestiers s'interrogent sur leur statut invasif. Notre objectif principal était d'évaluer si ces deux espèces ont étendu leur aire de répartition et leur domination relative au détriment des espèces indigènes et d'identifier les facteurs sous-jacents de cette expansion dans les forêts européennes.

Nous avons émis l'hypothèse i) que les deux espèces étendent leurs aires de répartition et ont augmenté leur présence et leur dominance au détriment des espèces indigènes ; et ii) que le climat favorise la présence et la dominance de ces deux espèces. Nous avons utilisé les données de six inventaires forestiers nationaux pour i) effectuer une comparaison directe entre les deux études en utilisant 7 indicateurs biotiques d'expansion et ii) développer des modèles de croissance absolue et relative de la surface terrière des peuplements afin d'identifier les facteurs sous-jacents de leur expansion.

Mes résultats montrent que les deux espèces ont augmenté de manière significative en termes de présence, d'abondance, de dominance relative et de densité relative entre les deux périodes d'inventaire, progressant considérablement dans les parcelles dominées par des espèces conspécifiques et dissemblables, confirmant leur capacité à se disperser et à s'établir dans les forêts européennes. Les perturbations humaines et le climat (conditions

plus chaudes et sèches) ont été respectivement les principaux moteurs de leur croissance absolue et relative, induisant une expansion de l'aire de répartition entre les deux périodes d'inventaire, à la fois vers le nord et vers le sud pour les deux espèces.
Ces résultats, considérés conjointement avec l'augmentation à venir de la fréquence et de l'intensité des sécheresses en Europe, l'intérêt croissant pour *Q. rubra* et *R.pseudoacacia* pour la culture à grande échelle, et le risque probablement accru de propagation induit par les incendies dans les zones non gérées suggèrent que de nouvelles opportunités pour l'établissement d'espèces exotiques et le changement rapide de la composition des espèces pourraient apparaître dans les décennies à venir avec des résultats écologiques et économiques négatifs concomitants.

Discussion générale

Dans l'ensemble, mes résultats soulignent que la sensibilité des arbres au changement climatique actuel dépend des caractéristiques spécifiques et diffère selon les aires de répartition des espèces. Alors que la partie méridionale des aires de répartition des espèces pourrait être façonnée par la mortalité induite par la sécheresse, le recrutement est lui, beaucoup moins affecté par la sécheresse.
Néanmoins, chez de nombreuses espèces, j'ai constaté que la sécheresse induit à la fois des taux de mortalité plus élevés et des taux de recrutement plus faibles. *Abies alba* et *Quercus robur*, par exemple, ont montré à la fois des taux de mortalité plus élevés et des taux de recrutement plus faibles en marge froide en réponse à l'augmentation de la température, ce qui indique une très probable contraction de l'aire de répartition à cet endroit.
Au contraire, *Pinus sylvestris* et *Alnus glutinosa* pourraient étendre leur aire de répartition en marge froide car les deux espèces présentent des taux de mortalité plus faibles dans cette partie de l'aire de répartition, en accord avec l'expansion de l'aire de répartition suggérée par d'autres études. Toutefois, il convient de noter que les preuves en faveur d'un déplacement d'aire de répartition induit par le climat en marge froide sont rares, principalement parce que de nombreux autres facteurs tels que les conditions du sol, la disponibilité des nutriments, l'histoire de l'utilisation des terres et les traits spécifiques aux espèces sont susceptibles de compenser l'effet du climat.
À l'inverse, les preuves de déplacements d'aires de répartition induits par la sécheresse dans le sud de l'Europe commencent à s'accumuler. Cette tendance est largement confirmée par nos résultats, au cours desquels nous avons mis en évidence à la fois des taux de recrutement plus faibles (chapitre 4) et des taux de mortalité plus élevés (chapitre 3) en marge chaude de nombreuses espèces, notamment *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* et *Quercus petrae*, ce qui suggère une forte probabilité de contraction de l'aire de répartition à leur marge chaude.

Dans l'ensemble, nos résultats, considérés avec la littérature actuelle, confirment que l'écotone méditerranéen-tempéré est fortement affecté par le changement climatique et que des changements d'aires de répartition se produisent probablement en réponse au climat, en particulier à la marge sèche de la distribution des espèces.
Un autre résultat important est qu'en réponse au climat, aucune des espèces étudiées n'a montré à la fois un recrutement plus élevé et une mortalité plus faible, ni en marge froide, ni en marge chaude. Ce résultat suggère une contraction de l'aire de répartition des espèces ayant tendance à laisser des espaces vacants. En outre, l'abandon des terres a été particulièrement élevé dans la région méditerranéenne et est particulièrement marqué dans les zones marginales et moins productives en Europe, y compris dans plusieurs zones montagneuses. Ces espaces nouvellement disponibles (par le non-remplacement des espèces ou l'abandon des terres) sont une opportunité pour les espèces invasives s'établissant habituellement dans ce type de zones ouvertes. C'est le cas de *Quercus rubra* et *Robinia pseudoacacia* qui en plus, bénéficient des climats plus secs et plus chauds (chapitre 5).
Par ailleurs, nos résultats du chapitre 5 indiquent que *Pinus sylvestris*, *Fagus sylvatica* et *Quercus petrae* sont les espèces qui coexistent le plus avec *Quercus rubra* et *Robinia pseudoacacia*, suggérant même qu'elles perdent de la couverture en faveur d'une augmentation de celle de l'une ou l'autre des espèces invasives. De même, *Quercus rubra* semble également augmenter son aire de distribution aux dépens d'*Abies alba* et de *Quercus robur*, qui toutes deux contractent leur aire de répartition (chapitres 3 et 4).
Dans l'ensemble, ces résultats suggèrent que les espèces dont l'aire de répartition se contracte, comme *Pinus sylvestris*, *Fagus sylvatica*, *Q. robur* et *Q. petraea* (en marge chaude) et *Abies alba* (en marge froide), seraient non seulement remplacées par des espèces de feuillus plus résistantes à la sécheresse, mais aussi par des espèces envahissantes, plus tolérantes à la sécheresse.
Un certains nombre de pratiques de sylviculture permettraient d'alléger l'impact du climat sur les espèces les plus affectées par la sécheresse, telle que la réduction de la compétition par l' éclaircissement selectif ou la réduction de la densité dépendance négative conspécifique via la culture de forêts mixes, présentant en plus des risques d'incendie plus faibles que les plantations en monoculture. La régénération naturelle devrait être également préférée aux stratégies de gestion intensive. Celles-ci pourraient être essentielles pour atténuer les effets négatifs du changement climatique sur la mortalité des arbres car les nouveaux arbres pourraient compenser nos émissions de carbone plus efficacement que les vieilles forêts.

Néanmoins, *Q.rubra* et *R.pseudoacacia* sont considérées comme des alternatives intéressantes dans les forêts tempérées gérées pour remplacer plusieurs autres espèces indigènes affectées par des événements climatiques extrêmes telles que *F. sylvatica* et *P. abies* et sont économiquement intéressantes et attractives pour la production de biomasse. Bien qu'elles puissent présenter un intérêt économique très important, leur culture à grande échelle induirait probablement des impacts négatifs sur les espèces indigènes, contribuant à la propagation de maladies et de ravageurs et altérant négativement la biodiversité et la fonction, la structure et la dynamique des écosystèmes forestiers si elles ne sont pas maintenues sous contrôle sylvicole.

Contents

"The Scientist must set in order. Science is built up with facts, as a house is with stones. But a collection of facts is no more a science than a heap of stones is a house." Henri Poincaré

Chapter 1

Introduction

1.1 Climate change and its effects on organisms

The acceleration of global emission of greenhouse gases at an unprecedented rate since the beginning of the industrial era (World Meteorological Organisation, 2014) has warmed the atmosphere and oceans, the sea level has risen, and increased the atmospheric CO2 concentration and nitrogen deposition (IPCC (2014), Figure 1.1a-c). As a consequence of recent climate change, we have observed an increase in droughts, unusual heavy rainfall, flooding and extreme events such as storms, late frosts, and fires (Trenberth et al., 2014; IPCC, 2014). From 1880 to 2012, the Earth temperature has warmed 0.85 °C and the period from 1983 to 2012 was very likely the warmest 30-year period of the last 800 years in the Northern Hemisphere (IPCC, 2014), which has likely affected living organisms.

Climate change has affected every continent and ocean and hence, and all major taxonomic groups inhabiting there. One major consequence of climate change on organisms is that species have changed their distribution ranges, community structures and demography (Parmesan et al., 2003; Parmesan, 2006). Furthermore, species distribution models based on the statistical relationship of the current occurrence of species with climate, predict that all organisms will need to change their distribution ranges to pace with future climate change (Thomas et al., 2004; Thuiller et al., 2011). Therefore, the fate of organisms under climate change is to persist *in situ* by evolutionary processes as adaptation and phenotypic plasticity (Nicotra et al., 2010; Aitken et al., 2008), to migrate (Aitken et al., 2008) or to die (Bussotti et al., 2015). In this context, organisms with long generation times as trees are less likely to adapt to fast climate change (Savolainen et al., 2007; Alberto et al., 2013). Likewise, sessile organisms as trees that rely on pollen dispersion to migrate, will have difficulties to migrate fast enough to track climate change (Lindner et al., 2010; Milad et al., 2011). Trees are, therefore, particularly affected by climate change and the resistance and resilience of forests is of high concern (Bonan, 2010, e.g.).

1.2 Disturbance and threats of European forests

European forests represent more than 25 % of the global forest area and cover more than 1 billion hectares. The forested area represents 45 % of the total land surface in Europe, reaching 70 % of the total land surface in Finland (FOREST-EUROPE (2011), Figure 1.2). In 2015, 4 % of Europe's forests were primary forests, 9 % were plantations

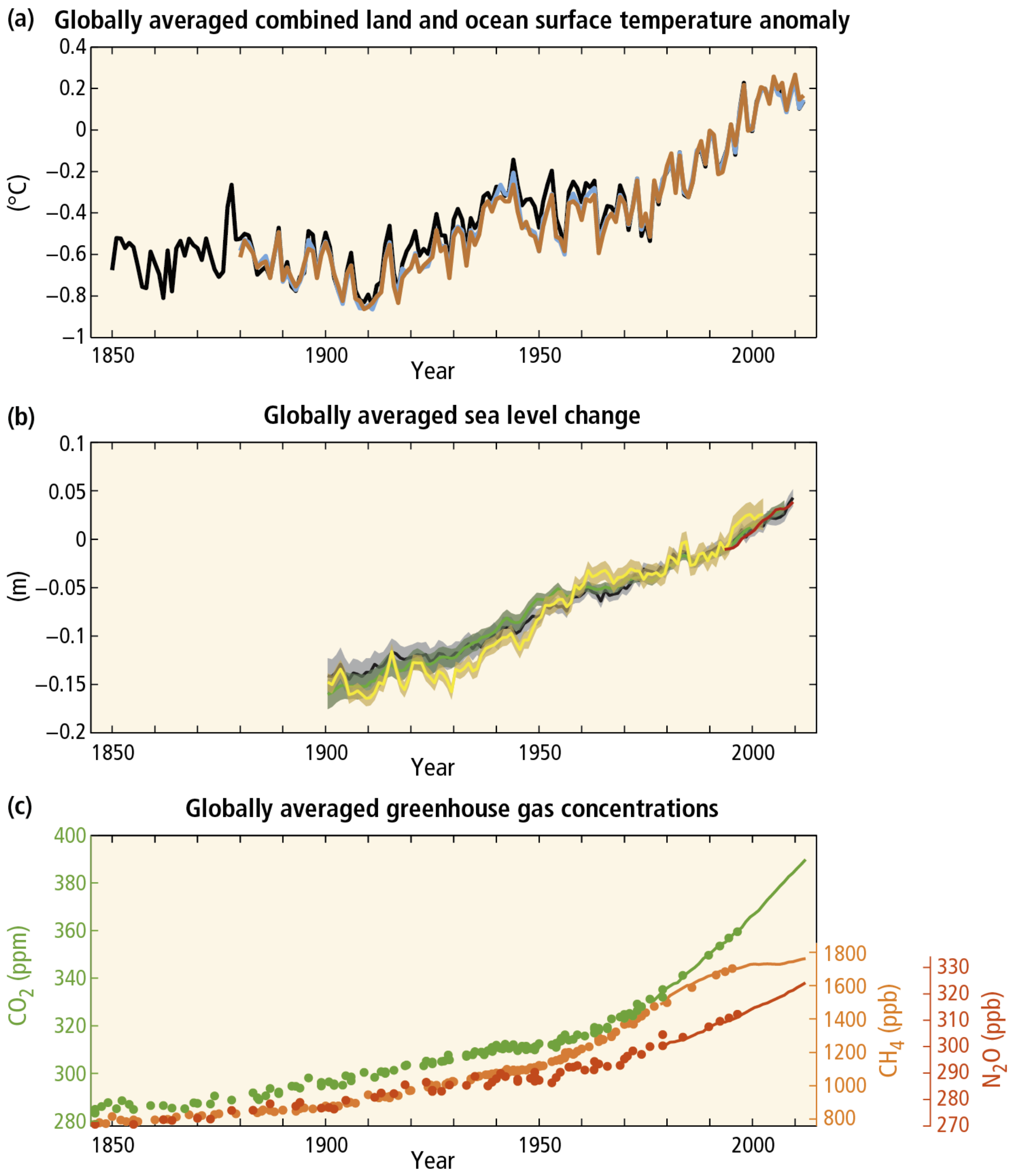

Figure 1.1: Observations of a changing global climate.(a) Annually and globally averaged combined land and ocean surface temperature anomalies relative to the average period 1986-2005.(b) Annually and globally averaged sea level change relative to the average period 1986-2005. Uncertainties are indicated by coloured shading. (c) Atmospheric concentrations of the main greenhouse gases: carbon dioxide (CO2, green), methane (CH4, orange) and nitrous oxide (N2O, red) determined from ice core data (dots) and from direct atmospheric measurements (lines). Source: IPCC (2014).

and 87 % were managed forests. Likewise, 46 % of European forests are predominantly coniferous, 37 % are broadleaved and the remaining ones are mixed-forests. Furthermore, European forests are mostly privately owned (about 51 % of the area, against 49 % of public forests, FOREST-EUROPE (2020)), which confers particular conditions compared with other countries forests that have mostly a public management, as it is the case of Canada.

European forests are an important source of renewable energy (FOREST-EUROPE, 2011), and provide renewal resources as furniture production, building material (Eurostat, 2015), paper production, etc, and therefore, represent an important economic sector. The estimated value of the forest sector alone is around 103 million euro and it provides a job and a sustainable living for 3 million people. In addition, they represent an important recreational value and provide important cultural services, among many other ecosystem services (FAO et al., 2015). This economic importance partially explains why forested areas in Europe are now increasing following the land abandonment that began in the second half of the 20th century (FOREST-EUROPE, 2011). For instance, an increase of 643 thousand hectares of forest per year was recorded on average from 1990 to 2020 (FOREST-EUROPE, 2020), half of which resulting from planted forests (Pereira et al., 2010; FOREST-EUROPE, 2011). This trend is expected to continue over the next few decades (Vuuren et al., 2006).

European forests main disturbances come from wildfires, pests, extreme climatic events (Pan et al., 2013), and those related to forests management and land abandonment. Anthropogenic factors such as land use and management may affect forests ecosystem services and functions. For instance, short rotation forestry can impact negatively biodiversity, soil erosion and acidification (De Rigo et al., 2016). In addition, land use and forest management can have repercussions on the local microclimate and exacerbate the effect of other non-anthropic disturbance. For instance, the spread of wildfire events are likely related to land abandonment patterns (Fernandez-Manjarres et al., 2018). Among the non-anthropic disturbance, wildfire strongly affect the Mediterranean countries (De Rigo et al., 2016) which leads to high mortality rates in several species in southern Europe such as *Pinus pinea* or *Pinus halepensis* (Baeza et al., 2007; Karavani et al., 2018). Overall, 3.7 million ha of forest are affected by forest damage, among which 0.5 million ha by fire damage, 0.8 million ha by storm wind and snow damage and 1.9 million ha are affected by insect or pathogens (FOREST-EUROPE, 2011).

Pathogens and insects outbreaks are increasing as a response to climate. This induces the decline of several species that are key to forests ecosystems such as *Fraxinus excelsior*, whose mortality is directly related to the spread of the pathogen *Chalara fraxinea* (Kowalski, 2006). Similarly, *Acer pseudoplatanus* is threatened by several pathogenic fungi spreading rapidly in Europe such as *Eutypella parasitica* and *Cryptostroma corticale* (Kelnarová et al., 2017; Ogris et al., 2006). These pathogens can boost tree mortality, growth and regeneration, leading to a cascade of negative consequences ultimately reducing the biodiversity and ecosystem services of forests (Hagen et al., 2012). Climate change is expected to trigger the frequency and intensity of all these disturbances in the coming

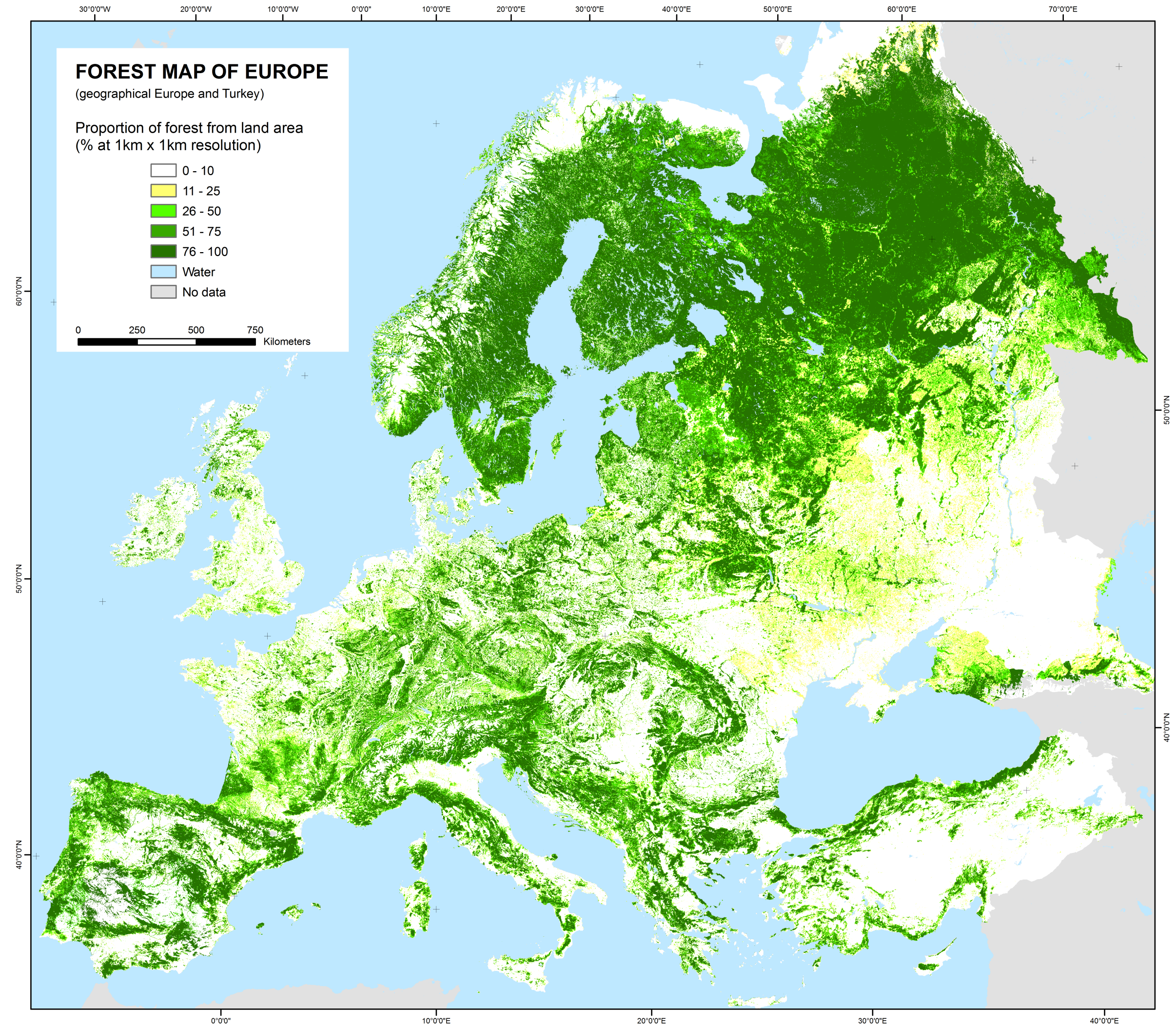

Figure 1.2: European forests distribution (Source: `https://efi.int/knowledge/maps/forest`

decades with disastrous consequences on forests (Dale et al., 2001). For instance, the burned forest area in southern Europe could double for the period 2071-2100 compared to 1961-1990 with a scenario of + 3.5°C temperature increase (Ciscar et al., 2014) and windstorm damages are also expected to increase (Lindner et al., 2014).

1.2.1 Climate change triggers tree mortality

Drought induced by climate change has increased the frequency of massive mortality events in all forested biomes in the world (Allen et al. (2010) and Allen et al. (2015), Figure 1.3 – Example for Europe). For instance, the sudden death of 7400 ha of mangrove vegetation in Australia (Duke et al., 2017), 29 Mt of dead biomass across the southern edge of Canadian boreal forest (Michaelian et al., 2011), up to 90 % mortality rate in central and southern Sierra Nevada (Stephens et al., 2018) or drastic increase in trees mortality in the Californian forests (Young et al., 2017) have all been induced by severe drought events. European forests are not spared: massive mortality events have been observed as a response to the warmer and drier conditions that forests are experiencing all across the latitudinal gradients (Figure 1.3). This includes mortality of *Picea abies* in boreal forest of Norway (Solberg, 2004), mortality of many hardwoods and coniferous species in the temperate forests of France (Allen et al., 2010) as well as strong decline of many species in Spain (Peñuelas et al., 2001).

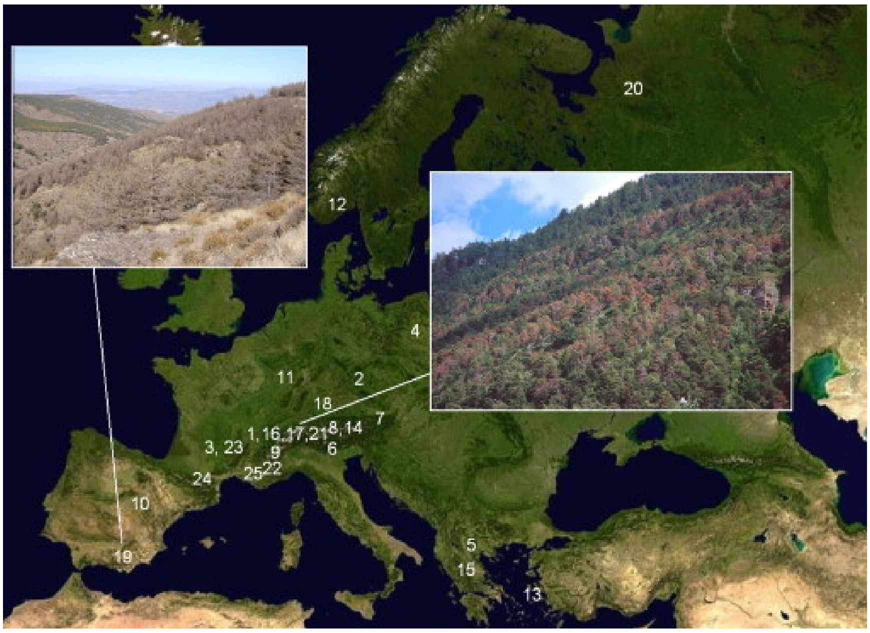

Figure 1.3: Satellite map of Europe documenting drought induce mortality areas. Right photo is *Pinus sylestris* mortality (Valais, Switzerland, 1999) and left photo is *Pinus sylvetris* die-off in Sierra de los Filbares, Spain, 2006. From Allen et al. (2010).

In addition to massive tree mortality (die-off mortality), the average tree mortality rate is increasing along with increased average temperatures and drought in recent decades (Van Mantgem et al., 2009; Peng et al., 2011). This is the case of European temperate forests, where tree mortality increases with warmer and drier summer conditions (Neumann et al. (2017), Figure 1.4a). Tree canopy mortality of temperate forest has doubled (+2.40 % year–1) since 1984 in central Europe (Senf et al. (2018), Figure 1.4b). This rising tendency in tree mortality is likely induce by the increase in average and extreme temperatures as for example in France, where the higher mortality rates of 18 species were correlated with increasing temperature or decreasing rainfall (Taccoen et al., 2019).

The increased intensity and frequency of both extreme events and average climatic conditions are crucial in the physiological process leading to tree death. Extreme temperatures favor hydraulic failure (i.e. the loss of conductance resulting from severe xylem embolism; Tyree et al. (1989) and Cruiziat et al. (2001)) that usually happens during short but intense drought stress period. Alternatively, chronic stress such as increased average climatic conditions leads to long and less intense period of drought stress that are likely to induce carbon starvation. Hydraulic failure and carbon starvation are the two main

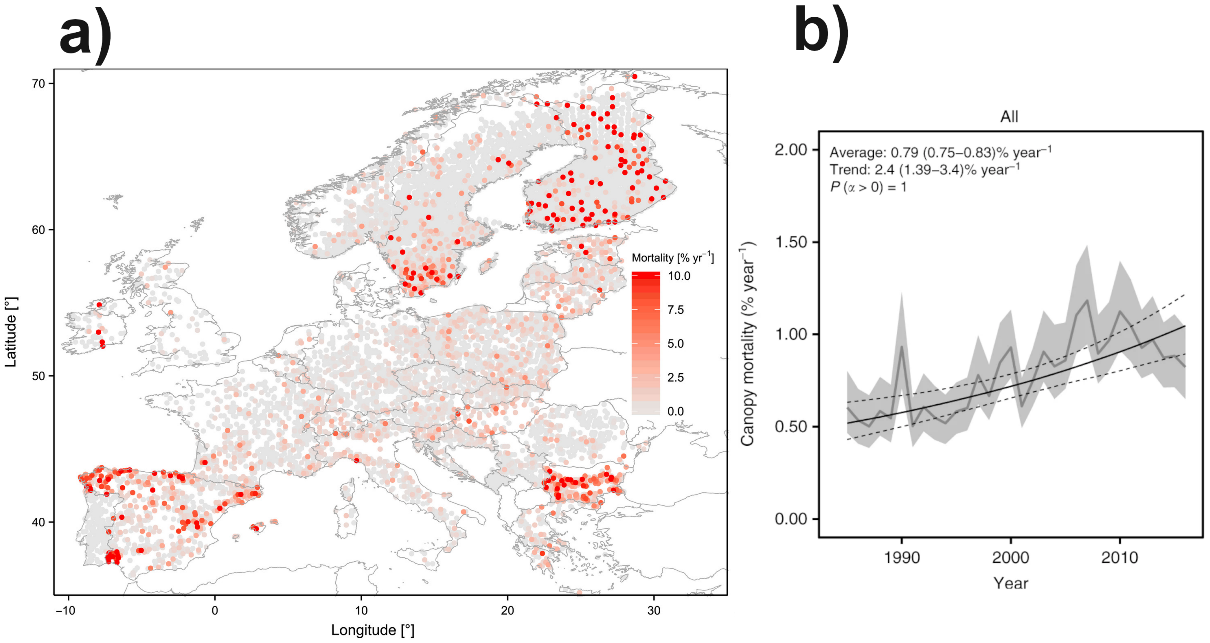

Figure 1.4: Patterns of tree mortality in Europe. a) Yearly mortality rate between 2000 and 2012 (from Neumann et al. (2017)). b) Annual rate of canopy mortality in temperate forests of Europe as a percentage of the forest area. Solid lines indicate median of the posterior probability distribution. Ribbons and dashed line indicate the 95 % credible interval of the annual estimates and the trend line, respectively (from Senf et al. (2020)).

processes leading to tree death and can also interact together and be triggered by pest and insect outbreak (McDowell (2008), McDowell et al. (2011), and Adams et al. (2017), Figure 1.5). In addition, increased temperature leads to heat stress which can exacerbate water stress on trees though reduce carbon assimilation (Anderegg et al., 2012; Teskey et al., 2015).

1.2.2 Tree recruitment is essential to cope with climate change

Tree populations' persistence and forest maintenance rely on many demographic processes that constitute the tree cycle: reproduction, regeneration, recruitment, growth and mortality (GRUBB, 1977). Recruitment is of particular importance because natural regeneration is essential to mitigate negative effects of climate change (Di Sacco et al., 2021) and is the most common regeneration strategy in European forests (i.e. 66 % of the total forest, FAO et al. (2020)). Moreover, recruitment is an essential limiting factor for the extension of the distribution of tree species (Morin et al., 2007). Recruitment reflects the new individuals added to a population. It is a major component of forest dynamics (Stephenson et al., 2005) directly related to the presence or absence of a species in a particular location and therefore a major component to understand species distributions (Bykova et al., 2012), future forest composition (Clark et al., 1999; Green et al., 2014) and assuring the entire ecosystem functioning (GRUBB, 1977). However, large scale recruitment data are scarce (Needham

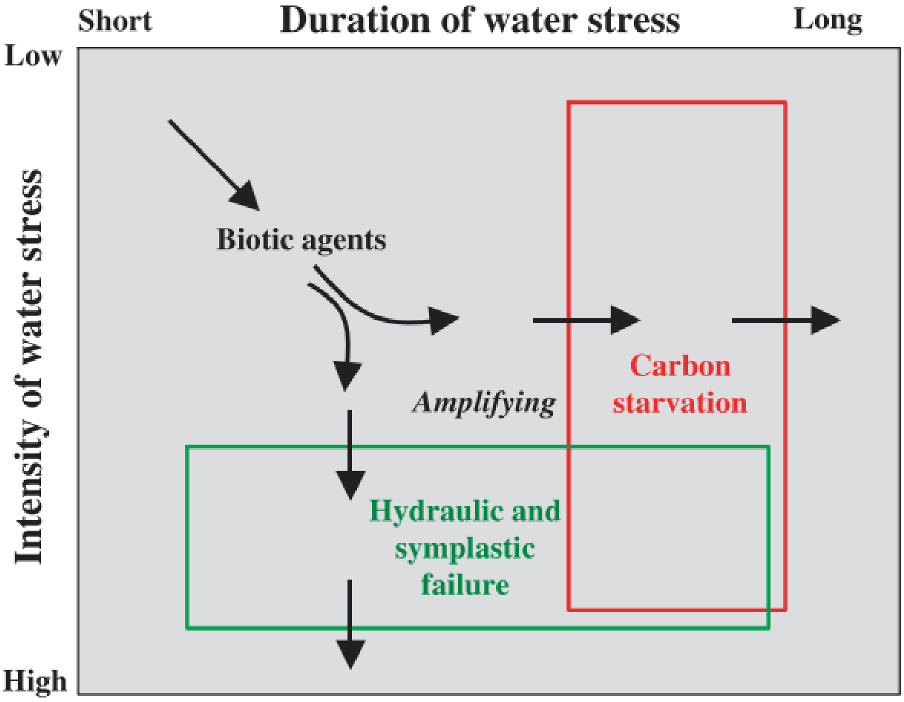

Figure 1.5: Theoretical diagram illustrating the two main hypotheses and the underlying ecophysiological processes leading to tree mortality during a period of water stress. The first is hydraulic failure, occurring during short and intense drought episodes, leading to total desiccation when a lethal species-dependent threshold is exceeded. The second hypothesis is carbon starvation, occurring during longer and less intense water stress episodes. It corresponds to the decrease in photosynthetic activity (and carbon stock) to a level below those of the total carbon reserves of the tree. Biotic agents such as insects may amplify both carbon starvation and hydraulic failure (Source McDowell (2008)).

et al., 2018) and studying the effect of climate change on recruitment is thus limited on selected regions and/or species (Vanclay, 1992; Adame et al., 2010; Klopcic et al., 2012; Yang et al., 2015). Nonetheless, recruitment is strongly affected by climate. For instance, increased temperatures are exacerbating decreased regeneration in the Iberian Peninsula of several oak species, that are already threatened by low recruitment rates (Plieninger et al., 2010; Urbieta et al., 2011) while spring temperatures and heterogeneity in soil moisture are key drivers of recruitment in five major species in the southern Appalachian mountain (Ibáñez et al., 2007). In addition, drought can threat plant recruitment in several species in the Mediterranean region (Mendoza et al., 2009). Climate can also act synergistically with biotic factors. For instance, increase in winter temperatures can reduce the reproductive success of *Pinus sylvestris* in southern Spain because it favors insect outbreaks such as the pine processionary caterpillar (Hódar et al., 2003).

1.3 The effect of climate change on tree demography along large climatic gradients

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Changes in mortality and recruitment are of major importance in explaining species ranges. In fact, the range of a species is defined by the geographical space occupied by the species, which is determined by the biotic and abiotic constrains explaining the species tolerance limits (Soberón et al., 2005). Species ranges strongly rely on climate, that changes across latitudinal and elevation gradients (Woodward et al., 1987). Therefore, forest trees with different life strategy and morphology occur in different places through a climatic gradient, from deciduous, evergreen, needle-leaved or broadleaved, that are better adapted to the environmental conditions of the geographic area where they occur (Whittaker, 1975; Woodward et al., 2004). In addition to the environmental conditions that fulfill the species requirements, distribution ranges are driven by the balance between extinction and colonization phenomena (Yackulic et al., 2015), relying on the balance between recruitment and mortality (Lloret et al., 2012), modified by biotic factors as competition, facilitation, etc (Louthan et al., 2015; Ettinger et al., 2017).

The changes in species ranges in response to climate change are particularly evident at the ecotones, defined as the bound or transition zone where two biomes converge (Allen et al., 1998; Elliott, 2017). These ecotones are of particular importance since they gather species at their northern margin (leading-edge) that could potentially benefit from climate change and species at their southern margin (trailing edge) that could be more affected by climate change and present for instance high rates of mortality (Rehm et al., 2015). The cold margins of the Northern Hemisphere (leading edge) are generally located at the limits of high latitude and altitude and conversely the warm margins (trailing edge) correspond to the range limits at low latitude and altitude (Figure 1.6a).

Likewise, the ecological margins of the species can also be structured along climatic gradients, with the climatic trailing edge representing the warmest margin and the climatic leading edge the coldest one (Hampe et al., 2005; Pironon et al., 2015). Shifts in species ranges are expected as a response to future climate, particularly at the drier margin of the distribution (Kunstler et al., 2016), that usually converges with the climatic trailing edge. For instance, changes in species composition occur in the Pyrenees, where oak species progressively replace beech trees (Peñuelas et al., 2007) and Scot pine in altitude. This is mainly because due to the high mortality recorded in *Pinus sylvestris* that is not compensated by recruitment (Vilà-Cabrera et al., 2013; Galiano et al., 2010). Similarly, the temperate *Quercus petraea* and the sub-Mediterranean *Q. faginea* (Urli et al., 2014) are moving northwards as a response to climate change. Likewise, *Quercus ilex* is progressively expanding northwards, limiting the recruitment of major Mediterranean pines (including *Pinus nigra, Pinus sylvestris, Pinus pinaster, Pinus halepensis and Pinus pinea*, Carnicer

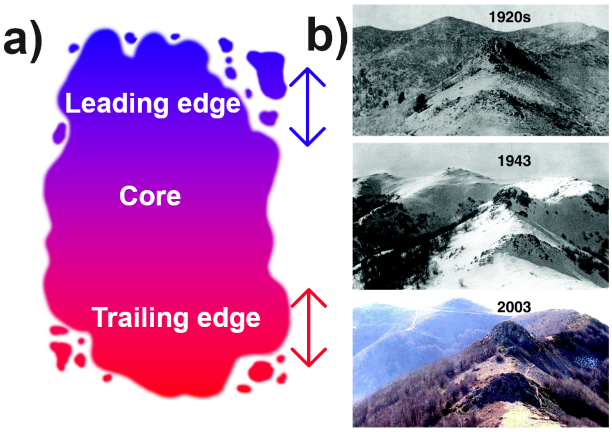

Figure 1.6: Latitudinal and altitudinal rangeshifts: a) Schematic representation of a species distribution range with the core, leading and trailing edge that can contract or expand. Adapted from Schneider (2019). b) Altitudinal upward shift of European beech forest towards the top (ca 1700 m) of the highest summits in the Turó de l'Home-Les Agudes ridge in the last century. From Peñuelas et al. (2007).

et al. (2014)). Furthermore, most of the observed increased mortality at the trailing edge of temperate species is related to drought and temperature (Benito-Garzón et al., 2013; Linares et al., 2012; Urli et al., 2014), associated with a decreased productivity (Härkönen et al., 2019).

These studies suggest that Mediterranean species are expanding northwards as a consequence of climate change (Delzon et al., 2013; Parmesan, 2006) and that the southernmost populations of temperate tree species in Western Europe are likely to experience increasing mortality, reduced growth and reproductive rates under future warming (Benito-Garzón et al., 2013; Benito-Garzón et al., 2018). In the long term, these species ranges changes following climate change would represent a northwards shift of the ecotone between Mediterranean and temperate ecosystems. As a consequence, temperate species are likely to contract their current distribution at the trailing edge and hence they would leave empty spaces available for other species in addition to the Mediterranean ones (Benito-Garzón et al. (2013) and Benito-Garzón et al. (2018), Figure 1.7).

An upward shift of the boreal–temperate forest ecotone has also been observed. In the Vernont mountains for instance, at the lower half of the ecotone, broadleaf species at their leading edge such as the sugar maple (*Acer saccharum*), the American beech (*Fagus grandifolia*) and the yellow birch (*Betula alleghaniensis*) increased their dominance and their recruitment at the expense of boreal species such as red spruce (*Picea rubens*), paper birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*), that declined. At the upper half, however, the boreal species increased their dominance and recruitment, consistent with an upward shift of the ecotone (Beckage et al., 2008). In the Swiss Alps upward shifts of the treeline are related to an increase in recruitment in many coniferous and broadleaved species (including *Acer pseudoplatanus, Abies alba, Fraxinus excelsior, Fagus sylvatica,* *Larix decidua, Picea abies Quercus petrae*), promoted by climate warming (Gehrig-Fasel et al., 2007; Hofgaard et al., 2009; Vitasse et al., 2012). Similarly, the lack of recruitment coupled with increased mortality induced a vegetation shift from *Pinus sylvestris* to *Quercus pubescent* at the lowest altitude of the Valais, Switzerland (Rigling et al., 2013). On the contrary, climate warming can limit tree recruitment, as it is the case at the alpine treeline for Norway spruce (Kueppers et al., 2017).

Many studies also confirm the treeline advance of boreal forests at the forest–tundra ecotone (MacDonald et al., 2008). In the Swedish Scandes Mountain for instance, treeline advance of *Pinus sylvestris* and *Picea abies* have been observed, likely driven by air and soil warming (Kullman et al., 2009). If the northern limit of species distributions is due to cold tolerance (Morin et al., 2008), the rising winter temperatures may trigger upward movement of boreal species at high altitude and latitude (MacDonald et al., 2008; Kullman et al., 2009). At lower latitude, however, climate warming would favor northwards expansion of broadleaved deciduous species at their leading edge, at the expense of evergreen coniferous species whose range could be reduced (Evans et al., 2017; Harsch et al., 2009). These movements could imply a northward shift of the ecotone between temperate and boreal species, likely to leave empty spaces for other species (Figure1.6b and 1.7). All in all, the ecotones constitute areas where changes in species composition will occur faster and whether local species already present at the ecotones or invasive species will take the place is still a matter of debate (Fernandez-Manjarres et al., 2018).

1.4 Climate change as an opportunity for invasive species

New climatic conditions such as those induced by climate change can pave the way to the invasion of opportunistic species, particularly at the ecotones. Therefore, while some species will likely suffer from the current climate change, others may benefit (Baxter et al., 2008). Hence, while Mediterranean species are likely to benefit from the changing climate, the new available spaces could also provide an opportunity for exotic species to expand their range and establish at the expanse of the weakened species.

Exotic species are those species that have successfully overcome the barrier to dispersal to expand their ranges, greatly assisted by humans, either accidental or intentionally in the last two centuries (Cousens et al., 2008; Baxter et al., 2008). They become invasive when they have reproductive offspring in large numbers over time and are able to spread over a considerable area (Blackburn et al., 2011; Richardson et al., 2011). The number of invasion cases is currently rising (Baxter et al., 2008). This is the case of *Robinia pseudoacacia*, introduced in Europe in the early 17th century (Sitzia et al., 2016) and *Querus rubra*,

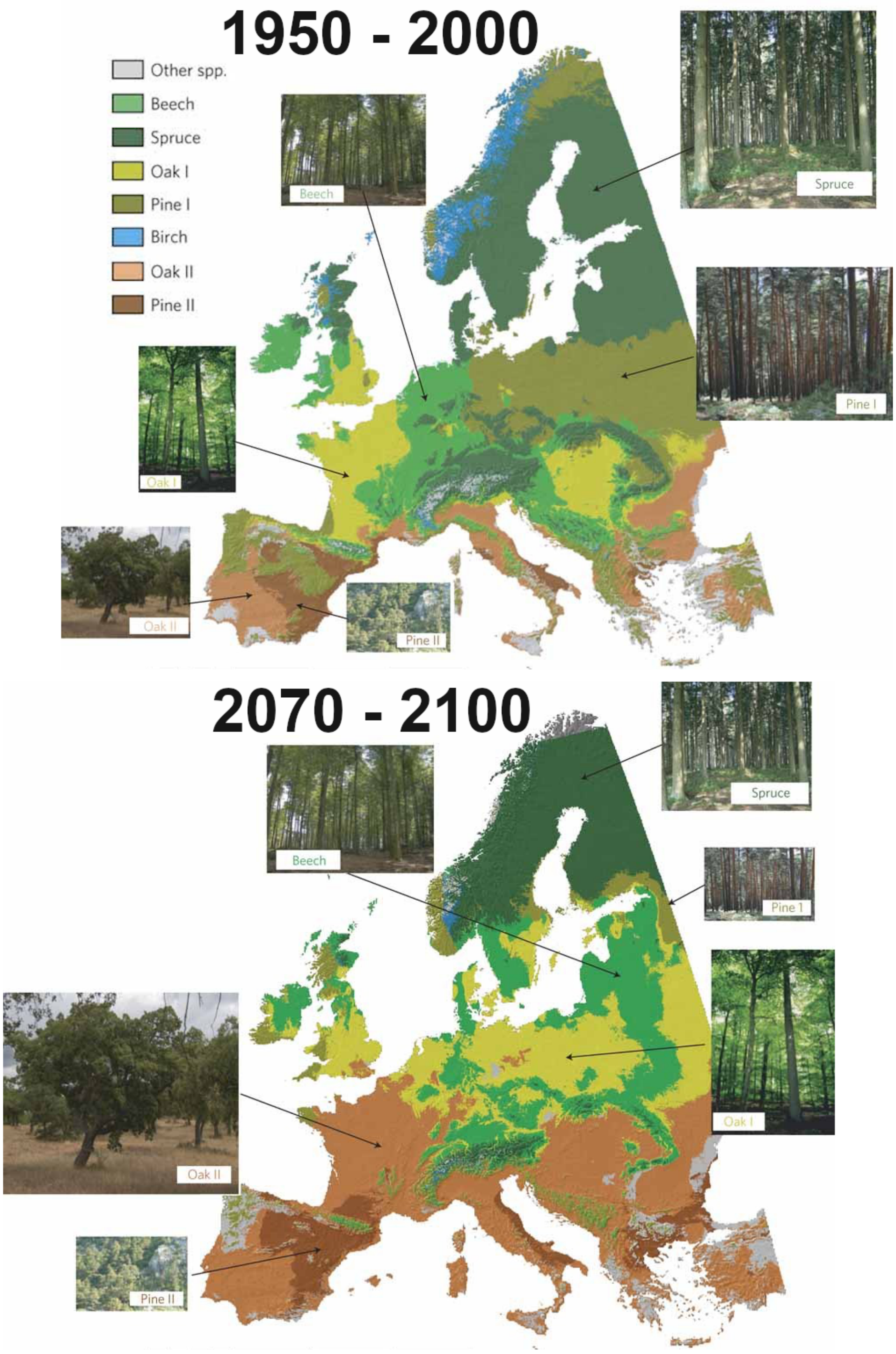

Figure 1.7: Predicted distribution of the main tree species groups in the European forest over the periods 1950 - 2000 and 2070 - 2100. The distribution over the period 2070 - 2100 is the projection under moderate warming scenario (scenario A1b from the ECHAM5 model). Adapted from Hanewinkel et al. (2013).

introduced from the USA to Europe in the late 17th century and 18th century (GOEZE, 1916; Timbal, 1994; Magni Diaz, 2004). Empirical studies have shown that both *Robinia pseudoacacia* and *Querus rubra* grow in detrimental of native species in their introduced areas. *Robinia pseudoacacia* changes plant, bird and lichen communities (Sitzia et al., 2016) while the high regeneration of *Q. rubra* in Central Europe impedes native tree species regeneration and negatively impact the understory biodiversity (Chmura et al., 2013; Woziwoda et al., 2014).

Despite both species are increasing their presence in Europe (Camenen et al., 2016), whether climate change would boost invasive tree range expansions remains an open question (Willis et al., 2010). Local conditions in the new habitats, including climate, are likely to play a role in the persistence, survival and establishment of invasive species (Colautti et al., 2004; Richardson et al., 2006). In Spain, for instance, temperature and distance to the sea have been identified as the main drivers constraining the spread of two invasive *Acacia* species into new areas (Hernández et al., 2014). Similarly, climate change has likely played an important role in facilitating invasion of tree species (Willis et al., 2010). Moreover, climate warming is likely to favor *Robinia pseudoacacia* and *Q. rubra* expansion in Central and Northern Europe whereas the risk of invasion is likely to decrease in the Mediterranean basin (Sitzia et al., 2016; Camenen et al., 2016).

1.5 Assessing demographic patterns at large geographical scales

Understanding tree demography at large geographical scales is key to understand the odds of tree populations to survive under climate change. As a consequence, different approaches exist to assess mortality, recruitment and more generally, the future distributions tree species under changing climate (Bugmann, 2001). Correlative models such as species distribution models (SDMs) have largely been used to assess species distributions, although they do not systematically include population demography (but see approaches by Pagel et al. (2012) and Normand et al. (2014)). Mechanistic approaches including ecophysiological processes such as gap models and dynamic vegetation models (DVGMs) aim to simulate the long term dynamic of forests. These models integrate a large number of ecological processes in a theoretical way (Bircher, 2018), which make them sensitive to the formulation of demographic processes (Albrich et al., 2020; Bugmann et al., 2019; Ruiz-Benito et al., 2020). Empirical models tackling demography at large geographical scales rely on dendrochronological data, remote sensing (Senf et al., 2020) or forest census such as systematic national forest inventories (NFIs) (Hülsmann et al., 2017), that every European country possess (Gschwantner et al., 2016) and from where several demographic processes can be inferred.

NFI consist on the census of individual trees according to a systematic grid of plots, re-measured every 5–15 years. They are used to characterize forest structure by several parameters that can be calculated as for example of density, volume, functional type, diversity, carbon and biomass. As a consequence, NFI have been used to understand tree demography (Ruiz-Benito et al., 2017a), ecosystem productivity (Ratcliffe et al., 2015), species ranges (Kunstler et al., 2020), forest dynamics (Vanderwel et al., 2013), biodiversity (Chirici et al., 2012) etc. A large part of the studies based on NFI's data have focused on relating demography to structure of forests and site conditions, showing a strong dependency of both mortality and recruitment to tree height (Holzwarth et al., 2013; Adame et al., 2010), or stand characteristic such as density or competition (Zell et al., 2019; Ruiz-Benito et al., 2017a), and the consequences of forests management on mortality and recruitment (Klopcic et al., 2012; Ruiz-Benito et al., 2017b). Likewise, they have been used to understand drought or water availability effects on forests. For instance in Spain, Ruiz-Benito et al. (2014) showed that growth and productivity changed upon water availability while Carnicer et al. (2014) showed a strong effect of drought on recruitment limitations. Similarly, carbon accumulation in European forests strongly depends on both stand structure and concomitant climate warming (Ruiz-Benito et al., 2014). Mortality and recruitment are more sensitive to competition than to climate (Ruiz-Benito et al., 2013; Zell et al., 2019), depending on species identity (Ruiz-Benito et al., 2013) and ecological strategy (Archambeau et al., 2020; Ruiz-Benito et al., 2017a; Zell et al., 2019), functional group, forest management and herbivory (Ruiz-Benito et al., 2017a).

1.6 Objectives and thesis structure

The main goal of my PhD thesis is to assess mortality and recruitment of European forests at large geographical scales, to anticipate the likely changes in forests structure, particularly those due to invasive tree species. The specific objectives corresponds to three chapters of the thesis. Chapter 2 describes the material and methods, detailing the steps taken to create the dataset used in the thesis, the methodological choices. The main results are presented in Chapters 3, 4 and 5 and the general discussion in Chapter 6.

Chapter 3: Identification of tree mortality spatial patterns and its main ecological drivers along large geographical gradient.

Objectives: i) identify the underlying drivers of mortality occurrence and intensity and how they are influenced by the climatic marginality of the population and ii) understand tree mortality occurrence and intensity patterns across species distribution ranges.

Hypotheses: i) marginal populations experience higher occurrence of mortality than core populations; ii) the intensity of mortality is more patchily distributed over the species distribution ranges than the average mortality reflecting the stochastic nature of die-off events.

Chapter 4: Identification of tree recruitment spatial patterns and its main ecological drivers along large geographical gradient.

Objectives: i) describe the spatial patterns of occurrence and amount of recruitment at the core, trailing and leading edge of species ranges; ii) identify the main drivers of tree recruitment and their interactive effects with climatic marginality; iii) identify the interaction effects of competition and drought with plot characteristics.

Hypotheses: i) more recruitment is found at the core than at the edges of the species ranges, with extensive zones of poor recruitment at the southernmost part, following mortality patterns; ii) interspecific and intraspecific competition are the most important drivers of recruitment in the ecological core while drought is expected to be more important in ecologically marginal populations; iii) competition changes along with drought and plot characteristics.

Chapter 5: Assessing invasive species expansion spatial patterns and its main ecological drivers along large geographical gradient.

Objectives: i) Quantify the ability of exotic species to spread at the expense of native species; ii) Analysing their presence, abundance and dominance relatively to that of the native species; iii) Determine the main drivers underlying the spread of these species; iv) evaluate how these drivers change along climate gradients.

Hypotheses: i) Both exotic species expand their ranges and have increased in presence and dominance relatively to the native species. ii) Climate triggers these expansions.

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"To doubt everything and to believe everything are two equally convenient solutions; each saves us from thinking" Henri Poincaré

Methods

2.1 Study area

All the analyses were done in the forested area of six European countries: Belgium, Finland, France, Germany, Spain and Sweden. The six countries, together covers a surface of 213,7 million km^2. The total area present an altitudinal gradient from 0 to 4809 m, and a latitudinal gradient from 36°N (Spain) to 70.05°N (Finland). The area is covered by 111,7 million hectares of forest (see Table 2.1 for the surface by country).

Country	Total land area (million ha)	Forest area (million ha)	Forest % of land area
Belgium	3.028	0.722	23.8
Finland	30.391	23.155	76.2
France	54.756	18.096	33.0
Germany	33.0	11.419	32.7
Spain	49.966	27.954	55.9
Sweden	40.731	30.344	74.5

Table 2.1: Description of the forest area by country: Total surface of the country, forest area are given in million ha. Forest is also expressed in % of the total land area, by country (FOREST-EUROPE, 2020)

The six countries cover forests belonging to three biomes, defined as large widespread areas with relatively homogeneous vegetation (Simons, 2005; FAO, 2012): boreal, temperate, and Mediterranean (Olson et al., 2001). The boreal biome was covered by boreal forests dominated by coniferous species such as *Picea abies* and *Pinus sylvestris* in Sweden and Finland. The temperate biome is occupied by deciduous broadleaved or mixed forest of numerous species as for example *Quercus petraea*, *Fagus sylvatica* in Germany, Belgium, France and Spain. Finally, the Mediterranean biome was mostly covered by sclerophyllous evergreen species such as *Quercus ilex*, *Q. suber* and Mediterranean pines as *Pinus pinaster*, *P. pinea*, *P. nigra* etc. in France and Spain. Some species, as *Pinus sylvestris* occurred in a large geographical gradient from boreal to Mediterranean biomes. Mountainous areas are characterized by high variation in vegetation formation and climatic conditions (Simons (2005) and FAO (2012), Figure 2.1)

2.2 Characteristic of the studied species

In my work I studied mortality and recruitment of 23 major forest tree species,

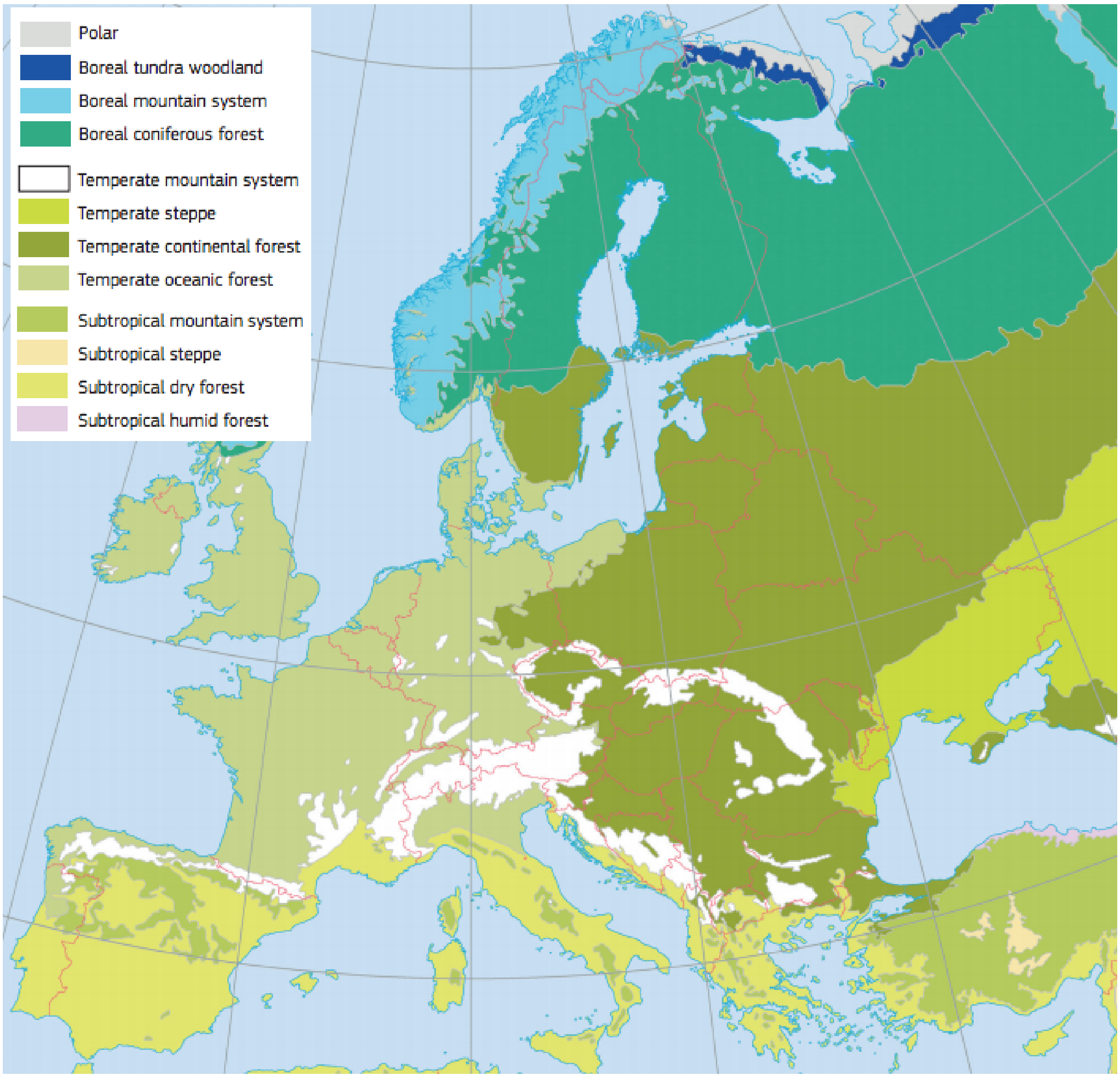


Figure 2.1: The three biome of European continents that can be split in 12 ecological zones according to temperatures and rainfall, (Trewartha, 1968; Köppen, 1931) adapted from De Rigo et al. (2016a).

gymnosperms or angiosperms. I chose them for their economic and ecological importance, and because the large availability of data in the National Forest Inventories. In the first chapters I focused on 21 native species. In the second chapter I had to remove *Populus nigra*, *Populus tremula* and *Quercus petraea* from the initial 21 natives because of lack of recruitment data. Finally, in chapter 3, I focused on the two invasive species *Quercus rubra* and *Robinia pseudoacacia*. Table 1 is a summary of their ecology, including their requirement in soil and climatic conditions and their vulnerability to frost, drought and fires.

Table 2.2: Main species studied and their ecological characteristics. Species: species latin name; Reference: Reference for species description Biome: Biome of the species (T=temperate; M=Mediterranean; B=boreal; E=exotic); Type: type of trees (evergreen or deciduous and coniferous or broadleaved); Requirements: soil and temperature requirements for growing; Drought sensitivity: drought sensitivity (intolerant, moderate or tolerant); Fire resistant: resistance to wildfire (yes or no); Frost tolerance: tolerance frost (yes or no); Shade: shade tolerance (Tolerance, medium, low tolerance or intolerant). Chapter: Chapter in which the species was studied. All characteristics were summarized based on the European Atlas of Forest Tree Species except for *Quercus rubra*. “ - “ Indicates the information was not available.

Species	Reference	Biome	Type	Requirement	Drought	Fire	Frost	Shade	Chapter
Abies alba Mill.	Mauri et al., 2016a	T	Evergreen coniferous	Cool temperature; high moisture	-	No	No	Tolerant	1-2
Acer pseudoplatanus L.	Pasta et al., 2016b	T	deciduous broadleaved	Good water supply	-	-	No	Tolerant	1-2
Alnus glutinosa L. Gaertn.	Durrant et al., 2016d	T	deciduous broadleaved	Moderate to cold climate and high water level	-	-	Yes	Intolerant	1-2
Betula pendula Roth.	Beck et al., 2016a	T/B	deciduous broadleaved	Light demanding; drained soil	intolerant	-	Yes	Intolerant	1-2
Castanea sativa Mill.	Conedera et al., 2016	M	deciduous broadleaved	Drained soil and mild temperature	intolerant	Yes	No	Intolerant	1-2
Fagus sylvatica L.	Durrant et al., 2016a	T	deciduous broadleaved	Humid atmosphere and well drained soil	intolerant	No	No	Tolerant	1-2

Species	Reference	Biome	Type	Requirement	Drought	Fire	Frost	Shade	Chapter
Fraxinus excelsior L.	Beck et al., 2016b	T	deciduous broadleaved	Moist or wet soil; mesophile and light demanding	intolerant	-	No	Intolerant	1-2
Picea abies L. H.Karst.	Caudullo et al., 2016b	T/B	Evergreen coniferous	Cool and moist conditions	intolerant	No	-	Tolerant	1-2
Pinus halepensis Mill.	Mauri et al., 2016b	M	Evergreen coniferous	Thermophilous and any soil	tolerant	Yes (but strongly affected)	No	Intolerant	1-2
Pinus nigra J.F.Arnold.	Enescu et al., 2016	M	Evergreen coniferous	Dry or humid conditions; light-demanding; large temperature tolerance	tolerant	No	Yes	Intolerant	1-2
Pinus pinaster Aiton.	Viñas et al., 2016	M	Evergreen coniferous	Light demaning; temperate-warm and humid conditions	tolerant	Yes	Yes	Intolerant	1-2

Species	Reference	Biome	Type	Requirement	Drought	Fire	Frost	Shade	Chapter
Pinus pinea L.	Viñas et al., 2016	M	Evergreen coniferous	Dryweather; high temperatures; light demanding	tolerant	Yes (but strongly affected)	-	Low tolerance	1-2
Pinus sylvestris L.	Durrant et al., 2016b	T/B	Evergreen coniferous	Light demanding; any soil and various climatic conditions	tolerant	-	Yes	Moderate	1-2
Populus nigra L.	De Rigo et al., 2016c	T	deciduous broadleaved	Light demanding and moist soil	intolerant	-	Yes	Intolerant	1
Populus tremula L.	Caudullo et al., 2016a	T/B	deciduous broadleaved	Light demanding; moist conditions	tolerant	-	Yes	Tolerant	1
Quercus ilex L.	De Rigo et al., 2016b	M	evergreen broadleaved	Light demanding; semi arid to humid and warm to cold conditions	moderate tolerance	Yes (but strongly affected)	-	Tolerant	1-2
Quercus petraea Liebl.	Eaton et al., 2016	T	deciduous broadleaved	Light demanding; mesoxerophile-mesophile soil	tolerant	-	No	Moderate	1-2

Species	Reference	Biome	Type	Requirement	Drought	Fire	Frost	Shade	Chapter
Quercus pubescens Willd.	Pasta et al., 2016a	T	deciduous broadleaved	Light demanding; thermophilous and any soil	tolerant	-	Yes	Moderate	1
Quercus pyrenaica Willd.	Quintano et al., 2016	M/T	Deciduous broadleaved	Light demanding; thermophilous and xérophile	intolerant	No	Yes	Tolerant	1-2
Quercus robur L.	Eaton et al., 2016	T	deciduous broadleaved	Light-demanding; mésophile-wet soil	intolerant	-	No	Intolerant	1-2
Quercus rubra L.	Nicolescu et al., 2020	E	deciduous broadleaved	light demanding; dry or most soil	tolerant	-	Yes	Moderate	3
Quercus suber L.	Durrant et al., 2016c	M	evergreen broadleaved	mild temperature; many conditions and soils	tolerant	Yes	No	Moderate	1-2
Robinia pseudoacacia L.	Sitzia et al., 2016	E	deciduous broadleaved	light demanding; wide variety of soil	intolerant	-	No	Intolerant	3

2.3 National forest inventories

National Forest Inventories (NFIs) provide a systematic large-scale representation of a country's forest structure. Their design ensures representation of the variability in forest types over large environmental and management gradients. Here I give details about the French inventory as an example and then, I summarized the difference that exist between the different countries used during this work (Table 2.2).

In France, the systematic sampling is based on a network of 1km^2 × 1km^2 grids covering the whole territory. Each inventory plot is attached to a 1 km^2 grid cell. The sampling follow a nested circular subplot design, where each plot is divided into 4 concentric circles of 6, 9, 15 and 25 m radius. Trees are measured on the three smallest subplots, depending on their diameter at breast height (DBH, i.e. diameter at 1.30 m height). Trees less than 7.5 cm of DBH are not measured. Trees with DBH between 7.5 and 22.4 cm are measured on the 6m radius subplot. Then trees with DBH between 22.5 and 37.4 cm and DBH larger than 37.5 cm are measured in the 9 and 15 m radius subplots, respectively. Individual tree measurements include DBH, height, and basal area increment in 5 years. Plot measurements include a floristic inventory and soil description in the 15 m radius circle. The geographic location, land cover, land use and stand description (composition, structure, age, logging possibilities, etc.) are noted on the largest circle (25 m radius). Finally, the dead wood on the soil is recorded along a 12 m transect centered on the inventory point (Figure 2.2).

Most NFIs follow a nested circular subplot design as the one described for France. However, subplots radius and the size of the DBH of the trees measured differ among NFI. Each NFI can use various sampling methods, plot sizes, sampling distances or grid sizes (Gschwantner et al., 2016). For instance, the Spanish National Inventory recorded single sample plots in a 1 km by 1 km grid whereas the Finnish National Inventory followed a cluster design, with number and grid size depending on location while the German NFI used a 4 x 4 km quadrangle grid where the samples lied on the intersection points. Moreover, the sampling years and the period between surveys differ substantially between countries. The NFIs from Spain, Germany, Finland, Sweden, Wallonia (Belgium) were harmonized in the FunDivEUROPE project (Baeten et al. (2013) and Ruiz-Benito et al. (2017), `http://www.fundiveurope.eu/`). All these countries have permanent plots sampled several years apart, ranging from 1981 to 2011. The main differences among inventories are summarized in Table 2.3.

Conversely with the other inventories, the French NFI come from temporary plots of annual campaigns 2005-2014. It was added to the FUNDIV dataset in Archambeau et al. (2020), (Annexes 1), which has constituted a significant time of my Ph.D. In the following section, I describe the steps I followed during the harmonization process.

Country	Belgium-Wallonia	Finland	France	Germany	Spain	Sweden
Sampling dates and plot type	1994-2003 2008-2011 PP	1985-1986 1995 PP	2005-2014 TP	1986- 1990, West Germany only 2001-2002 (West and East Germany)	1986-1996 1997-2007 PP	2005-2007 2008-2010 TP and PP
Grid size (km)	1x0.5	16x16 or 24x32 depending on the location	1x1	4x4, 2.83x2.83 or 2x2 depending on region	1x1	Vary
Sampling design (Distance between plots)	Single sample plots	Cluster design (100 or 300)	Single sample plots	Cluster design (150)	Single sample plots	Cluster design (vary)
Radius (m)	2.25, 4.5, 9, 12, 18	5.64, 9.77	6, 9, 15	1, 2, 5, 10, 25	5, 10, 15, 25	3.5, 10
Sample tree DBH threshold (cm)	6.4	0	7.5	10 (1st) 7 (2nd)	7.5	1
N Plots	1238	2487	60782	29914	48133	11338
N Trees	16011	39263	637830	295029	813464	187561
NdeadTrees (and %)	216 (1.35%)	490 (1.25%)	63178 (9.91%)	5725 (1.94%)	68896 (8.47%)	3136 (1.67%)

Table 2.3: Summary of the NFI design for each country: Belgium (Wallonia), Finland, France, Germany, Spain and Sweden Inventories. I included the sampling dates; plot type: permanent plots (PP) the years indicate the two campaigns used in the analysis, for temporary plots (TP) the years used in the analysis are indicated. Grid size: indicates the grid dimension in km for each country. Distance between plots: indicates the distance between the plots within the grid. Plot radius: indicates the different radius (m) used within plots to sample trees. Sample tree DBH threshold: indicates the minimum DBH of the trees selected to sample a tree within a plot. N plot: number of plots per country. N trees: number of trees per country

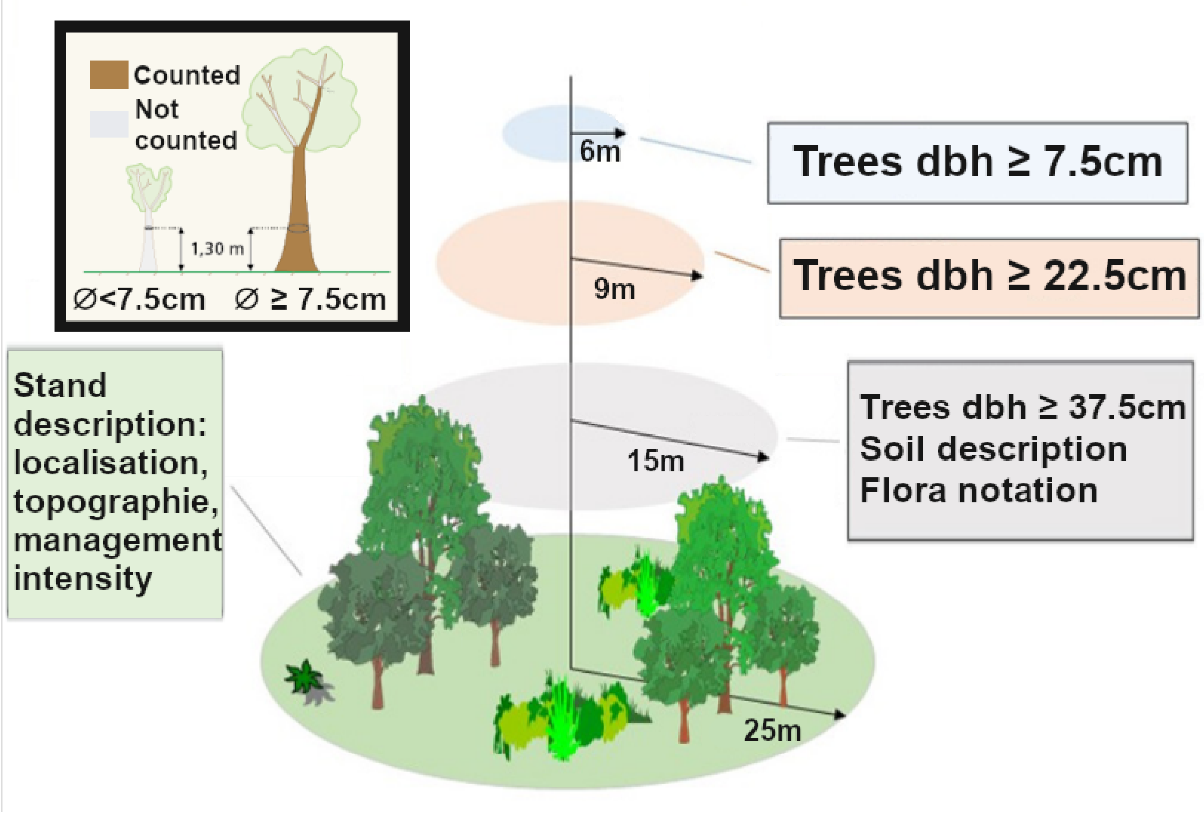


Figure 2.2: French national inventory of forest: sampling design. Adapted from Alberdi et al. (2017) and IGN (2020).

2.4 Harmonization of the French database

I developed a common species list based on the genera, species or sub-species found in the two databases (the FUNDIV and the French NFI). For instance, two subspecies of *Pinus nigra* were identified in FUNDIV while four were identified in the French one (*Pinus nigra* and *Pinus laricio* for french and *P. laricio calabre*, *P. laricio corse*, *P. nigra salzmann*, *P. nigra nigra* for FUNDIV). In this particular case, I considered all the subspecies together as there is no genetic differentiation between all the subspecies (Giovannelli, 2017). I corrected the names using Tela-botanica (`http://www.tela-botanica.org`) and followed the species nomenclature of the inpn (`https://inpn.mnhn.fr`). From 158 unique species code in the french database and 172 in FUNDIV, I obtained 212 species found across all inventories in the final list (Annexes 6.7).

In order to have comparable estimates, for example of basal area or density, I removed all trees with a diameter at breast height (DBH) less than 10cm which is the largest minimum DBH threshold that is found in the 1st German NFI (Table 2.3). I also removed plots with evidence of management during the period between the surveys, to avoid any confounding effect in the estimation of mortality (Chapter 3 and 4 only). However, it is important to note that despite harvested trees are not counted as dead, some of them might have been harvested alive or dead, which could make us underestimate the actual number of dead trees (Chapter 3).

The six NFI harmonized had a sample size of 153892 plots, 212 species and 1989158 trees varying from 10.18592 to 262.924 DBH (mm), with survey interval ranging from 2 (29 plots) to 20 years (46 plots).

2.5 Climatic data

We considered two types of climatic variables across the three chapters: first, we considered annual and extreme trends variables that were derived from monthly temperatures and rainfall measures (Fréjaville et al., 2018). To make the variables comparable between different survey dates and countries (table 3), we averaged them over the last 30 years before the first survey (chapter 3, Vayreda et al. (2012)). Besides, this allow to account for the fact that death of a tree can occur several years after climatic disturbance (Jump et al., 2017). To model growth of invasive species, we considered a more recent average climate based on the 15-years period before the first survey. Second, we considered Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. (2010)) that reflect the onset, duration and magnitude of drought conditions over the study period with respect to normal conditions during a period of reference, thus reflecting climate change (see Figure 2.3 for an example). We used the full period available as a reference period, from 1901 to 2015 (Ruiz-Benito et al., 2017). See Table 2.4 for the variable summary, by chapter.

2.6 Modeling tree demography

The three major demographic processes of forest trees and populations are reproduction, growth and mortality. The demographic processes that I studied in Chapters 3, 4, and 5 are shown in Table 2.5).

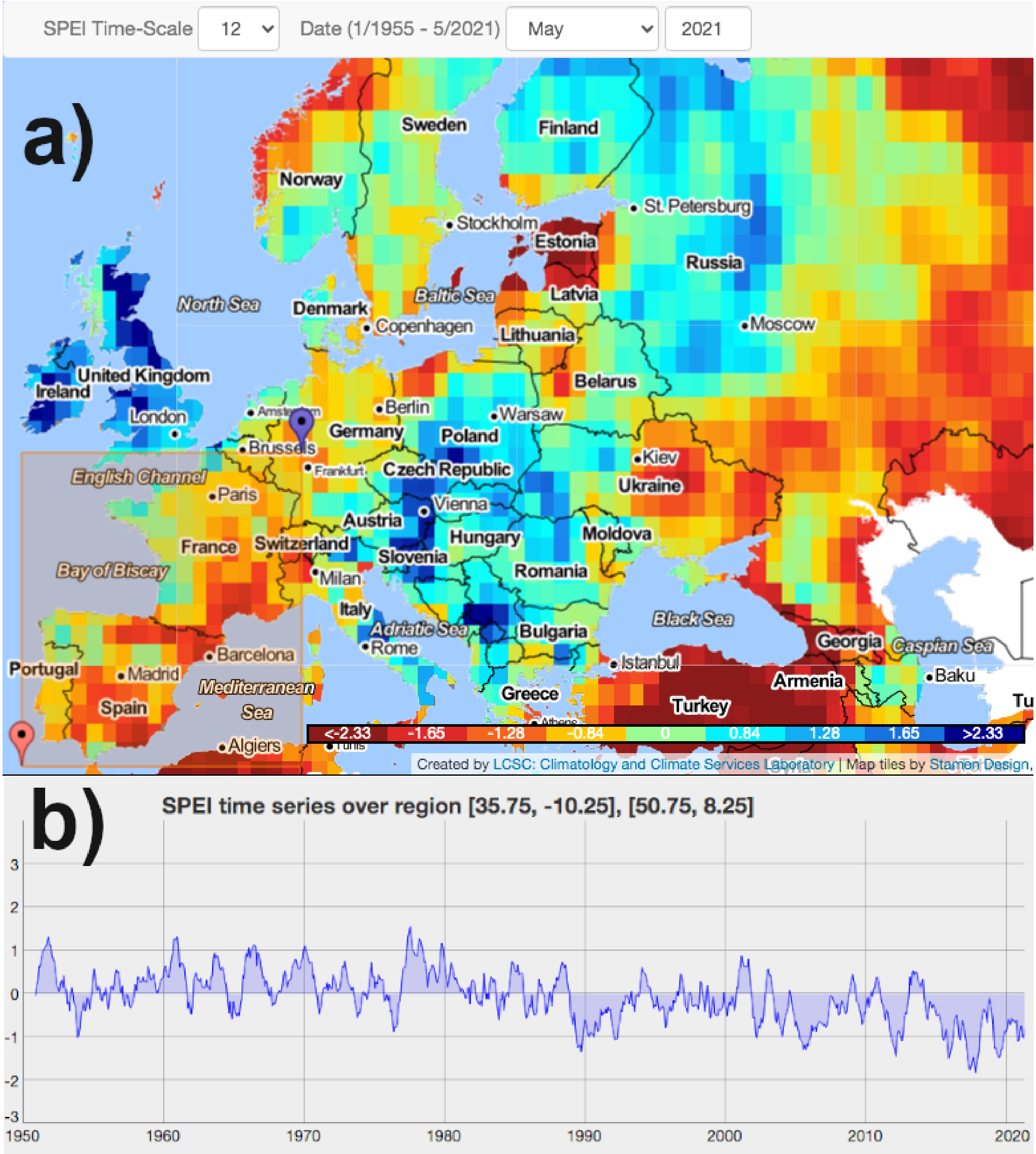
2.6.1 Mortality

I consider the following definition of dead tree: a tree that was present and above the minimum DBH (100mm) in the first survey but does not show any sign of life above 1.30 meters in the second survey (IGN; Gschwantner et al. (2016)). Hence, I only measured mortality in juvenile and mature trees.

As tree mortality is a rare event, the tree mortality recorded in the NFI is not very high, which implies that the distribution of mortality typically follows a zero inflated distribution

Description	Unit/Time period	Chapter
Annual mean temperature averaged over the last 30 years	°C	Chapter 3
Annual mean temperature averaged over the last 15 years	°C	Chapter 5
Mean diurnal temperature range averaged over the last 30 years	°C	Chapter 3
Maximal temperature of the warmest month averaged over the last 30 years	°C	Chapter 3
Winter mean temperature averaged over the last 30 years	°C	Chapter 3
Annual precipitation averaged over the last 30 years	mm	Chapter 3
Annual precipitation averaged over the last 15 years	mm	Chapter 5
Precipitation of the wettest month over the last 30 years	mm	Chapter 3
Precipitation of the driest month over the last 30 years	mm	Chapter 3
Annual water balance over the last 30 years	mm	Chapter 3
Monthly Standardised Precipitation-Evapotranspiration Index of the last 12 months	Averaged on the time period elapsed between the two-sampling procedure	Chapter 3-4-5
Monthly Standardised Precipitation-Evapotranspiration Index of the last 12 months	Minimum value on the time period elapsed between the two sampling procedure	Chapter 3

Table 2.4: climatic variables used as predictors in the three chapters, including 10 climatic variables averaged over the last 30 years before the first inventory (Chapter 3), 2 climatic variables averaged over the last 15 years before the first inventory (Chapter 5), 2 drought-related variables derived from SPEI indices calculated for the ith individual plot. We included the variable description/name, units/time period and the chapter of the manuscript in which the variable was used.



SPEI Time-Scale 12 Date (1/1955 - 5/2021) May 2021

Created by LCSC: Climatology and Climate Services Laboratory | Map tiles by Stamen Design,

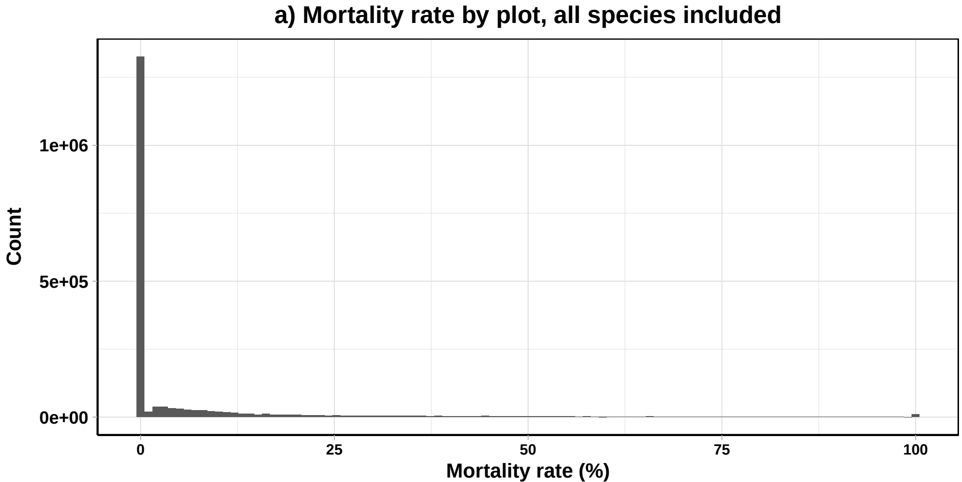
Figure 2.3: SPEI in Europe: a) The SPEI Global Drought Monitor gives near real-time information about drought conditions at the global scale, with a 1 degree spatial resolution and a monthly time resolution. Here is represented the SPEI calculated on 12 month with a reference period from January 1950 to June 2021. b) SPEI time series over the France and Spain (indicated by the rectangle). Generated on `https://spei.csic.es/map/maps.html`.

(Figure 2.4a). To handle it, I developed two separate models to estimate separately occurrence and intensity of mortality (i.e. zero-truncated models; Table 2.5; Benito-Garzón et al. (2018)). We choose this approach because 1) I assumed that occurrence of mortality (the occurrence of at least one mortality event in a given period, with zero when all trees in the plot survived; i.e. binomial part of the model) found in a plot reflects background mortality, whereas the intensity of tree mortality (the amount of trees that died in the same period, given that mortality occurred; i.e. conditional part of the model) found in a plot reflects die-off for the most intense events. 2) I assumed that zero outcome (no mortality event) can be produced in the binomial but not in the conditional part of the model, reflecting the fact that if conditions are favorable for the absence of mortality, it will always induce the absence of mortality (Zuur et al., 2009).

I expressed mortality as the number of dead individuals over the total number of individuals, which reflect well background mortality (Van Mantgem et al., 2009; Peng et al., 2011) rather than a volume of dead trees, better suited for economical purposes and related to carbon budget (Kurz et al., 2008). In addition, I estimated mortality as an annualized rate per area (nbr. Trees .ha-1.year-1) because 1) to avoid any bias related to the different country plot sizes, 2) I assumed a linear relationship between the census interval and the rate of mortality. However, census duration can have an influence on the estimates, longer intervals usually resulting in lower rate estimates (Sheil et al., 1996; Kohyama et al., 2018). For this reason, I included the number of years between survey as a predictor in the models (Table 2.5).

2.6.2 Recruitment

In silviculture, recruitment is understood as the process by which trees move from one size class to another (Helms, 1998) or by which saplings or young trees reach certain threshold value of height or DBH of a forest stand over a certain period (Lexerød et al., 2005; Zhang et al., 2012). As such, within the NFI designs, recruitment can be considered as the trees that appear from one census to the other. I defined recruitment as the number of trees that were either absent or below the minimum DBH (100mm) in the first survey but exceed the minimum DBH in the second survey (Gschwantner et al., 2016). As in the case of mortality, most of the plot do not contain recruited trees and recruitment estimated from NFI had a large proportion of zeros (Figure 5b). To handle them, I developed zero-inflated models (Table2.5). We used zero-inflation rather than zero truncation, assuming that zero outcome (no recruitment) can be produced both in the binomial and the conditional parts of the model, reflecting the fact that favorable conditions for recruitment do not always induce recruitment (Fortin et al., 2007; Li et al., 2011; Zell et al., 2019; Zhang et al., 2012). Similarly to mortality, we modeled recruitment as a number of new individuals that appear in the second survey in relation to the first one rather than a volume because we were



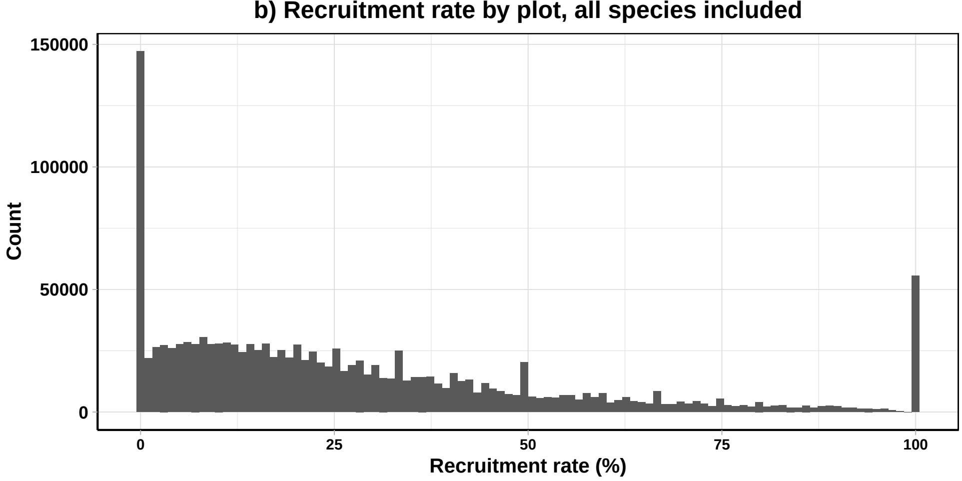


Figure 2.4: Histogram of a) mortality rate (in %) and b) recruitment rate (in %) representing the zero-inflation of both distributions.

interested in studing tree demography rather than productivity (Kurz et al., 2008). As for mortality, we modeled recruitment as an annualized rate per area (nbr. Trees.ha-1.year-1) assuming a proportional increase of recruitment along elapsed time and plot size. However, instead of using an annualized rate as for mortality, we used an offset on census time (CI) and variable plot size, to make the model interpretability easier (Li et al. (2011) and Vanclay (1992), Table 2.5).

2.6.3 Stand basal area growth as a measurement of invasion trait

Stand basal area growth and relative stand basal area growth are good traits to measure the invasive capacity of species (Daehler, 2003; Hernández et al., 2014). In chapter 5, I calculated stand basal area growth and relative stand basal area growth to measure the invasibility of *Robinia pseudoacacia* and *Quercus rubra* in the plots where they appeared. I calculated stand basal area growth of a given species (BAG_{ij}) as the sum of the conspecific basal area in the second inventory ($BAj.ha2$) minus the conspecific basal area in the first inventory ($BAj.ha1$). This is given by the increment of individual basal area of the trees present in both inventories (i.e. survivor growth) plus the total basal area of the trees present in the second survey only (i.e. recruited trees) minus the basal area of trees present only in the first survey (i.e. dead trees); See equation 2.1.

$$\begin{aligned} BAG_{ij} = &\sum_{i,k=survivor} BA.ha2_j + \sum_{i,k=recruited} BA.ha2_j - \sum_{i,k=dead} BA.ha2_j \\ &- \sum_{i,k=alive} BA.ha1_j \end{aligned} \tag{2.1}$$

I calculated relative stand basal area growth ($RBAG_{ij}$)as the stand basal area growth of the target species divided by the sum of the stand basal area growth of all species in a plot ($BA.tot.ha$); See equation 2.2

$$\begin{aligned} RBAG_{ij} = &\frac{\sum_{i,k=survivor} BA.ha2_j + \sum_{i,k=recruited} BA.ha2_j - \sum_{i,k=dead} BA.ha2_j}{BA.tot.ha2} \\ &- \frac{\sum_{i,k=alive} BA.ha1_j}{BA.tot.ha1} \end{aligned} \tag{2.2}$$

We developed linear mixed-effects models of basal area growth and relative basal area growth to account for the different countries and census interval in the random effect. To remain consistent with the other chapters, we expressed the absolute tree growth *per area* rather than *per capita* in $\text{cm}^2.\text{ha}^{-1}$ (Ruiz-Benito et al., 2017). As for recruitment, we used an offset on census time (CI) assuming a proportional increase of growth along elapsed time (Table 2.5). In all chapters we used the same general structure for our models:

$$\eta_{1-6}(Y) = \alpha_0 + \sum_{h=1}^{n} \beta_h x_{h.i} + \sum_{h=1}^{n} \gamma_h x_{h.i} z_{h.i} + \alpha_{\text{country}} + \text{offset}(Years_i) + \epsilon_i \tag{2.3}$$

Whereα_0 is an intercept term, α_{country} s the random country intercept that account for sampling differences between each NFI (this effect follows a Gaussian distribution $\alpha_{\text{country}} \sim \mathcal{N}(0, \sigma^2_{\alpha_{\text{country}}})$); ϵ_i is the residual error following a Gaussian distribution $\epsilon_i \sim \mathcal{N}(0, \sigma^2_{\epsilon_i})$. β_h is the regression coefficient for the h$^t h$ of the fixed effect predictors x_h and γ_h the regression coefficient of the h$^t h$ interaction between fixed effect predictors x_h and z_h. To avoid the potential bias caused by the different years of NFIs campaigns (See Supplementary table S1), we used an offset on census time (Years) (Chapter 2 and 3).

2.7 Climatic marginality

To account for the effect of the climatic marginality on tree mortality and recruitment

Response	Distribution	Response calculation	η_{1-6}	Chapter
Species mortality occurrence (presence/absence at the plot level)	Binomial (BIN)	Probability of mortality $p(Y1_{ij} = 1)$ if at least one event recorded, and $p(Y1_{ij} = 0)$ if no event recorded	logit	1
Species mortality intensity (Number of trees per ha per plot per year)	Zero-truncated negative binomial (NB)	Annual mortality rate given that mortality occur $\mu1_{ij} = \frac{\sum dead\ trees_{ij}}{\sum number\ trees_{ij}} \times \frac{1}{years_i}$	log	1
Species recruitment occurrence (presence/absence at the plot level)	Binomial (BIN)	Probability of recruitment $p(Y2_{ij} = 1)$ if at least one event recorded, and $p(Y2_{ij} = 0)$ if no event recorded	logit	2
Species recruitment count (Number of trees per ha per plot)	Zero-inflated negative binomial (NB)	Average count of recruitment given that recruitment occurs $\mu2_{ij} = \sum recruited\ tree_{ij}$	log	2
Stand basal area growth ($\mathrm{m}^2\mathrm{ha}^{-1}$)	Normal	$Y3_{ij} = BAj.ha2_{ij} - BAj.ha1_{ij}$	Identity	3
Relative stand basal area growth ($\mathrm{m}^2\mathrm{ha}^{-1}$)	Normal	$Y4_{ij} = \frac{BAj.ha2_{ij}}{BAtot.ha2_i} - \frac{BAj.ha1_{ij}}{BAtot.ha1_i}$	Identity	3

Table 2.5: Response variables analyzed. Response variables are calculated for ith individual plot of the jth species. Response: Response description and unit. Distribution: distribution used to model the corresponding response. Response calculation: calculation of the response and name given for within the model. η_x: Link function used in the corresponding model. Chapter: Chapter of the manuscript in which we used the given model.

I divided the core, trailing and leading edge of the species ranges based on their climate. I calculated a climatic marginality index to categorize populations based on climate and geography following these steps: I use species distribution ranges from Caudullo et al. (2017) or EUFORGEN (`http://www.euforgen.org/`; Figure 2.5a). Within each range, I characterized the climate using a weighted principal components analysis (WPCA; Benito-Garzón et al. (2014)) based on 21 climatic variables averaged over the 2000–2014 time period at each point in a grid with a pixel size of 1km×1km (Annexes 3, Supporting Information Table S3; Fréjaville et al. (2018)). The WPCA was calculated using 10,000 randomly selected points within each of the species' ranges. The variance explained by the two first axes of the WPCA ranged from 71.53% for *Fagus sylvaticata* 87.42% for *Larix decidua* (Annexes 3, Supporting Information Table S4).

Based on the weighted scores of the two first WPCA axes, I defined three climatic groups: core, transition and marginal regions (Figure2.5b; Annexes 3, Supporting information Table S4). Species-specific thresholds for attributing the core (C), climatic marginal (M) and transition (T) areas were calculated based on the WPCA scores (Annexes 3, Supporting Information Table S2). Values between 0 and 60% were attributed to core areas, between 60 and 80% to transition areas and $>$ 80% to marginal areas. To separate climatic marginal areas (M) further into the climatic trailing edge (TE) for the southernmost edge and the climatic leading edge (LE) for the northernmost, we used a discriminant principal components analysis (DPCA) and an attribution test to check whether individual points were reassigned successfully to their attributed group based on the discriminant functions (Jombart (2008); Figure2.5c). Finally, NFI plots were linked to WPCA scores and classified as core (C), leading or trailing edge (LE or TE). Plots lying in transition (T) regions between C and LE or C and TE were not used in the analysis (Figures 6d and Annexes 3: Supporting Information Table S2 and figure S3). We used species-specific thresholds to have enough populations in the margins.

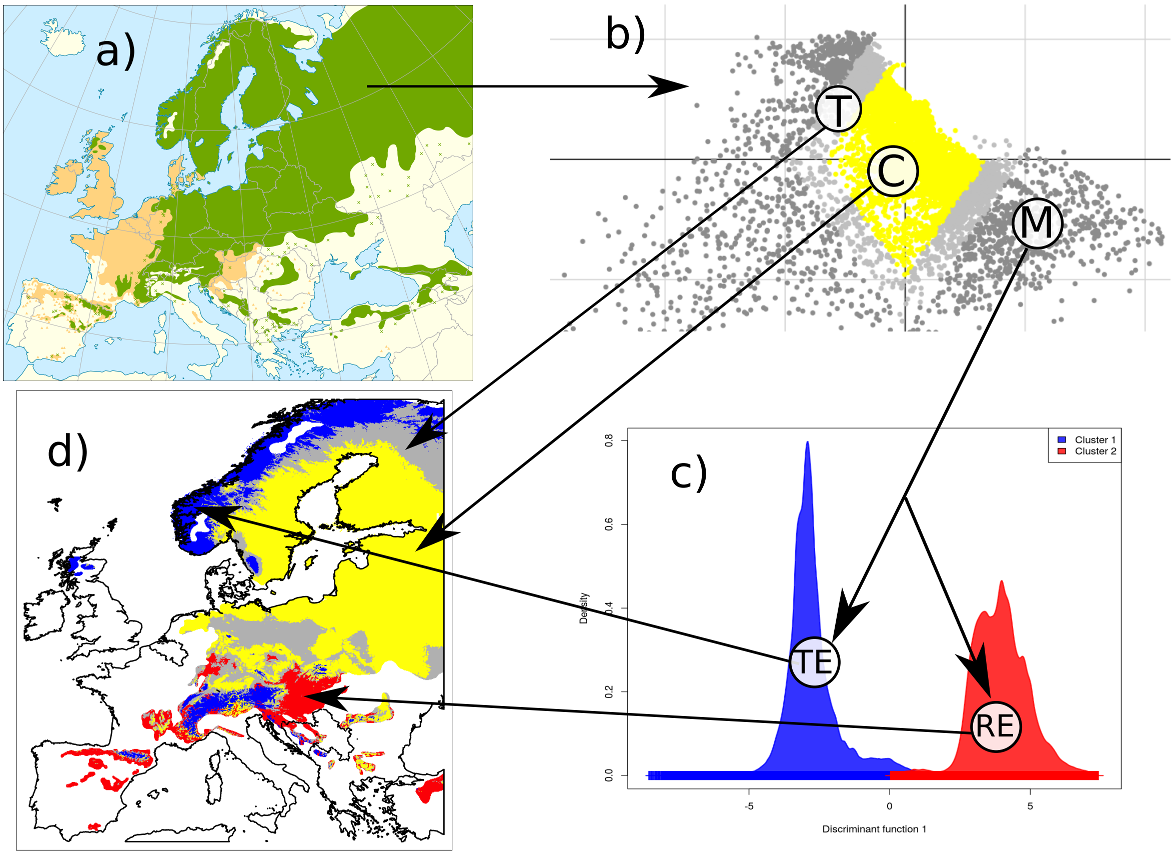


Figure 2.5: Climatic characterization of the species distribution ranges into core, transition and marginal (leading or trailing) areas. We show an example for *Pinus sylvestris* from from Caudullo et al. (2017) including: a) Species distribution range; b) the climatic variables within the species range are analysed using a Weighted PCA to define three clusters including C = Core areas with C: the lowest weighted scores within the range calculated on the two first axis of the PCA; M = Marginal areas with M: the largest weighted scores within the range (extremes individuals) calculated on the two first axis of the PCA; T = Transition areas with T: weighted scores that fall between the lowest values (core) and largest values (marginal areas); c) results of the Marginal climatic areas that were clustered into: TE trailing edge (TE) and (leading edge (LE) areas with a Discriminant Principal Component Analysis (DPCA).; d) map of the areas defined within the species range with their respective colors. ("Core" in yellow, "trailing edge" in blue, "leading edge" in red and "transition" zone in gray).

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Chapter 3

Occurence but not intensity of mortality rises towards the climatic trailing edge of tree species ranges in European forests

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RESEARCH PAPER

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Occurrence but not intensity of mortality rises towards the climatic trailing edge of tree species ranges in European forests

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Abstract

Aim: Tree mortality is increasing world-wide, leading to changes in forest composition and altering global biodiversity. Nonetheless, owing to the multifaceted stochastic nature of tree mortality, large-scale spatial patterns of mortality across species ranges and their underlying drivers remain difficult to understand. Our main goal was to describe the geographical patterns and drivers of the occurrence of mortality (presence of a mortality event) and the intensity of tree mortality (amount of mortality related to that mortality event) in Europe. We hypothesized that the occurrence of mortality represents background mortality and is higher in the margin than in core populations, whereas the intensity of mortality could have a more even distribution according to the spatial and temporal stochasticity of die-off events.

Location: Europe (Spain, France, Germany, Belgium, Sweden and Finland).

Major taxa studied: More than 1.5 million trees belonging to 20 major forest tree species.

Methods: We developed binomial and truncated negative binomial models to tease apart the occurrence and intensity of tree mortality in National Forest Inventory plots at the range-wide scale. The occurrence of mortality indicated that at least one tree had died in the plot, whereas the intensity of mortality referred to the number of dead trees per plot.

Results: The highest occurrence of mortality was found in peripheral regions and the climatic trailing edge linked with drought, whereas the intensity of mortality was driven by competition, drought and high temperatures and was scattered uniformly across species ranges.

Main conclusions: We show that tree background mortality, but not die-off, is generally higher in the trailing-edge populations. It remains to be explored whether other demographic traits, such as growth, reproduction and regeneration, also decrease at the trailing edge of European tree populations.

KEYWORDS

background mortality, climatic edges, die-off mortality, drought, European forests, hurdle models, National Forest Inventory, tree mortality

1 | INTRODUCTION

Tree mortality is increasing world-wide, particularly following summer drought (Allen et al., 2015; van Mantgem et al., 2009). Tree mortality can change the forest community, ecosystem dynamics and function; hence, it can alter biodiversity (McDowell et al., 2008). Nonetheless, tree mortality remains difficult to predict at large spatial scales (Hartmann et al., 2018) because it is a multifaceted, stochastic process (Franklin et al., 1987). Background tree mortality is defined as the occurrence of individual tree mortality within a given region in the absence of catastrophic events, such as fires, wind, heatwaves, drought or disease outbreaks (Csilléry et al., 2013; Franklin et al., 1987). It is a complex process driven by the combination of drought, climate warming, forest composition, trees interactions and age (Hülsmann et al., 2017; Ruiz-Benito et al., 2013). In contrast, die-off mortality is a local phenomenon whereby many trees die together as a response to exceptional events (Mueller-Dombois, 1987). Die-off mortality has been related to extreme localized events, disturbances or environmental conditions, such as intense drought, heatwaves, storms or fire (Allen et al., 2010; McDowell et al., 2008), and is exacerbated by pest and disease outbreaks (Anderegg et al., 2015).

Climate change, especially an increase in the number and duration of drought events, has been linked to increases in both background mortality rates and the extent of die-off events (Allen et al., 2010, 2015; Taccoen et al., 2019). However, identification of the drivers of die-off and background mortality along large environmental gradients remains challenging because tree sensitivity to biotic and abiotic factors depends on the species identity (Ruiz-Benito et al., 2013), their age (Hülsmann et al., 2017) and their ecological strategies (Archambeau et al., 2020; Benito Garzón et al., 2018; Ruiz-Benito, Ratcliffe, Zavala et al., 2017).

Demographic performance generally decreases toward both the leading and trailing edges of species ranges (Sexton et al., 2009), although exceptions have been found (Pironon et al., 2017). Throughout the manuscript, we call “marginal populations” the populations located at the climatic edges, with the trailing edge representing the backward-moving front of the population and the leading edge the forward-moving front. In the Northern Hemisphere, demographic processes in the trailing edge can be affected more by drought, whereas those at the leading edge are likely to be affected more by cold and photoperiod. In the context of climate change, we expect an increased mortality rate in trailing-edge populations owing to increased drought and rising temperatures (Benito-Garzón et al., 2013; Purves, 2009; Young et al., 2017), and in the leading edge owing to warmer conditions that can promote insect attacks (Kliejunas et al., 2009). Additionally, we could expect higher background mortality at the margins than at the core of the distribution (Neumann et al., 2017), with the most intense events of mortality distributed evenly across species ranges (Allen et al., 2010, 2015; Jump et al., 2009, 2017). However, very little is known about the differential drivers of background tree mortality and die-off events at large geographical scales, and both processes can occur throughout species ranges (e.g., Allen et al., 2010; Greenwood et al., 2017; Jump et al., 2009).

Here, we analyse tree mortality of 20 major forest tree species from > 1.5 million trees recorded in the National Forest Inventories (NFIs) from Spain, France, Germany, Belgium (Wallonia), Sweden and Finland to understand mortality patterns across species distribution ranges. The mortality observed in NFIs can be considered as background mortality (Taccoen et al., 2019) because it reflects the occurrence of individual tree mortality within a given region. However, intense events of mortality in the same plot may also reflect die-off mortality (Hülsmann et al., 2017). With this rationale, we assumed that the occurrence of mortality (the occurrence of at least one mortality event in a given period) found in a plot reflects background mortality, whereas the intensity of tree mortality (the amount of trees that died in the same period) found in a plot reflects die-off for the most intense events. We developed hurdle models of mortality occurrence and intensity to understand the effect of climatic marginality defined as areas exhibiting the highest or the lowest values of several climatic variables and its interaction with drought. The aims of our study were as follows: (a) to identify the underlying drivers of mortality occurrence and intensity and how they are influenced by the marginality of the population; and (b) to evaluate tree mortality occurrence and intensity patterns across species distribution ranges. We hypothesized that marginal populations will have higher occurrence of mortality than core populations, and that the intensity of mortality will show a patchy distribution over the spatial range, reflecting the stochastic nature of die-off events.

2 | MATERIALS AND METHODS

2.1 | Harmonization of NFIs

We used mortality records and biotic data from the NFIs of six European countries [Spain, Germany, Finland, Sweden, Wallonia (Belgium) and France] compiled by Archambeau et al. (2020). Plots with repeated measurements were originally harmonized in the FunDivEUROPE project (http://www.fundiveurope.eu/) (Baeten et al., 2013; Ruiz-Benito, Ratcliffe, Jump et al., 2017) for all the NFIs except France. Archambeau et al. (2020) subsequently added the French NFI to the dataset. These data vary between NFIs owing to differences in sampling methods, plot sizes and densities. The French NFI has temporary plots recorded between 2005 and 2014, whereas the other countries have permanent plots sampled several years apart, ranging from 1981 to 2011 (Supporting Information Table S1). Data from the six NFIs together cover a latitudinal gradient from 36° N (Spain) to 70.05° N (Finland).

2.2 | Plot-level tree mortality recorded from NFIs

We used individual tree mortality data for 20 major forest tree species from a total of 1,989,158 trees (141,641 dead) ranging from 10 to 263 cm (mean =28 cm) diameter at breast height (d.b.h.; in centimetres) and 153,892 plots and with a mean census interval of

10.7 years, ranging from 2 (29 plots) to 20 years (46 plots; Supporting Information Table S2). We included only trees that died of natural mortality (standing and fallen) and excluded trees missing for unknown reason and trees that had been harvested. Mortality occurrence was calculated as a binary variable, with zero when all the trees in the plot survived and one when at least one tree died in the plot during the census interval. Mortality intensity was calculated in each plot as the percentage of trees that died between the first and second survey in the NFIs with permanent plots, divided by the number of years between the surveys and calculated at the hectare level. In the French NFI, tree mortality per plot was calculated as the percentage of trees that died within the 5 years before sampling in the temporary plot. We removed plots with trees recently recorded as harvested or managed between consecutive inventories and individual trees < 100 mm d.b.h. to make the tree measurements consistent across countries with different d.b.h. thresholds. Finally, we had 1,595,968 trees (105,798 dead) and 134,590 plots for further analysis.

To avoid the potential bias caused by the different years of the NFI campaigns and the different sizes of the plots between the NFIs (Supporting Information Table S1), we upscaled tree mortality from plot to hectares per year using a weighted index provided by each NFI and dividing this value by the number of years between campaigns for the NFIs with repetitive measurements or by five for the French NFI (Supporting Information Figure S1). The weighted index reflected the size of the plot or the density of the grid or both, depending on the country (Supporting Information Table S1; http://project.fundiveurope.eu/).

2.3 | Model predictors

2.3.1 | Indexes of climatic marginality and climatic areas

We determined the distribution range of each species using information available from Caudullo et al. (2017) or EUFORGEN (http://www.euforgen.org/). Within each range, we characterized the climate using a weighted principal components analysis (WPCA; Benito-Garzón et al., 2014) based on 21 climatic variables averaged over the 2000–2014 time period at each point in a grid with a pixel size of 1 km × 1 km (Supporting Information Table S3; Fréjaville & Benito Garzón, 2018). The WPCA was calculated using 10,000 randomly selected points within each of the species' ranges. The variance explained by the two first axes of the WPCA ranged from 71.53% for *Fagus sylvatica* to 87.42% for *Larix decidua* (Supporting Information Table S4). Based on the weighted scores of the two first WPCA axes, we defined three climatic groups: core, transition and marginal regions (Supporting Information Figure S2; Table S4). Species-specific thresholds for attributing the core (C), climatic marginal (M) and transition (T) areas were calculated based on the WPCA scores (Supporting Information Table S2). Values between 0 and 60% were attributed to core areas, between 60 and 80% to transition areas and > 80% to marginal areas.

To separate climatic marginal areas (M) further into the climatic trailing edge (TE) for the southernmost edge and the climatic leading edge (LE) for the northernmost, we used a discriminant principal components analysis (DPCA) and an attribution test to check whether individual points were reassigned successfully to their attributed group based on the discriminant functions (Jombart, 2008; Supporting Information Figure S2).

Finally, NFI plots were linked to WPCA scores and classified as core (C), leading or trailing edge (LE or TE) accordingly, based on their coordinates. Plots lying in the transition (T) region were not used in the analysis (Supporting Information Table S2; Figures S2 and S3).

2.3.2 | Climatic data

We characterized the long-term climate of each plot with annual temperature- and precipitation-related variables (Fréjaville & Benito Garzón, 2018) that are known to affect both background and die-off tree mortality (Archambeau et al., 2020; Benito Garzón et al., 2018; Ruiz-Benito, Ratcliffe, Zavala, et al., 2017). To make the variables comparable between different survey dates and countries, we averaged them over the last 30 years before the first survey. We selected four temperature variables that were not correlated with the other four precipitation-related variables chosen among the 21 variables mentioned above (correlation not shown, but see VIF in Supporting Information Table S5). For each species, we then chose the precipitation- and temperature-related variables that explained the most variance (Table 1). These variables were derived from monthly temperatures and rainfall measures and represented both annual and extreme trends. Following WorldClim conventions for the variable names (https://www.worldclim.org/data/bioclim.html), we used: annual mean temperature (bio1), maximal temperature of the warmest month (bio5), winter mean temperature (tmean.djf), autumn mean temperature (tmean.son) (temperature-related variables); and annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), annual water balance (precipitation minus potential evapotranspiration; ppet.mean) (precipitation-related variables; Supporting Information Table S3).

In addition, we used the standardized precipitation evapotranspiration index [SPEI v.2.5 (2017); http://hdl.handle.net/10261/104742]. SPEI is a multi-scalar drought index based on potential evapotranspiration and precipitation over the time-scale considered (12 months to match our annual mortality estimation), relative to median values for a long-term reference period that reflects the average climate during the last century (from 1901 to 2015). Negative SPEI values indicate lower water availability in the specific period of time than for the reference period (Vicente-Serrano et al., 2010). Here, we used 1901–2015 as a reference period and a 12-month time-scale. For each month during the time interval between inventory campaigns, we calculated the annual means and extracted the minimum and mean values (hereafter, SPEI variables; for summary statistics by species, see Table 1; Supporting Information Table S3).

TABLE 1 Mean, standard error, minimum and maximum values of plot-level variables included in the best full model by species

Species	M (trees. ha-1.yr-1)	DBH (mm)	BAIj.mean (cm^2. ha-1.yr-1)	D (trees.ha-1)	SPEI12	BA.O (cm^2.ha-1)	BA (cm^2.ha-1)	BAj (cm^2.ha-1)	T° (°C)	P° (mm)
ABIALB									Winter T°	Driest month P°
	5.06	357.84	.08	14.28	−.01	18.33	35.12	–	.29	69.95
	(16.89)	(140.26)	(.05)	(7.03)	(.38)	(15.07)	(15.36)		(1.33)	(16.75)
	0–172	101–1,277	0–.47	1–82	−1.44 to .87	0–98.35	.72–110.6		−4.81 to 6.13	13.19–132.09
ACEPSE									Annual T°	Driest month P°
	1.37	271.74	.08	11.92	.08	–	28.32	5.85	8.97	65.44
	(10.19)	(121.15)	(.05)	(6.16)	(.32)		(14.81)	(5.44)	(1.56)	(17.17)
	0–185	99.5–824.42	0–.42	1–59	−1.28 to .78		.72–110.6	.41–48	2.94–14.42	22.58–127.85
ALNGLU									Annual T°	Driest month P°
	6.77	241.74	.07	14.12	.07	15.26	25.03	–	10.3	51.02
	(20)	(98.49)	(.05)	(9)	(.39)	(12.76)	(14.71)		(2.19)	(15.34)
	0–171	100–710	0–.43	1–62	−1.16 to 1.32	0–91.78	.27–131.14		4.39–17.08	.95–91.52
BETPEN									Annual T°	Driest month P°
	4.26	219.18	.06	12.53	.09	–	23.71	5.64	9.51	52.98
	(17.97)	(92.3)	(.05)	(7.68)	(.34)		(13.05)	(5.63)	(2.28)	(13.06)
	0–182	101.86–646.67	0–.4	1–62	−1.44 to 1.28		.3–90.43	.26–50.94	−1.47 to 14.93	10.5–113.72
CASSAT									Annual T°	Driest month P°
	16.07	275.63	.08	14.83	−.13	15.26	27.71	–	11.65	54.7
	(32.9)	(170.19)	(.08)	(8.72)	(.33)	(12.89)	(14.67)		(1.15)	(14.99)
	0–196	100–1,702.96	0–1.34	1–85	−1.37 to .89	0–105.31	.44–118.25		7.88–17.08	.99–93.46
FAGSYL									Warmest month T°	Driest month P°
	1.66	336.94	.08	12.19	.06	–	29.02	13.16	23.27	58.88
	(8.62)	(157.1)	(.05)	(7.17)	(.32)		(13.68)	(11.19)	(1.54)	(14.68)
	0–172	100–1,556.54	0–.77	1–82	−1.3 to 1.17		.31–123.17	.27–90.73	16.25–28.59	12.35–126.73
FRAEXC									Warmest month T°	Annual P°
	2.06	281.95	.08	11.56	0	18.05	–	7.61	24.33	843.74
	(11.94)	(131.65)	(.05)	(6.21)	(.36)	(13.43)		(7.59)	(1.62)	(157.33)
	0–172	101–923.1	0–.57	1–65	−1.37 to 1.22	0–119.91		.26–103.91	17.11–30.06	506.36–1,535.75
PICABI									Warmest month T°	Wettest month P°
	3.88	251.22	.06	17.43	.24	–	26.37	16.47	21.21	101.61
	(14.32)	(128.98)	(.05)	(10.15)	(.37)		(17.43)	(16.49)	(1.64)	(24.87)
	0–183	100–872.17	0–.74	1–82	−1.32 to 1.33		.25–123.17	.25–114.35	15.07–28.07	56.49–200.48

(Continues)

TABLE 1 (Continued)

Species	M (trees. ha-1.yr-1)	DBH (mm)	BAIj.mean (cm^2. ha-1.yr-1)	D (trees.ha-1)	SPEI12	BA.O (cm^2.ha-1)	BA (cm^2.ha-1)	BAj (cm^2.ha-1)	T° (°C)	P° (mm)
PINHAL									Warmest month T°	Annual WB
	4.11	226.83	.03	12.69	−.21	–	8.57	6.78	29.12	−517.52
	(13.77)	(83.98)	(.02)	(9.36)	(.27)		(7.52)	(6.45)	(1.88)	(256.76)
	0–187	99.5–955	0–.27	1–69	−1.3 to .53		.39–58.27	.39–54.81	23.79–35.55	−1029.7–124.03
PINNIG									Warmest month T°	Annual P°
	3.28	244.07	.02	18.71	−.18	–	12.74	8.56	26.8	610.5
	(11.34)	(101.69)	(.02)	(12.38)	(.23)		(10.51)	(9.35)	(2.19)	(118.12)
	–106	99.5–1,305.07	–.34	1–87	−1.16 to .58		.39–95.27	.39–95.27	19.15–33.35	385.94–1,084.96
PINPIN									Warmest month T°	Driest month P°
	5.47	273.24	.03	17.73	−.07	–	11.55	6.99	30.24	15.36
	(15.44)	(109.73)	(.02)	(10.95)	(.18)		(7.87)	(6.69)	(3.16)	(12.51)
	0–99	100.5–1,101	0–.21	1–74	−1.12 to .28		.4–52.37	.39–52.37	24.01–36.67	0–45.11
PINPINA									Annual T°	Driest month P°
	12.23	273.13	.05	22.29	−.13	3.07	17.56	–	12.87	30.03
	(21.93)	(103.95)	(.06)	(15.7)	(.29)	(6.37)	(12.03)		(1.61)	(19.99)
	0–180	99.5–967.66	0–.82	1–97	−1.3 to .51	0–60.96	.4–87.01		7.87–18.39	.99–80.61
PINSYL									Annual T°	Wettest month P°
	5.3	242.02	.04	18.92	.08	–	19.37	12.14	7.35	86.33
	(16.85)	(97.72)	(.03)	(13.21)	(.43)		(14.08)	(11.26)	(3.2)	(13.64)
	0–188	99.5–805.32	0–.51	1–107	−1.44 to 1.33		.25–104.1	.25–84.23	−2.63 to 15.08	49.29–170.65
POPNIG									Warmest month T°	Annual P°
	7.35	442.38	.11	11.23	−.09	–	24.57	11.38	25.8	780.13
	(22.13)	(218.96)	(.08)	(7.12)	(.37)		(15.11)	(10.23)	(2.03)	(106.31)
	0–152	108.23–1257.32	0–.48	1–54	−1.3 to .67		.86–80.74	.48–52.65	18.93–30.69	547.86–1,215.08
POPTRE									Annual T°	Driest month P°
	6.47	236.14	.08	14.37	.07	17.66	22.92	–	9.44	52.7
	(22.72)	(104.23)	(.06)	(8.97)	(.38)	(11.99)	(12.62)		(2.8)	(15.1)
	0–177	100–736.21	0–.92	1–76	−1.44 to 1.23	0–84.03	.26–87.33		−2.27 to 15.49	11.05–112.42
QUEILE									Annual T°	Annual P°
	2.48	244.47	.02	10.73	−.014	3.97	–	5.32	13.52	599.87
	(10.75)	(153.72)	(.05)	(9.52)	(.27)	(7.15)		(6.24)	(2.07)	(147.99)
	0–157	99.5–1,522	0–1.55	1–68	−1.3 to .66	0–101.74		.39–100.08	6.68–18.85	346.56–1,249.9

(Continues)

TABLE 1 (Continued)

Species	M (trees. ha-1.yr-1)	DBH (mm)	BAIj.mean (cm^2.ha-1.yr-1)	D (trees.ha-1)	SPEI12	BA.O (cm^2.ha-1)	BA (cm^2.ha-1)	BAj (cm^2.ha-1)	T° (°C)	P° (mm)
QUEPET									Annual T°	Annual P°
	4.37	364.87	.06	11.33	.07	–	25.38	11.96	10.39	796.93
	(16.63)	(161.58)	(.04)	(6.32)	(.28)		(11.81)	(9.29)	(1.14)	(120.18)
	0–176	100–1,686	0–.6	1–65	−1.23 to .89		.46–97.76	.39–73.19	4.79–16.25	530.05–1,343.66
QUEPYR									Annual T°	Driest month P°
	4.43	261.27	.03	17.04	−.05	–	14.3	7.21	11.58	34.04
	(14.9)	(150.85)	(.02)	(12.96)	(.25)		(11.57)	(7.3)	(1.66)	(19.23)
	0–172	99.5–1,321	0–.25	1–89	−.96 to .79		.39–67.27	.39–67.27	6.67–16.24	3.77–77.35
QUEROB									Warmest month T°	Wettest month P°
	5.09	390.31	.06	11.68	.01	15	25.19	–	24.45	95.81
	(18.24)	(170.5)	(.05)	(7.31)	(.34)	(12.51)	(13.11)		(1.67)	(26.48)
	0–183	99.5–1,532	0–.56	1–78	−1.23 to .89	0–107.83	.45–118.88		18.64–30.35	56.08–257.12
QUESUB									Annual T°	Annual P°
	4.03	333.11	.02	14.62	−.12	–	12.45	7.65	15.5	662.5
	(13.45)	(156.88)	(.01)	(10.59)	(.24)		(8.55)	(6.81)	(1.19)	(152.47)
	0–141	99.5–1,465	0–.2	1–69	−1.3 to .45		.43–53.15	.39–50.1	10.64–18.84	329.17–1,547.02

BA = total basal area of the plot; BAj = conspecific basal area of the plot; BAIj.mean = plot growth rate; BA.O = heterospecific basal area of the plot; D = plot density (number of trees); DBH = plot mean diameter at breast height; M = annual mortality rate per hectare; P° = precipitation-related variable (with name according to the species); Species = species code (defined in Table 2); SPEI12 = mean relative drought index; T° = temperature-related variable (with name according to the species); WB = water balance (precipitation minus potential evapotranspiration).

2.3.3 | Stand and competition variables

All stand variables were calculated using NFI data, transformed where necessary to meet the model assumptions of normality (Table 1; Supporting Information Table S6): total basal area increment of the species (BAI_j; in square metres per hectare per year), calculated as the difference in basal area between two inventory periods for all NFIs except France, where 5-year cores were used; mean basal area increment of the species (meanBAI_j; in square metres per hectare per year); mean diameter at breast height (DBH; in millimetres), tree density calculated as the number of trees per hectare (treenumber; number of trees per hectare); total conspecific stand basal area (BA; in square metres per hectare; estimated as the basal area of all individuals of the species in the plot, BAj; in square metres per hectare) and heterospecific stand basal area (estimated as basal area of all individuals excluding the studied species, BA.O; in square metres per hectare).

The DBH, BAI_j and meanBAI_j were included in the model because they reflect the stage of maturity (DBH) and growth (BAI variables) in the plot. These variables together with tree density (treenumber) influence tree mortality (Dietze & Moorcroft, 2011; Hülsmann et al., 2017). The number of years between surveys (years between survey) was also included in the model to account for the increase in the probability of mortality with elapsed time. We used BA, BAj and BA.O as proxies of total competition and intraspecific and interspecific competition (Kunstler et al., 2016).

2.4 | Statistical analyses

2.4.1 | Selection of climatic and competition covariates in the mortality models

For each species, we ran 48 competing occurrence of mortality models. In each model, we included the climatic marginality as a qualitative variable (i.e., the core, leading or trailing edge of each plot), the five stand covariates and the minimum and mean SPEI indexes. We added all the possible combinations of one precipitation-related, one temperature-related and two competition variables. We included all interactions between marginality, the two SPEI indexes, the two competition-related variable and the two climate variables.

We included both precipitation- and temperature-related variables in the models, in addition to marginality, because they could vary within the species margins and thus capture variations not accounted for by the marginality variable. We found no signal for collinearity between the precipitation- and temperature-related variables and marginality because none of the calculated variation inflation factors was > 10 (Supporting Information Table S5a,b).

2.4.2 | Statistical models of mortality

We used two species-specific models to handle the zero-inflated distribution of tree mortality (Archambeau et al., 2020; Benito Garzón et al., 2018; Ruiz-Benito, Ratcliffe, Zavala et al., 2017). Consequently, we analysed separately the mortality occurrence between two censuses (0/1 = at least one tree is dead in the plot/all trees are alive in the plot) and the intensity of mortality in plots where mortality occurs (the proportion of trees dead in the plot; Young et al., 2017), which is equivalent to a hurdle model. First, mortality occurrence was analysed with a binomial model (equivalent to the binomial part of the hurdle model; $Y1_i$, Supporting Information Table S7) where p_i is the probability of occurrence of a mortality event in an individual plot, i (among n), during the census interval ($Y1_i = 1$) following a binomial distribution (*Bin*). We used a binomial generalized linear mixed model (GLMM) with a logit link (BIN model) to estimate the parameters of the species-specific linear function $\eta_{1i,sp}$ with sp being a given species (Hülsmann et al., 2017):

$$Y1_i = 1 \approx Bin\left(n, p_i\right)$$

$$\text{logit}\left(p_i\right) = \eta_{1i,sp}$$

Second, we analysed the intensity of mortality as the annual rate of mortality in plots where at least one tree was recorded as dead ($Y2_i$; Supporting Information Table S7) with a zero-truncated negative binomial mixed-effect model (NB model), which corresponds to the second part of hurdle model $Y2_i$, where μ_i is the mean number of mortality events per year per hectare and k is the inverse of the dispersion, following a negative binomial distribution (*NB*). We used NB models with a log link to estimate the parameters of the species-specific linear function $\eta_{2i,sp}$:

$$Y2_i \approx NB\left(\mu_i, k\right)$$

$$\log\left(\mu_i\right) = \eta_{2i,sp}$$

Functions $\eta_{1i,sp}$ and $\eta_{2i,sp}$ take the same general form:

$$\eta_{i,sp} = \alpha_0 + \sum_{h=1}^{16} \beta_h x_{hi,sp} + \sum_{n=1}^{21} \gamma_n x_{sp} z_{sp} + \alpha_{\text{country},sp} + \varepsilon_{i,sp}$$

where α_0 is an intercept term, $\alpha_{\text{country},sp}$ is the random country intercept to account for sampling differences between each NFI and follows a Gaussian distribution, $\alpha_{\text{country},sp} \approx N\left(0, \sigma^2_{\alpha_{\text{country},sp}}\right)$; $\varepsilon_{i,sp}$ is the residual error following a Gaussian distribution, $\varepsilon_{i,sp} \approx N\left(0, \sigma^2_{\varepsilon}\right)$; β_h is the regression coefficient for the h^{th} of 16 fixed effect predictors x_{sp} (including five stand covariates, two climatic variables and their respective quadratic effect, two drought-related (SPEI) variables and their respective quadratic effect, two competition variables and marginality; see details below and Table 1); and γ_n is the regression coefficient of the n^{th} interaction between fixed effect predictors x_{sp} and z_{sp} (including all interactions between climatic variables, drought-related variables, competition variables and marginality).

2.4.3 | Model selection

To select the most parsimonious model, we applied the following procedure for each species. First, we calculated the variance inflation factor (VIF) for all 48 possible combinations of variables and removed combinations with VIF > 10 (Dormann et al., 2013). Second, we ran BIN models including each remaining combination of variables and selected the combination with the best predictive ability using the Akaike information criterion (AIC < 2) and the log H-likelihood (largest values; Lee et al., 2018). Third, given that we wanted to compare the relative importance of drivers between the occurrence and intensity of mortality, we assumed initially that both processes are driven by the same factors and fitted the NB model including the same variables as those in the BIN model with the best predictive ability. Fourth, we used a stepwise approach for both the BIN and NB models (i.e., we removed the least significant variable to fit a new model) to obtain the most parsimonious models.

All models were fitted with the spaMM package (Rousset et al., 2014; Table 2) in R v.3.6.1 (R Core Team, 2020).

2.4.4 | Model validation

The goodness-of-fit was evaluated with the area under the curve (AUC) for BIN models (Hurst et al., 2011) and with cross-validation for the NB models [models were fitted on 66% of the data, and the remaining 33% were used to validate the predictions (Table 2; for comparison between observed and predicted distribution of mortality values for the NB models, see Supporting Information Figure S4)].

The percentage of the variance explained by the BIN and NB models was estimated by the marginal and conditional R^2 including fixed effects and fixed plus random effects, respectively (Nakagawa & Schielzeth, 2013). The proportion of change in explained variance between the full model and the null model (PCV) indicates the variance retained by the selected model. All these metrics were calculated from the spaMM objects using a personal script adapted from the piecewiseSEM package (Lefcheck, 2016), following Nakagawa and Schielzeth (2013) and Nakagawa et al. (2017).

2.4.5 | Comparison of spatial predictions and climatic marginality

We used the selected models to predict the occurrence and intensity of mortality across the range of NFI plots (Supporting Information Figures S5–S7). For visual inspection of the differences in the climatically marginal populations, we split the predicted values into three groups based on the quartiles, in order to indicate high (first quartile), medium (second and third quartile) and low levels (fourth quartile) of mortality (Figure 1; Supporting Information Figure S8).

To test statistically for heterogeneity in the distribution of the predicted probability between the three areas (core, leading edge and trailing edge), we compared the predicted distribution (Figure 1) against the expected distribution under the assumption of no spatial structure in mortality occurrence (null hypothesis) with a chi-square test. Under the null hypothesis, we expected the distribution to be distributed uniformly within the three areas (25% of the values in each quartile) (Supporting Information Figure S9a). Values of $p < .05$ indicate that predicted mortality was different from that expected under the null hypothesis. The same approach was used to test for patterns across the three areas in predicted mortality intensity (Supporting Information Figures S8 and S9b).

3 | RESULTS

3.1 | Climatic marginality across species ranges

The variables that contributed the most in defining the core, trailing and leading areas were annual evapotranspiration for 10 species, maximum temperature of the warmest month for four species and annual precipitation for four species (Supporting Information Table S4). Marginal areas, as expected, exhibited extreme climatic values (generally highest at the trailing edge and lowest at the leading edge).

We observed that our climatic marginality did not match systematically with the commonly used geographical marginality (northern part of species distribution corresponding to the geographical leading edge and southern part to the geographical trailing edge), particularly in the mountainous areas, which were in the climatic leading edge for most species although they tended to be located in the central part of the range (geographical core) (Supporting Information Figure S3).

3.2 | Underlying drivers of the occurrence and intensity of tree mortality

The variance explained by BIN models ranged from 6% for *Acer pseudoplatanus* to 46% for *Pinus pinaster*, and the AUC ranged from .769 for *Quercus ilex* to .850 for *Acer pseudoplatanus* (Table 2). The variance explained by NB models ranged from 13% for *Castanea sativa* to 48% for *Fraxinus excelsior*, and the cross-validation scores ranged from .256 for *Quercus pyrenaica* to .735 for *Betula pendula*.

An increased probability of mortality (BIN models; Figure 2a) was commonly associated with increased intraspecific competition (BAj; nine species) but also with decreased total competition (BA; 10 species). We also found that the probability of mortality was positively associated with increases in precipitation (10 species), temperature (10 species) and relative drought conditions (decreased SPEI; seven species).

We found contrasting patterns in mortality intensity models (Figure 2b). The most intense mortality events were associated with high interspecific competition (BA.O; six species) and low intraspecific competition (BAj; eight species). Increases in mortality intensity were also related to high SPEI values (low drought relative conditions; six species) and low precipitation (seven species).

TABLE 2 Statistical evaluation of occurrence and intensity of mortality models for each species

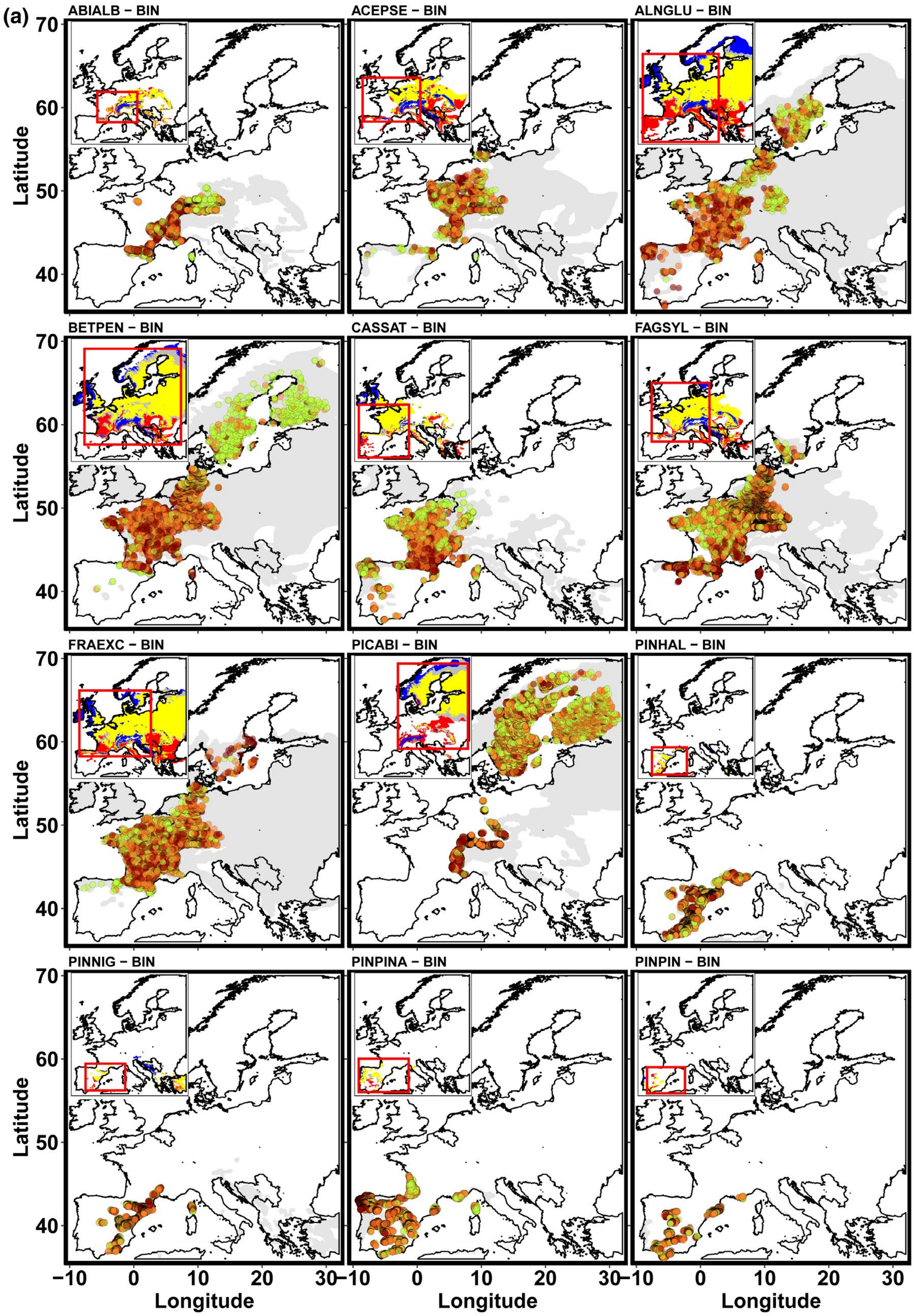
Species	Code	Model	Marginal R^2	Conditional R^2	PCVObs	AUC	CV
Abies alba Mill.	ABIALB	Occurrence	.13	.42	−1.98	.82	–
Acer pseudoplatanus L.	ACEPSE	Occurrence	.06	.20	−9.25	.85	–
Alnus glutinosa (L). Gaertn.	ALNGLU	Occurrence	.20	.26	−1.45	.81	–
Betula pendula Roth.	BETPEN	Occurrence	.09	.34	−5.55	.83	–
Castanea sativa Mill.	CASSAT	Occurrence	.21	.56	−1.18	.82	–
Fagus sylvatica L.	FAGSYL	Occurrence	.11	.12	−3.55	.82	–
Fraxinus excelsior L.	FRAEXC	Occurrence	.07	.38	−5.59	.84	–
Picea abies (L.) H. Karst.	PICABI	Occurrence	.15	.19	−1.68	.78	–
Pinus halepensis Mill.	PINHAL	Occurrence	.22	.22	−1.46	.80	–
Pinus nigra J.F. Arnold.	PINNIG	Occurrence	.19	.24	−1.74	.81	–
Pinus pinea L.	PINPIN	Occurrence	.24	.24	−1.20	.81	–
Pinus pinaster Aiton.	PINPINA	Occurrence	.46	.46	−.52	.85	–
Pinus sylvestris L.	PINSYL	Occurrence	.22	.26	−1.17	.80	–
Populus nigra L.	POPNIG	Occurrence	.19	.46	−1.39	.84	–
Populus tremula L.	POPTRE	Occurrence	.12	.24	−2.83	.82	–
Quercus ilex L.	QUEILE	Occurrence	.12	.37	−2.98	.77	–
Quercus petraea Liebl.	QUEPET	Occurrence	.13	.36	−2.63	.83	–
Quercus pyrenaica Willd.	QUEPYR	Occurrence	.17	.17	−2.04	.79	–
Quercus robur L.	QUEROB	Occurrence	.28	.52	−1.37	.83	–
Quercus suber L.	QUESUB	Occurrence	.15	.15	−1.20	.77	–
Abies alba Mill.	ABIALB	Intensity	.20	.50	.31	–	.58
Acer pseudoplatanus L.	ACEPSE	Intensity	.21	.92	.70	–	.51
Alnus glutinosa (L). Gaertn.	ALNGLU	Intensity	.39	.44	.40	–	.53
Betula pendula Roth.	BETPEN	Intensity	.42	.66	.53	–	.73
Castanea sativa Mill.	CASSAT	Intensity	.13	.78	.38	–	.57
Fagus sylvatica L.	FAGSYL	Intensity	.23	.46	.25	–	.37
Fraxinus excelsior L.	FRAEXC	Intensity	.46	.46	.52	–	.64
Picea abies (L.) H. Karst.	PICABI	Intensity	.22	.41	.33	–	.57
Pinus halepensis Mill.	PINHAL	Intensity	.26	.26	.33	–	.60
Pinus nigra J.F. Arnold.	PINNIG	Intensity	.20	.41	.32	–	.32
Pinus pinea L.	PINPIN	Intensity	.24	.34	.30	–	.56
Pinus pinaster Aiton.	PINPINA	Intensity	.29	.29	.38	–	.62
Pinus sylvestris L.	PINSYL	Intensity	.27	.51	.35	–	.57
Populus tremula L.	POPTRE	Intensity	.29	.29	.34	–	.59
Quercus ilex L.	QUEILE	Intensity	.26	.48	.35	–	.40
Quercus petraea Liebl.	QUEPET	Intensity	.29	.77	.40	–	.57
Quercus pyrenaica Willd.	QUEPYR	Intensity	.26	.26	.32	–	.26
Quercus robur L.	QUEROB	Intensity	.26	.38	.33	–	.61
Quercus suber L.	QUESUB	Intensity	.33	.33	.34	–	.73

AUC = area under the curve, measuring the capacity of generalization for mortality occurrence models; Code = acronym used for each species; CV = cross-validation score, measuring the capacity of generalization for intensity of mortality models; Model = model type (occurrence or intensity model); PCVObs = proportional change in variance between null model and fixed effect model (expressed as a percentage); Species = name of the species.

In addition, DBH was important in explaining both the occurrence and the intensity of mortality (positive association in 14 and 11 species, respectively). We found similar results for tree density (treenumber), because it was positively associated with increased mortality occurrence and intensity (14 and 10 species, respectively, for BIN and NB models). Average growth rate (meanBAIj) was also significant in both models (negative associations in 18 species for BIN models and in seven species for NB models). Finally, an increase in the number of years between surveys (years between survey) was associated with increased intensity of mortality but not with mortality occurrence (14 species, NB model; Supporting Information Table S8a,b; Figures S10–S13).

3.3 | Interacting drivers underlying the occurrence and intensity of tree mortality

Interactions between marginality and SPEI variables were the most frequent in BIN models (nine significant interactions at the trailing



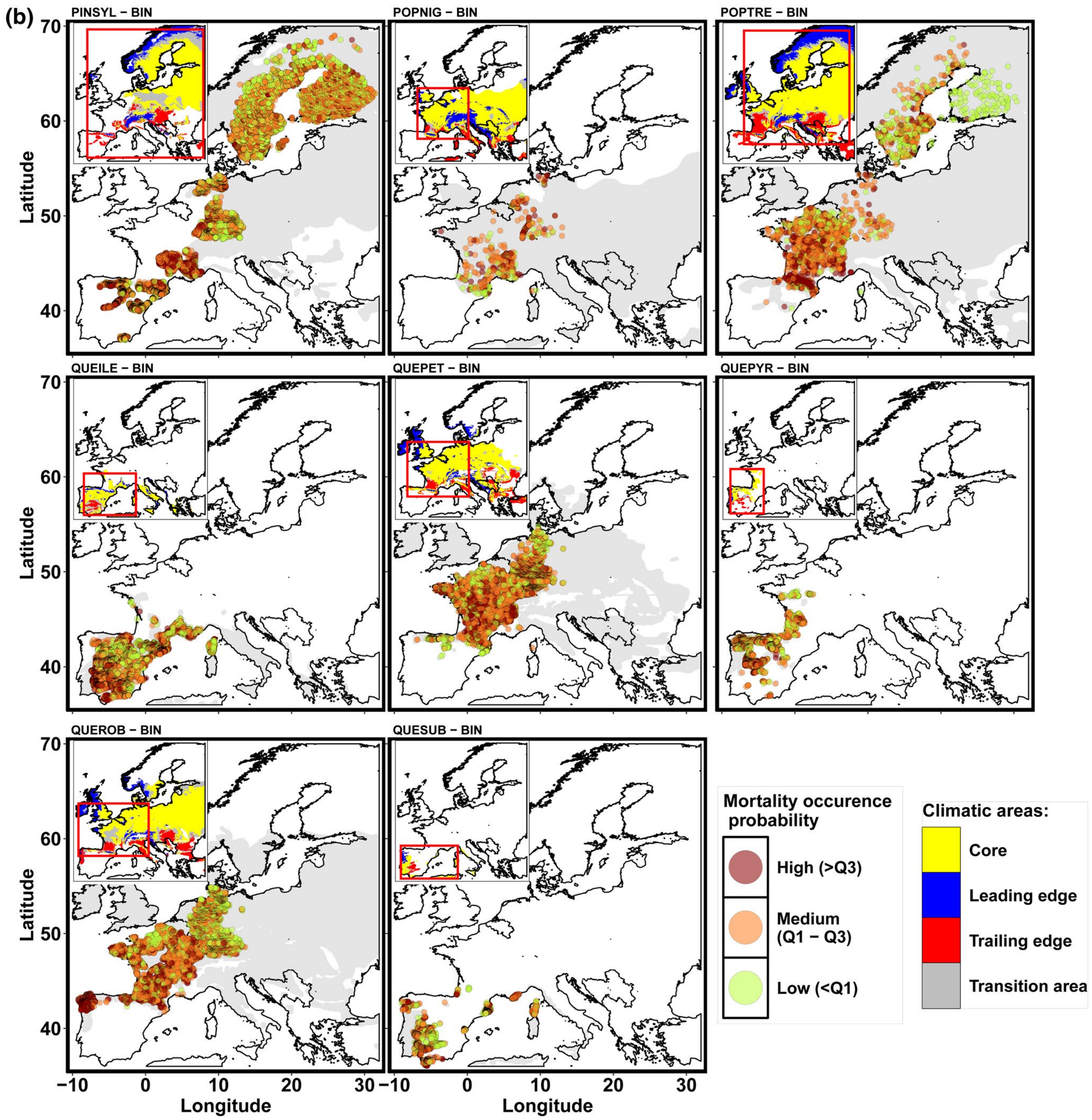


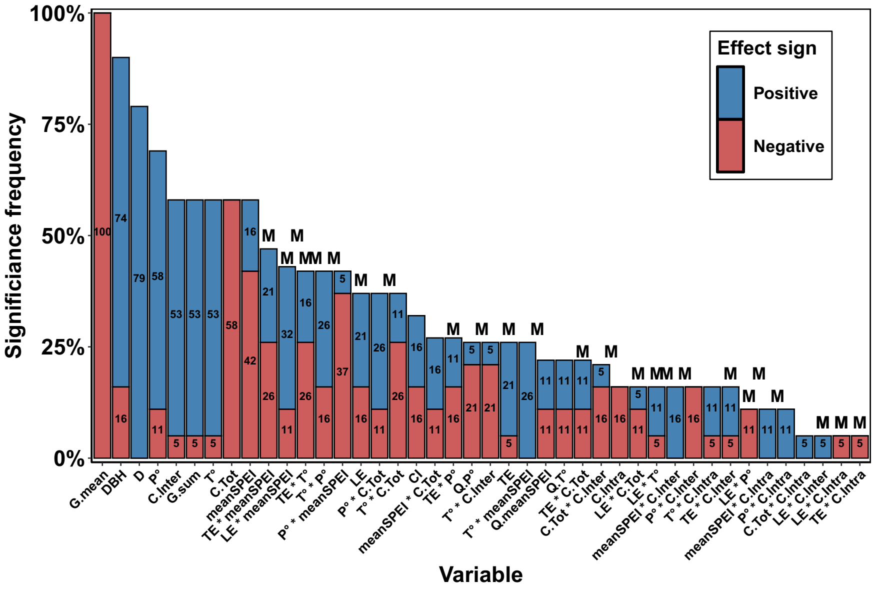
FIGURE 1 Predicted occurrence of mortality [binomial GLMM with a logit link (BIN) model] for each species organized in alphabetical order from (a) ABIALB to PINPIN and (b) PINSYL to QUESUB. Species codes are defined in Table 2. Green dots correspond to mortality prediction values lower than the first quartile (lowest values); orange dots represent values ranging from the first to the third quartile (medium values); and red dots represent values higher than the third quartile (highest values). Light grey areas display species distribution ranges. Climatic marginality maps are shown in the top left corner of each panel, with red squares showing the areas with National Forest Inventory (NFI) mortality records

edge and eight at the leading edge). Under increased relative drought (i.e., negative SPEI values), we found a higher probability of mortality occurrence (BIN models) in marginal areas than in core areas, particularly at the trailing edge (for both temperate and Mediterranean species: *Abies alba*, *Picea abies*, *Pinus sylvestris*, *Castanea sativa*, *Pinus pinea* and *Pinus nigra*; Figure 3a–f). However, we also found increased relative drought to be associated with a higher probability of mortality in the core areas than in marginal areas for some temperate (*Populus tremula*, *Quercus robur* and *Betula pendula*; Figure 3g–i) and Mediterranean species (*Pinus halepensis* and *Q. pyrenaica*; Figure 3j; Supporting Information Table S8c).

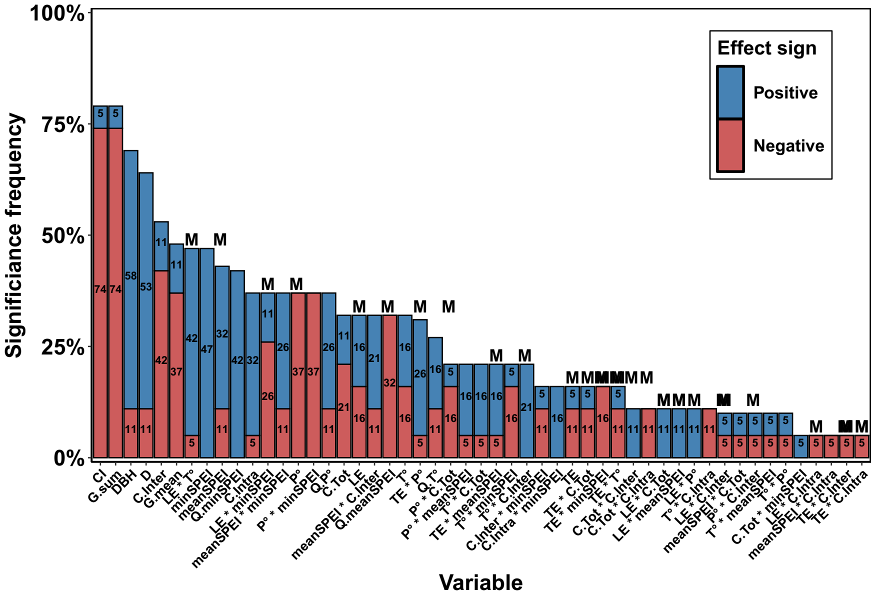
To a lesser extent, interactions between marginality and temperature or precipitation were often significant (eight significant interactions at the TE and three at the LE for temperature, and two at

FIGURE 2 Frequency of the different variables and their interactions explaining tree mortality in the 20 tree species studied. Red colours indicate negative effects, and blue colours indicate positive effects. The "M" indicates main effects and interactions involving climatic marginality. C.Inter = interspecific basal area of the plot; C.Intra = conspecific basal area of the plot; C.Tot = basal area of the plot; D = plot density (number of trees); DBH = plot mean diameter at breast height; G.mean = plot growth rate; G.sum = sum of plot growth rate; LE = leading edge; meanSPEI = mean relative drought index; minSPEI = minimum relative drought index; Q.P° = quadratic effect of precipitation related variable; Q.T° = quadratic effect of temperature-related variable; T° = temperature-related variable; P° = precipitation-related variable; TE = trailing edge. (a) Occurrence of mortality [binomial GLMM with a logit link (BIN) model]. (b) Intensity of mortality [negative binomial mixed-effect (NB) model] [Colour figure can be viewed at wileyonlinelibrary.com]

(a) Main effects and interaction importance across species (BIN)



(b) Main effects and interaction importance across species (NB)



the LE and five at the TE for precipitation). For instance, we found the highest probability of mortality at the climatic margins at low precipitation in *Fagus sylvatica* or when temperatures were high in *Pinus pinaster* and *Quercus suber* (Supporting Information Figure S14a–c).

Interactions between climatic marginality and temperature-related variables were the most frequent in NB models (three significant interactions at the TE and nine at the LE). We found more intense predicted mortality at the leading edge than in the core areas under increased temperatures in *A. alba*, *Fraxinus excelsior*, *Pinus halepensis*, *Pinus nigra*, *Pinus pinea*, *Q. ilex*, *Q. petraea* and *Q. robur* (Figure 4a–f; Supporting Information Table S8d). Moreover, the intensity of mortality was higher in the trailing edge than in the core in some species, associated with various variables, such as competition (three species), increase in relative drought (four species) or lower precipitation (six species); for example, *B. pendula*, *Fagus sylvatica* or *Picea abies* (Supporting Information Figure S15a–c).

For other significant interactions, see the Supporting Information [Figure S16 (BIN models) and S17 (NB models)].

3.4 | Spatial patterns of occurrence and intensity of mortality across tree species ranges

The predicted probability of the occurrence of mortality (BIN models) was the highest in the trailing edge part of the range for eight temperate (*Alnus glutinosa*, *B. pendula*, *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Fagus sylvatica*, *Q. robur* and *Q. petraea*) and three

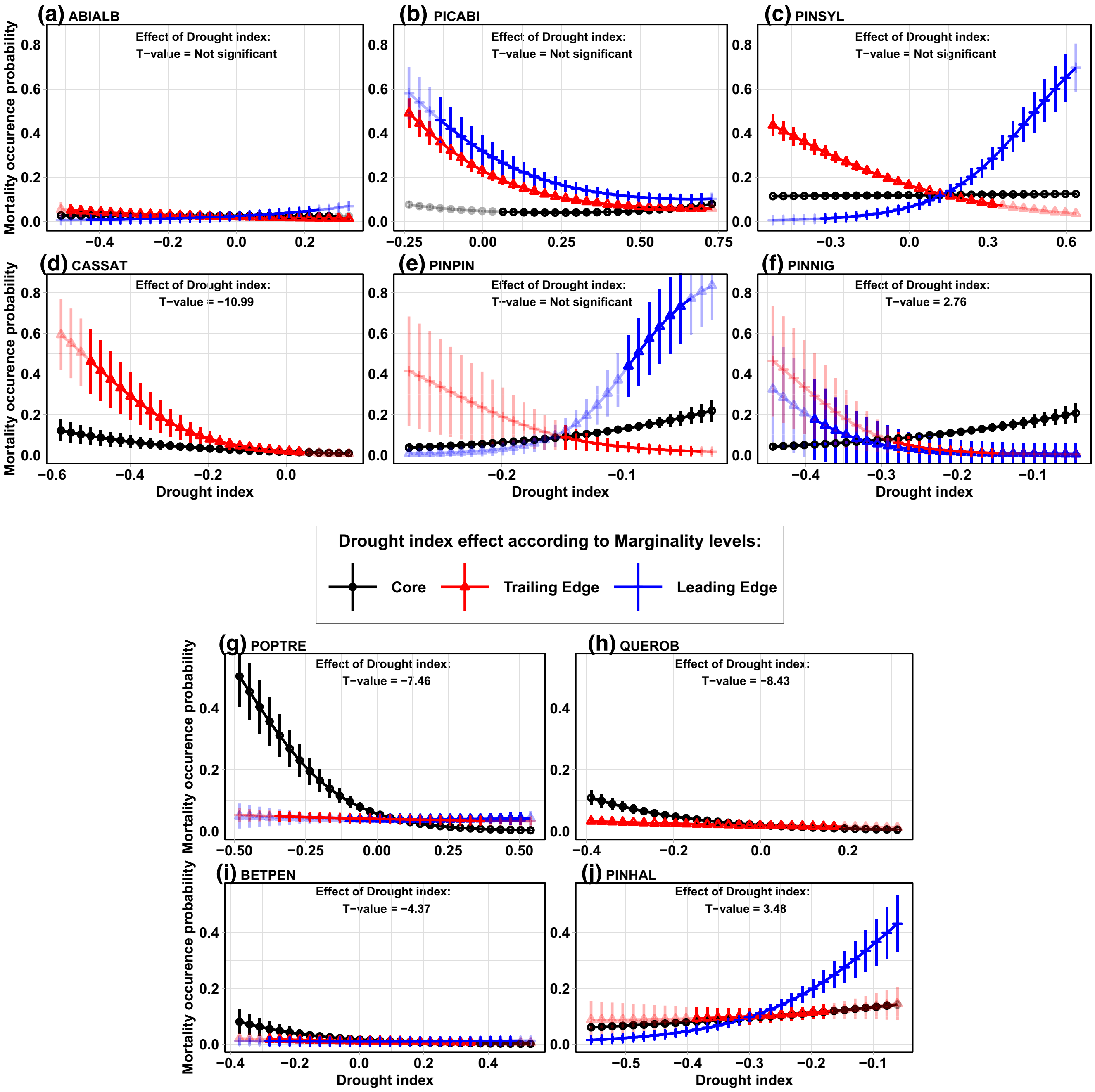


FIGURE 3 Effect of the interaction between drought [mean standardized precipitation evapotranspiration index (SPEI) index] and marginality on predicted occurrence of mortality per plot (expressed as a probability) across the core (black lines), trailing edge (red lines) and leading edge (blue lines) of the following 10 species: (a) *Abies alba*, (b) *Picea abies*, (c) *Pinus sylvestris*, (d) *Castanea sativa*, (e) *Pinus pinea*, (f) *Pinus nigra*, (g) *Populus tremula*, (h) *Quercus robur*, (i) *Betula pendula* and (j) *Pinus halepensis*. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colours, and extrapolations outside the environmental gradients covered by the species are shown in pale colours. In the case of *Castanea sativa*, our data did not cover the leading edge of the species. T-values of the main effects interacting with marginality are reported [Colour figure can be viewed at wileyonlinelibrary.com]

Mediterranean species (*Q. ilex*, *Q. pyrenaica* and *Castanea sativa*). None of the species had a higher probability of occurrence of mortality in the core than in the margins, and two temperate species (*Picea abies* and *Pinus sylvestris*) had a lower probability of occurrence of mortality in the core than expected under the assumption of uniformity across the species range. Four temperate species (*Alnus glutinosa*, *Pinus sylvestris*, *Pinus nigra* and *Q. robur*) and four Mediterranean species (*Castanea sativa*, *Pinus nigra*, *Pinus pinea* and *Q. ilex*) had a lower probability of occurrence of mortality in the LE part of their range than in the core (Figure 1; Supporting Information Figure S9a).

We did not find any spatial patterns in the intensity of mortality (NB models) in temperate species. However, the highest predicted intensity of mortality was at the LE part of the species range for

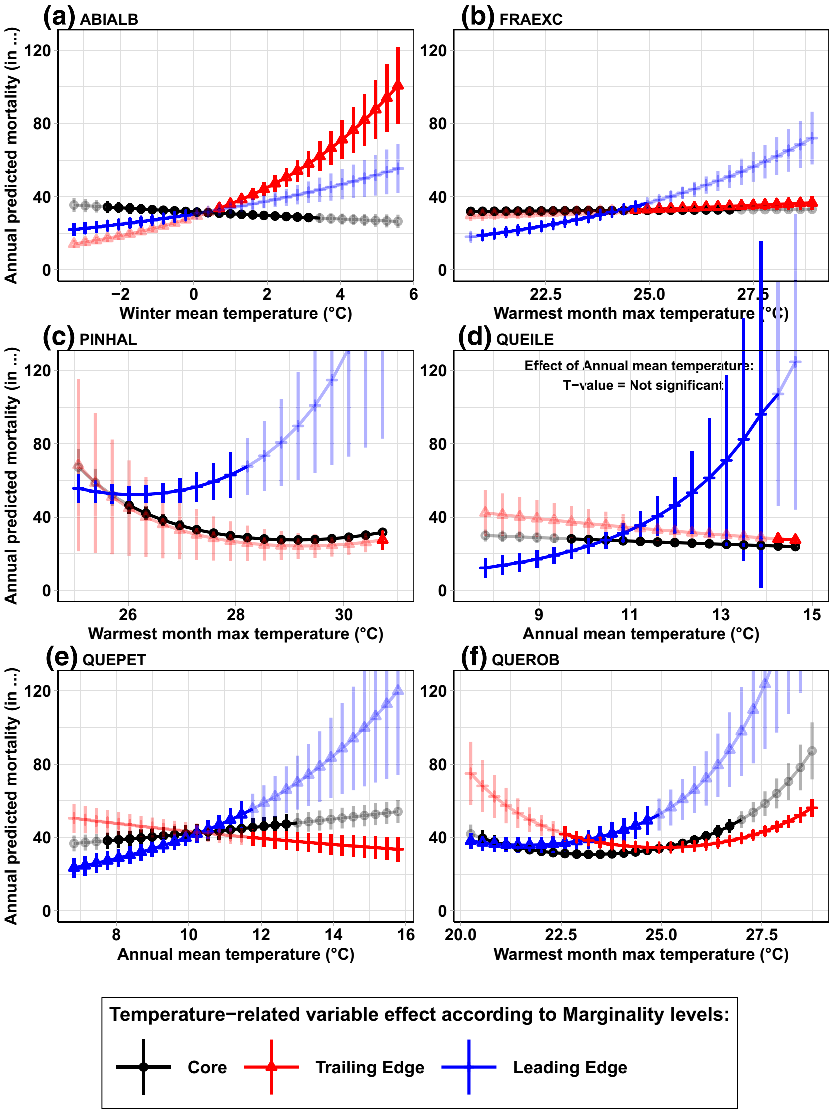


FIGURE 4 Effect of the interaction between temperature-related variables and marginality on the predicted intensity of mortality across the core (black lines), trailing edge (red lines) and leading edge (blue lines) of the following six temperate species: (a) *Abies alba*, (b) *Fraxinus excelsior*, (c) *Pinus halepensis*, (d) *Quercus ilex*, (e) *Quercus petraea* and (f) *Quercus robur*. Values are expressed as the proportion (‰), by year and by plot. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colours, and extrapolations outside the environmental gradients covered by the species are shown in pale colours. T-values of the main effects interacting with marginality are reported [Colour figure can be viewed at wileyonlinelibrary.com]

six Mediterranean species (*Pinus halepensis*, *Pinus nigra*, *Pinus pinaster*, *Pinus pinea*, *Q. pyreneica* and *Q. suber*; Supporting Information Figures S8 and S9b).

4 | DISCUSSION

4.1 | Stand variables drive the occurrence and intensity of tree mortality

Despite large variations in mortality rates between species, we found that the occurrence of mortality was higher in slow-growing than in fast-growing trees. These results are consistent with previous work on the occurrence of mortality (Stephenson et al., 2011) and support the results of Das et al. (2016), highlighting that biotic-induced background mortality decreases with growth rate (meanBAIj). These results are, therefore, likely to reflect growth-dependent background mortality.

The occurrence of mortality was higher in large trees than in small trees, as reported by Das et al. (2016). However, this positive association of the occurrence of mortality with mean d.b.h. is inconsistent with previous work, which has usually reported a negative association of d.b.h. with mortality (Neumann et al., 2017; van Mantgem et al., 2009). This might be explained by the high threshold we used to include trees in the analyses (10 cm d.b.h.), resulting in absence of the juvenile peak of mortality (Dietze & Moorcroft, 2011; Ruiz-Benito et al., 2013). Hence, our largest d.b.h. trees reflect the plots approaching maturity (Condés & del Río, 2015) and correspond to the right side of the typical U-shaped relationship described with lower d.b.h. thresholds than ours, that is, 4 and 7 cm in the study by Hülsmann et al. (2017). This is supported further by previous work reporting increased mortality with plot age in several species in boreal forests (Luo & Chen, 2011).

Interestingly, we found the occurrence of mortality to be higher in plots with more conspecific neighbours, which is consistent with the work of Luo and Chen (2011), who inferred a strong intraspecific competition for light. In contrast, the negative relationship between the occurrence of mortality and both total and interspecific competition indicates facilitative processes that change along latitudinal gradients, most likely to be the result of access to light or resources or niche complementarity between species. We observed this in *Fagus sylvatica*, suggesting facilitative mechanisms such as those already observed in dry conditions, where *Fagus* individuals benefit from the presence of *Pinus sylvestris* (Condés & del Río, 2015), and from *Pinus sylvestris*, *Quercus pyrenaica* and *Castanea sativa*, but they can turn into competition processes when released from drought conditions (Archambeau et al., 2020). The change from facilitation to a competitive process across species ranges is thus driven mainly by environmental conditions and can modulate tree relationships in mixed forests (Pretzsch et al., 2013). Therefore, other environmental drivers might also induce facilitation processes along latitudinal gradients; for instance, the impact of herbivory or pathogenic agents (HilleRisLambers et al., 2013) could be mitigated by the presence of other species in comparison to monospecific stands (Jactel et al., 2017).

The intensity of mortality was independent of the growth rate in most (13) species, although for the seven remaining species it was higher in slow-growing trees than in fast-growing trees. This growth–mortality independence suggests that, in most species, plots containing trees growing at all rates are equally likely to experience large mortality events, which could reflect die-off events (Ozolincius et al., 2005). For the other seven species, the large dependence between growth and the intensity of mortality could be driven by competition or other biotic factors (Das et al., 2016). Hence, this intensity of mortality could reflect either growth-independent dieback events or growth-dependent mortality.

Overall, our results confirm the major importance of stand variables in driving both components of mortality (Dietze & Moorcroft, 2011; Lutz & Halpern, 2006) and, therefore, the potential beneficial effect of management practices such as basal area reduction to mitigate high mortality rates (Bradford & Bell, 2017).

4.2 | Inconsistent effect of climatic drivers across species

Our results are in agreement with previous studies showing that climatic factors (high temperature, high rainfall or drought conditions) can exacerbate the probability of the occurrence of mortality, in addition to competition and stand variables (Condés & del Río, 2015; Luo & Chen, 2013; Ruiz-Benito et al., 2013). However, we found unexpected relationships between climate and the intensity of mortality. For instance, both drought and precipitation had a negative effect on the intensity of mortality. This is surprising because it is expected that intense events of mortality will be found in dry areas (Young et al., 2017). These patterns could be attributable to a lower sensitivity to our long-term averaged precipitation than seasonal fluctuations (Neumann et al., 2017), which we did not take into account. Moreover, an absence of effects of drought on mortality have been reported at high elevations (Etzold et al., 2019; Ruiz-Benito et al., 2013), where mortality is impacted more by frost damage and winter desiccation (Barbeito et al., 2012).

We also found that the importance of temperature depended on the identity of the species, which could be explained by the many confounding effects associated with temperature. For instance, high temperatures are often associated with insect damage, which could lead to increased mortality (Anderegg et al., 2015; Wood et al., 2018). Likewise, low temperatures are associated with low management intensity in mountainous areas, where higher mortality rates are expected in comparison to managed forests (Bravo-Oviedo et al., 2006). Nonetheless, the intensity of mortality was correlated more strongly with increasing temperatures, especially in leading-edge populations, which could be related to high pest survival owing to warm winters in these areas (Kliejunas et al., 2009). An increase in background mortality associated with warmer temperatures has been found at the northern margin of species ranges (Neumann et al., 2017; Ruiz-Benito et al., 2013), but not in the intensity of mortality, as we have shown here.

4.3 | Interactions between drought and climatic marginality

Our results suggest that trailing-edge populations are the most likely to experience mortality with increasing drought, but occasionally, drought was more detrimental for core populations. An explanation for this is that marginal populations of some species could be better adapted to harsh climatic conditions, such as drought (Rehm et al., 2015; Vizcaíno-Palomar et al., 2019), although maladaptation of marginal populations is more common (Fréjaville et al., 2020).

However, drought had a small impact on the intensity of mortality, which could be explained by the mismatch between rapid fluctuations in drought-related stress and the slow mortality responses of trees, resulting in an important time lag (Jump et al., 2017).

4.4 | Placing tree mortality on large geographical gradients

We found that the occurrence of mortality was the highest in the trailing edge of temperate species and the lowest in the leading edge for half of the Mediterranean species. This suggests that the Mediterranean–temperate ecotone could be a hotspot of changes in forest composition, as previously suggested (Ruiz-Benito, Ratcliffe, Zavala et al., 2017). Overall, our results suggest that the southern parts of the species ranges can be shaped by drought-induced mortality (Benito-Garzón et al., 2013; Benito Garzón et al., 2018; Kunstler et al., 2016). Conversely, the most intense events of mortality in temperate species were distributed evenly across the studied countries, as expected for die-off events (Allen et al., 2010, 2015; Jump et al., 2017).

4.5 | Limitations and perspectives

Tree mortality can be affected by other factors, such as wind disturbance, snow damage, pest emergence, fires or pathogens, which we did not include in our study. For instance, *Fraxinus excelsior* mortality has been related directly to the pathogen *Chalara fraxinea* (Kowalski, 2006), and *Acer pseudoplatanus* is threatened by several pathogens spreading rapidly in Europe [e.g., *Eutypella parasitica* and *Cryptostroma corticale* (Kelnarová et al., 2017; Ogris et al., 2006)]. The relatively low variance explained by our models for some species (*Acer pseudoplatanus*, *Fraxinus excelsior*, *B. pendula*, *Castanea sativa* and *Pinus nigra*) could be related directly to these missing factors.

Although recently managed forests have been removed from our analysis, the removal of weak and senescent trees by forest managers in anticipation of natural mortality could alter our results (Csilléry et al., 2013). Likewise, the temporally restricted and uneven duration of the data in some countries is a limitation, because the data might not account for recent impacts of climate change on forests, resulting in an underestimation of mortality in some areas (Clark et al., 2011). In addition, the lack of data from southern countries, other than Spain, might have skewed our climatic areas toward northern climates, and our definition of climatic marginality (constrained to a 1 km grid) leaves out the influence of microclimate (Hampe & Jump, 2011), which could result in an underestimation of the marginality effect. However, our patterns are likely to be maintained across wide regions despite these methodological issues, because heterogeneity in sampling strategies (various countries, various years) had little effect on variation in mortality (Supporting Information Figures S12 and S13).

Further studies should look at more recent data from NFIs and investigate whether drivers of mortality are changing over time, especially in the last decades, because temperatures, drought frequency and drought intensity are increasing (Astigarraga et al., 2020; Trenberth et al., 2014). Further investigation could also focus on whether drivers of mortality differ between deciduous and evergreen trees, as reported in other regions (Clark et al., 2011), or between shade-tolerant and shade-intolerant species (Luo & Chen, 2011). Finally, it remains an open question whether other demographic traits, such as growth, reproduction and regeneration, could also decrease at the trailing edge of European tree populations and to what extent this is related to drought.

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DATA AVAILABILITY STATEMENT

The French, German and Spanish inventories are available for download through each NFI website (Spanish National Forest Inventory: https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2_descargas.aspx and https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx; French National Forest Inventory: https://inventaire-forestier.ign.fr/spip.php?article532; and German National Forest Inventory: https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/). The Swedish and Finnish data are available from the Dryad Digital Repository at: https://doi.org/10.5061/dryad.wm37pvmkw (Ratcliffe et al., 2020). All the R script codes used in this manuscript are available at: https://github.com/ChangenetAlex/Fundiv.project

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BIOSKETCH

The authors' research is focused on forest ecology and global change. The authors use modelling and experimental approaches to understand complex processes in ecology at large geographical scales.

SUPPORTING INFORMATION

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

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CHAPTER 4

RECRUITMENT IN EUROPEAN FORESTS IS MORE LIMITED BY COMPETITION THAN DROUGHT

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Abstract

Forest distribution and composition are expected to change in composition as a response to climate change, with strong impacts on ecosystem dynamics and biodiversity. To predict the impact of on forest dynamics, tree mortality and growth have been extensively studied. In contrast, recruitment has largely been neglected in part due to data availability and its stochastic and multi-step nature. Hence, the main factors driving recruitment across a species distribution range are poorly understood. The center-periphery hypothesis (CPH) predicts that recruitment in marginal populations is lower than in core populations, while the competition environment gradient hypothesis (CEGH) states that range limits are shaped by competition in favorable conditions and by environment in harsh conditions. Following the CPH and the CEGH, we expect recruitment to be higher in the core than in the climatically marginal populations, and competition to be the most important driver in the core and drought to be the most important driver at the leading and trailing edges. Here, we analyze recruitment occurrence and abundance of 18 major forest tree species from more than 1.5 million trees recorded from National Forest Inventories from Spain, Germany, Belgium, Sweden and Finland. We developed zero-inflated models to tease apart recruitment occurrence and abundance at the plot scale, assess their spatial variation and determine how environment and competition shape recruitment patterns. Our results show that for most species, recruitment occurrence and count did not differ between the core and the climatic margins. In most species, both recruitment occurrence and count were mostly driven by competition. Drought was not an important driver of recruitment alone, but strongly interacts with inter- and intra-specific competition. Synthesis: the strong interactions between biotic and environmental conditions makes it difficult to test the CPH and the CEGH . Future work should assess trees' demographic traits by accounting for these interactions as well as populations positions within the range.

4.1 Introduction

Forests are key ecosystems for both terrestrial biodiversity and global carbon cycling (Bonan, 2010; Harris et al., 2021). However, climate change is threatening forests composition and tree species distributions, with concomitant impacts on biodiversity, ecosystem functioning and dynamics (McDowell, 2008; Lindner et al., 2014) . Climate change is altering the major demographic processes structuring forests, with different effects on tree mortality, growth and recruitment across time and space (Lloret et al., 2012). In the last decades, tree mortality has increased in all forested biomes globally, often related to climate change (Allen et al., 2015; Van Mantgem et al., 2009). Tree mortality can be particularly strong/intense towards the climatic trailing edge of the species ranges (Changenet et al., 2021), with further studies suggesting that climate change and tree mortality can lead to changes in forest composition (Ruiz-Benito et al., 2017) and carbon storage (Astigarraga et al., 2020). Similarly, evidence for widespread increase in tree growth, forest productivity and standing stock accumulation are growing as a response to rising temperatures and extended growing seasons when water is not limiting (Boisvenue et al., 2006; McMahon et al., 2010; Pretzsch et al., 2014). However, the beneficial effect of climate change can be both species- and site-specific (Pasho et al., 2011) and numerous studies point out the negative effects of climate change on growth at local scales (Lindner et al., 2014) and in water-limited forests (Ruiz-Benito et al., 2014).

Recruitment is a major component of forest dynamics (Stephenson et al., 2005) upon which future forest composition (Clark et al., 1999) and the entire ecosystem rely (GRUBB, 1977), but the information available at large spatial scales and the main patterns are much less known than for tree mortality or growth (see e.g. Lines et al. (2020)). Recruitment is the outcome of seed production, dispersion, seedling emergence, survival, growth and establishment (Castro et al., 2004; Merges et al., 2020). It reflects the new individuals added to the population, defined as the number or volume of trees that reach the smallest measured size class of a forest stand over a certain period (Lexerød et al., 2005; Zhang et al., 2012). The number of individuals recruited depend on the outcomes of biotic interactions such as density dependence (Fortin et al., 2007; Ibáñez et al., 2007; Xiang et al., 2016; Yang et al., 2015), intraspecific competition (Jevon et al., 2020) or grazing pressure (Boulant et al., 2008; Gehrig-Fasel et al., 2007). The species dominating the canopy (Granda et al., 2014) and functional dissimilarity in foliar traits (Muledi et al., 2020) also modulates seedling survival and therefore recruitment through change in light quality or reduction of water stress during drought.

Recruitment rates strongly rely on the environment and its interaction with biotic interactions (Schupp et al., 1995). For instance, decreased recruitment can result from a lack of forest management (Plieninger et al., 2010) and drought (Castro et al., 2004; Mendoza et al., 2009) while warm spring temperature (Camarero et al., 2007; Ibáñez et al., 2007) and increased annual precipitation (Klopcic et al., 2012; Matías et al., 2012) can lead to increased recruitment.

Species abundance and demographic performance largely depend on latitudinal and altitudinal gradients, due to variation in climate and ecological conditions (Purves, 2009; Sexton et al., 2009; Vilà-Cabrera et al., 2019), where the contribution of tree recruitment is a critical component but less understood than other demographic processes (Angert et al., 2011; Sexton et al., 2009). Along the latitudinal gradient, seedling establishment of broadleaved species is more sensitive to drought at the trailing edge than the core of its distribution (Castro et al., 2004). Along altitude, recruitment underlines range-shifts of the treeline. In the Scandes mountains and the Swiss Alps upward shifts of the treeline were related to an increase in recruitment and climate warming (Gehrig-Fasel et al., 2007; Hofgaard et al., 2009; Vitasse et al., 2012). Conversely, climate warming limits tree recruitment at the alpine treeline in Norway spruce, suggesting a possible range contraction (Kueppers et al., 2017). These altitudinal range-shift may imply changes in species composition, as in the Pyrenees, where oak species progressively replace beech trees (Peñuelas et al., 2007) and Scot pine (Galiano et al., 2010; Vilà-Cabrera et al., 2013) and the lack of recruitment induced vegetation shift from Scots pine to pubescent oak at the lowest altitude of the Valais, Switzerland (Rigling et al., 2013). Besides, climate change has generally boosted tree species ranges at the range margins through altitudinal shifts (Lenoir et al., 2008), for instance in the temperate *Quercus petraea* and the sub-Mediterranean *Q. faginea* (Urli et al., 2014). Latitudinal shifts at the range margins are also reported both in boreal forests (Chapin et al., 2004) and temperate forests. For instance, Holm oak progressively shifts northward of its northern distribution margin along the Atlantic coast at the expense of other tree species (Delzon et al., 2013).

The center periphery hypothesis (CPH) states that populations at the backward-moving front (i.e. trailing edge) and at the forward-moving front (i.e. leading edge) of the species distribution should exhibit weaker demographic performance than those in the core. However, little support for the hypothesis has been found in the literature, mainly because geographic periphery and ecological marginality are not always concordant (Pironon et al. (2017), but see Purves (2009) and Vanderwel et al. (2013)). The competition-environmental gradient hypothesis (CEGH) states that populations inhabiting favorable environmental conditions are more constrained by biotic factors, such as competition, than populations living in less favorable conditions (i.e. ecological marginality, Ettinger et al. (2017)). In fact, biotic interactions can lead to competition reducing species ranges (Ettinger et al., 2017; Kunstler et al., 2020), or facilitation, expanding hence species ranges (Batllori et al., 2009).

However, a clear understanding of the role of biotic and abiotic gradients in influencing recruitment is lacking (Bulleri et al., 2016; Alexander et al., 2016). Understanding how these biotic and abiotic gradients interact and drive recruitment along the species range is therefore of crucial importance.

As recruitment may or may not occur during any time period, its variability is usually very large. Therefore, it is needed to use a two-step model to estimate recruitment occurrence probability first, and the amount of recruitment afterwards. Here, we developed Zero inflated models to analyze the occurrence and amount of recruitment of 19 major forest tree species from more than 1.5 million trees recorded in the National Forest Inventories from Spain, Germany, Belgium (Wallonia), Sweden and Finland.
We aimed to better understand if recruitment patterns along large environmental gradients were better explained by CPH or CEGH. For this aim, we address the following questions and hypotheses i) What are the spatial patterns of recruitment occurrence and abundance at the core, trailing edge and leading edge of species range? We expect more recruitment at the core than at the edges of the range (CPH) with extensive zones of poor recruitment at the southern part of the species ranges, following mortality patterns (Changenet et al., 2021); ii) What are the main drivers of tree recruitment and what are the interactive effects (if any) of competition and drought with climatic marginality on tree recruitment? We expect interspecific and intraspecific competition to be the most important drivers of recruitment in the ecological core while drought to be more important in ecologically marginal populations (CEGH, Ettinger et al. (2017)); iii) Can we identify the interactive effects (if any) of competition and drought with plot characteristics? We hypothesize that competition effects depend on drought and plot characteristics.

4.2 Material and methods

4.2.1 National Forest Inventories

We estimated recruitment from National Forest Inventories (NFIs) from five countries (Spain, Germany, Finland, Sweden, Belgium Wallonia) harmonised in FunDivEUROPE and available for download through each NFI website (see Data Accessibility statement; Baeten et al. (2013) and Ratcliffe et al. (2020). These countries have permanent plots sampled several years apart, ranging from 1981 to 2011 (Supplementary table S1). Data from the five NFIs cover a latitudinal gradient from 36° N (Spain) to 70.05° N (Finland).

4.2.2 Plot-level tree recruitment recorded from NFI

We calculated species recruitment per plot as the number of trees that appeared in the second inventory but were not present in the first one, exceeding the DBH size threshold (100mm). The recruitment count was then extrapolated from plot to hectare level using a weighted index provided by each NFI that reflected the size of the plot or the density of the grid or both depending on the country (Supplementary table S1 and `http://project.fundiveurope.eu/`). We calculated individual tree recruitment data for 18 species, gathering a total of 1,128,416 trees (and 78,745 plots (Supplementary table S2)) varying from 100 mm to 1,686 mm diameter at breast height (DBH) and with census intervals (CI) ranging from 2 (29 plots) to 20 years (46 plots; Supplementary table S3 for CI and DBH according to the country).

4.2.3 Model drivers

Indices of climatic marginality and drought

To characterize the climatic marginality of the species distribution area, we classified NFIs plots in three categories using the climatic information corresponding to their distribution range (Caudullo et al., 2017): climatic core (C), climatic leading or climatic trailing edge (LE and TE; see Supplementary Table S2 for the number of plots that belongs in each categories; Changenet et al. (2021)). Specifically, we used 21 climatic variables (EuMedClim; Fréjaville et al. (2018); Supplementary Table S4) averaged over the 2000-2014 period at each plot in a 1 x 1 km pixel size grid. Firstly, we classified the climatic core (C) from the climatic margins (LE + TE, hereafter = M) using a Weighted Principal Component Analysis. Secondly, we used a Discriminant Principal Component Analysis (DPCA) to separate M plots into LE and TE plots, depending on the different climates that they reflected.

We used a relative drought index, the Standardized Precipitation Evapotranspiration Index (SPEI v.2.5 (2017) (`http://hdl.handle.net/10261/104742`), where negative values reflect drier conditions in a specified time relative to a reference period (Vicente-Serrano et al., 2010). We used 1901–2015 as a reference period and a 12-month time-scale. Then, we calculated the annual mean values over the time interval between inventory campaigns and extracted the average value (Hereafter SPEI variables; Supplementary Table S4).

Plot variables

Mean basal area increment was calculated as the difference in basal area between two survey periods for all NFIs (G, cm2 ha yr-1); plot mortality rate was calculated as the percentage of trees that died between the first and second surveys divided by the number of years between the surveys (M, trees. ha-1.yr-1); mean diameter at breast height (DBH, cm); tree density was calculated as the number of trees of all species in the plot (D, No. trees ha-1); conspecific and heterospecific plot basal area (INTRA and INTER, respectively, cm2 ha-1). DBH, G and D are proxies of stand density and maturity (Muledi et al., 2020; Yang et al., 2015). INTRA and INTER plot basal area are proxies of intra-specific and inter-specific competition (Kunstler et al., 2016). See Supplementary Table S5.

4.2.4 Statistical analyses

Statistical models of tree recruitment

We used a species-specific zero-inflated negative binomial model (ZINB) because it handles the excess of zero and the over-dispersion of the recruitment process. ZINB is a two-part conditional model, where the occurrence of recruitment p (zero inflated part) and the number of events conditioned by the occurrence mu (conditional part) are considered as two different processes in a single model. Both parts can contain zeros, reflecting the fact that even if conditions are favorable for recruitment, it may not occur in a given plot (Fortin et al., 2007; Li et al., 2011; Zell et al., 2019; Zhang et al., 2012). All analyses were performed using the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2021).

The zero inflated part of the model describes the probability of observing a zero count:

$$P(y_i = 0) = p_i + (1 - p_i) \times (\frac{k}{\mu_i + k})^k$$

and relates p_i (the probability of observing no recruitment) to the covariates following a binomial distribution with $logit(p_i) = \eta_{1i}$. The conditional part of the model describes the differences in the occurrence of the number of recruited trees conditional on the probability of a non-zero observation:

$$P(y_i | y_i > 0) = (1 - p_i) \times (\frac{\Gamma(y_i + k)}{\Gamma(k) \times \Gamma(y_i + 1)}) \times (\frac{k}{\mu_i + k})^k \times (1 - \frac{k}{\mu_i + k})_i^k$$

relates μ_i (the average count of recruitment) to covariates following a Negative binomial distribution with $log(\mu_i) = \eta_{2i}$. The total number of recruited trees in a plot is therefore given by the product of both parts of the model: $Y_i = (1 - pi) \times \mu_i$.

Model structure

We included the same variables in both parts of the model and functions η_1 and η_2:

$$\eta_k = \alpha_0 k + \sum_{h=1}^{8} \beta_{hk} x_{h.i} + \sum_{n=1}^{11} \gamma_{nk} x_{h.i} z_{h.i} + \alpha_{\text{country}.k} + log(CI_i) + log(Weight_i)$$

With $\alpha_0 k$, an intercept term, $\alpha_{\text{country}.k}$, a random effect that accounts for sampling

differences between each NFI (this effect was not included for species only present in a single country, i.e.: *Pinus pinaster*, *Pinus nigra*, *Pinus halepensis*, *Pinus pinea*, *Quercus suber*, *Quercus pyreneica*, *Quercus ilex*); β_{hk} the fixed effect coefficients for the h^{th} of 8 predictors x_{hi} (including CM, INTRA, INTER, DBH, D, G, M and SPEI; see Supplementary Tables S4-S5 for the variable description, Supplementary Table S6 for summary statistics and VIF in Supplementary Table S7; Dormann et al. (2013)) and γ_{nk} the regression coefficient of the n^{th} of the 11 interactions between predictors x_{hi} and z_{hi}. We focused on the interactions: i) between drought and competition with climatic marginality as we expect interspecific and intraspecific competition to be the most important drivers of recruitment in the ecological core while drought to be more important in ecologically marginal populations (this is our second hypothesis); ii) between mortality and climatic marginality because mortality is a strong driver of recruitment; iii) between SPEI and Competition because these biotic and abiotic factors interact together impacting forest demography (Clark et al., 2014), with important implications in driving species range-shift (Lett et al., 2018; Tomiolo et al., 2018); iv) INTRAxG and INTERxDBH, which corresponds to our third hypothesis because the outcome of these interactions can also change across life stages and size of the individuals (Andivia et al., 2018; Tredennick et al., 2018). Hence, we included the following interactions: CM*SPEI; CM*INTRA; CM*INTER; CM*G; CM*M; INTRA*SPEI; INTRA*DBH; INTRA*G; INTER*SPEI INTER*DBH and INTER*G.
Due to the limited data in marginal areas, the CM*M interaction was removed from the equations for the following species: *Betula pendula*, *Fraxinus excelsior*, *Quercus petraea*, *Pinus nigra*. To avoid the potential bias caused by the different NFI survey years and plot sizes (Supplementary Table S1), we used an offset on census time (CI) and variable plot size, respectively $log(CI_i)$ and $log(Weight_i)$. We therefore assumed a proportional increase of recruitment along elapsed time and plot size (Li et al., 2011; Vanclay, 1992).

Model performance and validation

We calculated the goodness-of-fit with a chi-square test between observed and fitted values (Zhang et al., 2012). We then assessed the variance explained by the models with both the marginal and conditional r-squared, Pearson squared correlation and the normalized square root of the residuals variance (RMSE) using R 3.6.3 (R Core Team, 2021) and the package Performance (Lüdecke et al. (2020); Table 4.1).
In addition, we plotted the observed versus predicted distribution (Supplementary Figure S1) and the Pearson residuals against fitted values to visually inspect the residuals (Supplementary Figure S2). Finally, we used the DHARMa package (Hartig et al., 2017) to test for dispersion, uniformity and the presence of outliers on 3000 sets of simulated residuals for each model (Supplementary Figure S3-S5 and Supplementary Table S8).

4.3 Results

4.3.1 Model performance and validation

We found no significant deviation between observed and fitted distribution of recruitment (p-value > 0.05, chi-square tests, Table 1 and Figure S1).The marginal r-squared in tree recruitment models ranged from 17% (*Fagus sylvatica*) to 69% for (*Pinus sylvestris*) and the Pearson correlation test between observed and predicted values ranged from 0.78 (*Quercus suber*) to 0.95 for (*Acer pseudoplatanus*) (Table 1). Finally, the unexplained variance (RMSE) ranged from 5% (*Quercus suber*, *Quercus pyrenaica*) to 2% (*Quercus robur*, *Quercus petraea*, *Picea abies*, *Betula pendula* and *Acer pseudoplatanus*; Table 4.1). None of the simulated residuals presented zero-inflated distribution when compared to the fitted residuals (Zero inflation tests, Supplementary Table S8). Seven species displayed significantly over-dispersed simulated residuals compared to fitted residuals (p-value < 0.05). Nevertheless, the associated dispersion ratio values were relatively low (ranging from 1.08 to 1.41), indicating that significance is likely induced by the large number of simulations (3000). Similarly, simulated residuals showed significant deviation from fitted residuals in all 18 species (p-value < 0.05, KS test for uniformity, Supplementary Table S8).

4.3.2 Spatial patterns of tree recruitment

In 9 of the 18 species, neither of the recruitment components (μ and p, i.e. recruitment abundance and occurrence) was lower at the climatic margins than at the core: occurrence of recruitment p was significantly lower at the trailing edge than at the core in *Fagus sylvatica*, *Pinus sylvestris* and *Quercus suber*, and lower at the leading edge than at the core in *Abies alba* and *Acer pseudoplatanus.* We found no significant difference in recruitment occurrence between the core and any of the climatic margins for twelve species.

Average recruitment abundance μ was significantly lower in the trailing edge than in the core in five species (*Alnus glutinosa*, *Betula pendula*, *Pinus halepensis*, *Pinus sylvestris* and *Quercus robur*) and lower at the leading edge than in the core in *Pinus pinaster* and *Quercus robur.* On the contrary, *Picea abies*, *Pinus pinea*, *Quercus ilex* showed larger μ in the trailing edge than in the core and *Acer pseudoplatanus* showed larger μ in the leading edge than in the core (Figure 4.1) (trailing edge effect TE and leading edge effect LE) and Supplementary Figure S6; Supplementary Tables S9a-b); Moreover, in eight species we found no significant difference in μ between core and any of the climatic margins. This absence of significant difference in most species was also represented by the absence of strong spatial patterns in recruitment rate for most species (Figure 4.2, Supplementary

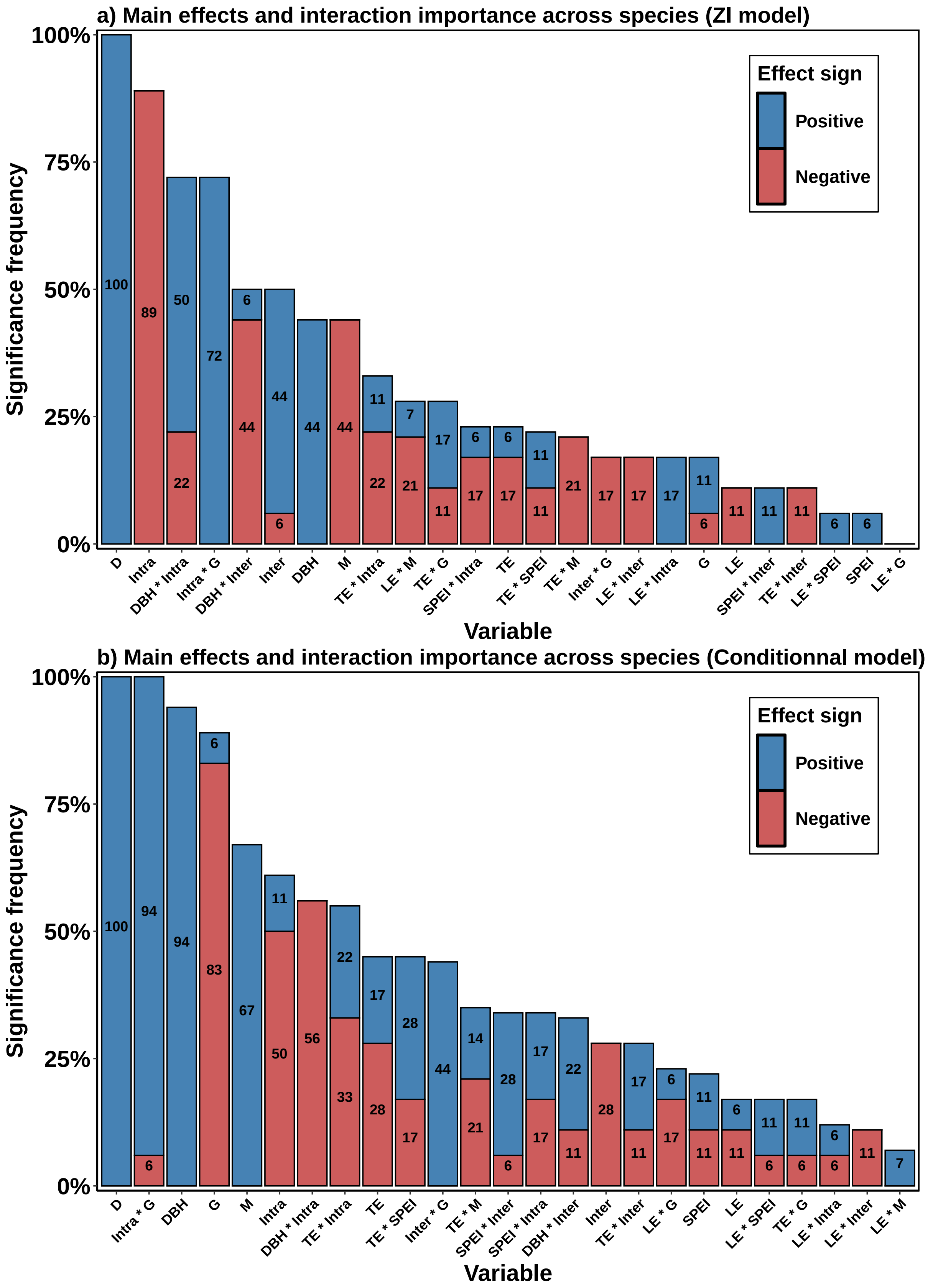


Figure 4.1: Proportion of species exhibiting significant variables explaining tree recruitment (i.e. main effects and interaction). Red colors indicate negative coefficient estimates and blue colors indicate positive coefficient estimates. a) For occurrence of recruitment (BIN) and b) abundance of recruitment (NB). D = tree density; DBH = plot mean dbh; Intra = conspecific basal area; Inter = heterospecific basal area; G = growth rate; LE = leading edge; M = mortality rate; SPEI= mean spei; TE = trailing edge; * indicate an interactive effect between two variables.

Species	Code	Chi square (p.value)	AIC	R2C	R2M	r	RMSE(n)
Abies alba Mill.	ABIALB	804068 (0.39)	14471.62	0.66	0.45	0.85	0.03
Acer pseudoplatanus L.	ACEPSE	196560 (0.37)	3638.07	0.48	0.31	0.95	0.02
Alnus glutinosa (L). Gaertn.	ALNGLU	175536 (0.36)	4997.43	NA	0.52	0.89	0.04
Betula pendula Roth.	BETPEN	321550 (0.39)	4515.20	0.66	0.49	0.93	0.02
Castanea sativa Mill.	CASSAT	110160 (0.39)	5336.82	NA	0.51	0.88	0.03
Fagus sylvatica L.	FAGSYL	7262658 (0.42)	69256.77	0.51	0.17	0.83	0.04
Fraxinus excelsior L.	FRAEXC	347622 (0.38)	6539.59	1.00	0.30	0.92	0.03
Picea abies (L.) H.Karst.	PICABI	7141995 (0.42)	69751.95	0.75	0.68	0.89	0.02
Pinus halepensis Mill.	PINHAL	1912190 (0.44)	55256.15	NA	0.58	0.85	0.04
Pinus nigra J.F.Arnold.	PINNIG	1164160 (0.43)	33850.34	NA	0.64	0.85	0.03
Pinus pinaster Aiton.	PINPINA	293496 (0.41)	11568.66	NA	0.66	0.85	0.03
Pinus pinea L.	PINPIN	2629662 (0.41)	47959.36	NA	0.66	0.85	0.04
Pinus sylvestris L.	PINSYL	9764352 (0.44)	95481.38	0.76	0.69	0.85	0.03
Quercus ilex L.	QUEILE	1310902 (0.46)	50884.93	NA	0.55	0.87	0.04
Quercus petraea Liebl.	QUEPET	1009280 (0.41)	14856.46	0.75	0.43	0.88	0.02
Quercus pyrenaica Willd.	QUEPYR	435200 (0.41)	17753.80	NA	0.61	0.85	0.05
Quercus robur L.	QUEROB	892737 (0.42)	14968.23	0.65	0.50	0.86	0.02
Quercus suber L.	QUESUB	299880 (0.44)	13586.40	NA	0.55	0.78	0.05

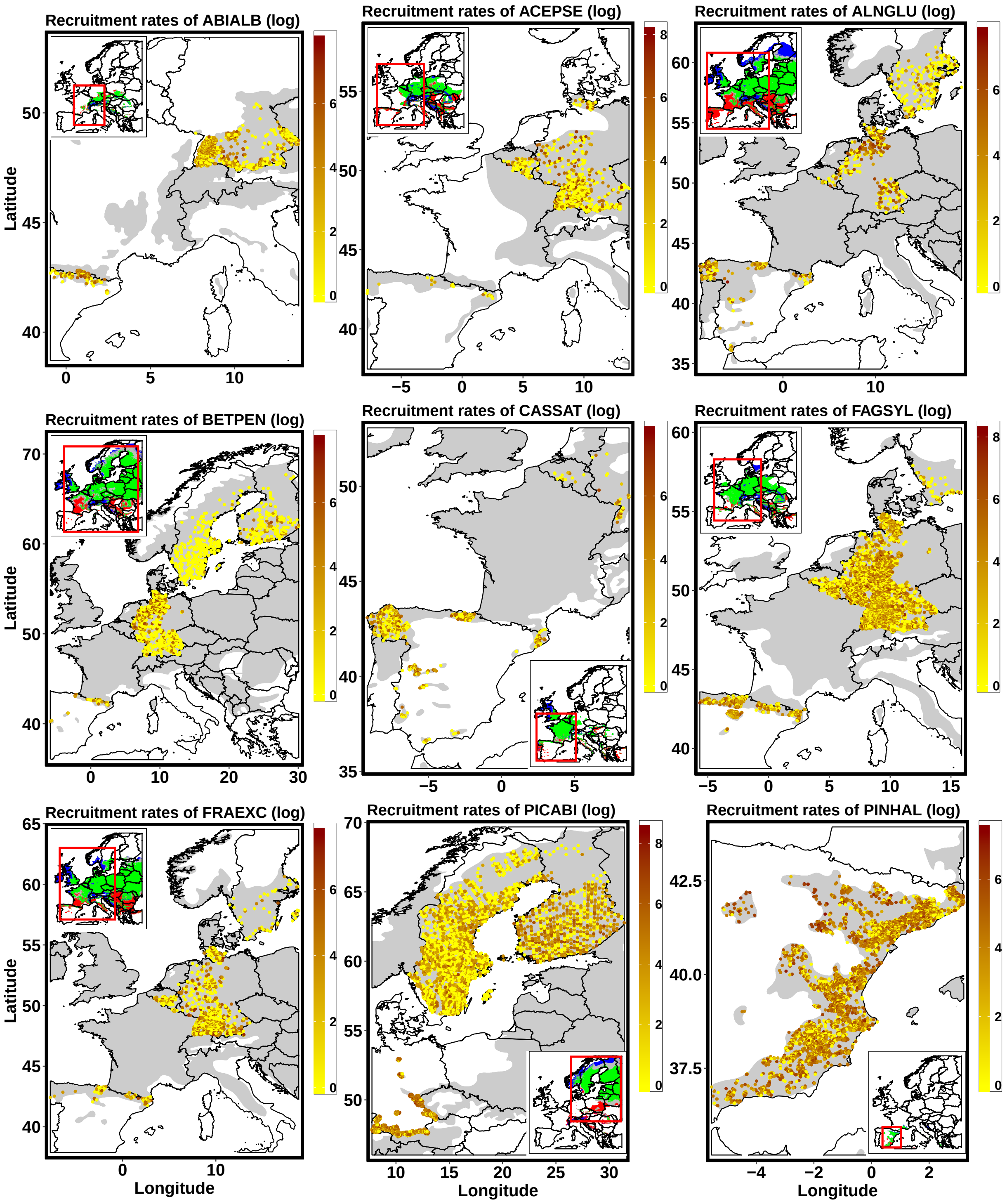
Table 4.1: Statistical evaluation of recruitment models, by species. Species: Name of the species. Code: Acronymused for each species; Chi-square (p-value): Statistic and associated p-value of the chi-square test between fitted and observed distribution of regeneration values; AIC: Akaike Information Criterion; R2C: Conditional r-squared. R2M: Marginal r-squared. r: The Pearson squared correlation between the model's actual and predicted response. RMSE (normalized): square root of the variance of the residuals which indicates the absolute fit of the model to the data. The normalized RMSE is the proportion of the RMSE related to the range of the response variable and can be interpreted as the standard deviation of the unexplained variance.

Tables S9a-b).

4.3.3 Underlying drivers of tree recruitment occurrence and abundance

Increased recruitment occurrence was associated with an increase in density for all species, and an increase in tree size and basal area of other species, for eight species (see positive effect signs in Figure 4.1a). Increased recruitment occurrence was also associated with decreases in both basal area of conspecifics (16 species) and mortality rate (eight species, see negative effect signs in Figure 4.1a). Increased p was associated with an increase in SPEI (lower relative drought) in *Fagus sylvatica* only. (Figure 4.1a and Supplementary Figure S7a; Supplementary Table S9a).

Recruitment abundance μ was associated with increase in density for all species, increase in mean tree size for 17 species and with decrease in basal area of other species (9 species). In contrast to recruitment occurrence p, we found an increase in recruitment abundance with increased mortality (12 species) and a decrease in basal area of other species in five


Recruitment rates of ABIALB (log)
Recruitment rates of ACEPSE (log)
Recruitment rates of ALNGLU (log)
Recruitment rates of BETPEN (log)
Recruitment rates of CASSAT (log)
Recruitment rates of FAGSYL (log)
Recruitment rates of FRAEXC (log)
Recruitment rates of PICABI (log)
Recruitment rates of PINHAL (log)
Latitude
Longitude

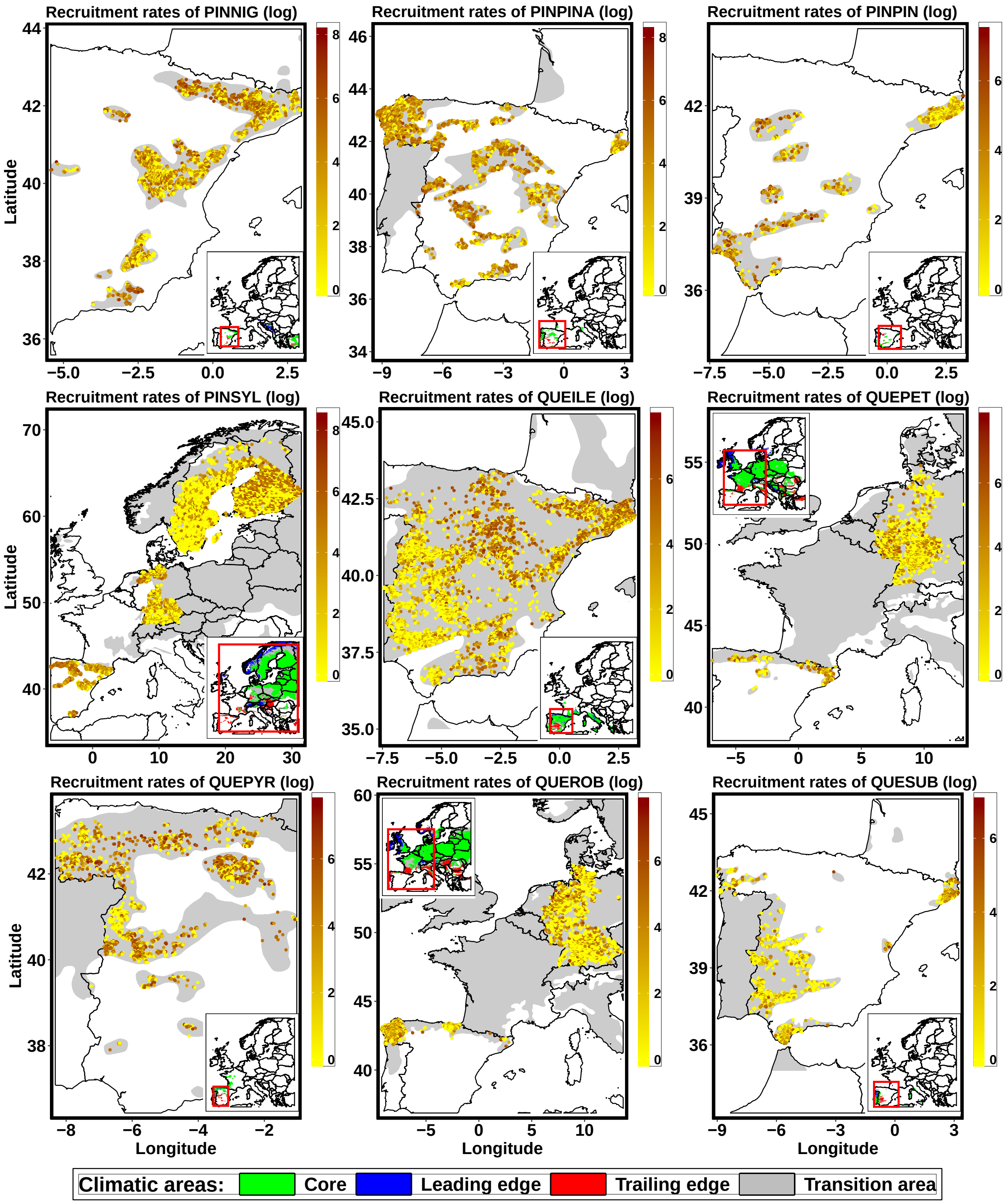


Figure 4.2: Predicted recruitment abundance for each species on a log scale (tree ha-1). Yellowest dots correspond to the lowest recruitment rates while redest dots represent the highest recruitment rates. Light grey areas display species distribution ranges from Caudullo et al. (2017). Climatic marginality maps are shown on the top left or bottom right corner with core area in green, leading edge area in blue and trailing edge area in red. Red squares show the areas with NFI recruitment records.

species (all of which had recruitment probability recruitment abundance mu positively associated with an increase in basal area of other species). In addition, increased μ was associated with decreasing average growth rate G in 15 species; with increasing SPEI in *Fagus sylvatica* and *Pinus sylvestris*; with decreasing SPEI in *Fraxinus excelsior* and *Quercus robur* (Figure 4.1b and Supplementary Figure S7b; Supplementary Table S9b).

4.3.4 Competition, drought and mortality interactions with climatic marginality on recruitment

The probability of recruitment occurrence was affected by the interaction between SPEI and climatic marginality in a small number of species (significant effect of SPEI in four species at the TE and one positive at the LE; Figure 4.1a): when relative drought increases (i.e. low SPEI), recruitment occurrence decreases in the margins (in the LE for *Q. robur* and in the TE for *Q. robur* and *Q. petraea*) but increases in the core areas. However, we also found the opposite pattern in *F. sylvatica* and *F. excelsior* (p increases with relative drought in the TE while p decreases in the core) (Figure 4.3a).

The recruitment abundance mu was affected by the interaction between SPEI and climatic marginality in several species (significant effect in eight species at the TE, three at the LE; Figure 4.1b). When relative drought increased (i.e. low SPEI), recruitment abundance strongly decreased in the LE of *F. sylvatica* and *P. pinaster* and in the TE of *A. glutinosa*, *F. excelsior*, *P. pinaster*, *P. pineae* and *P. sylvestris* while remaining stable or slightly increasing in the core. On the contrary, when relative drought increases, recruitment abundance strongly increases in the LE (*P. abies*), or in the TE (*B. pendula*, *P. abies*, *P. halepensis*) while decreasing slightly in the core (Figure 4.3b).

The effect of conspecific basal area varied with climatic marginality on both recruitment occurrence (significant effect in six species at the TE, three at the LE; Figure 4.1a) and abundance (significant effect in 11 species at the TE, two at the LE; Figure 4.1b). When conspecific basal area increases, recruitment occurrence decreases faster in the TE than in the core in *A. pseudoplatanus*, *A. glutinosa*, *Q. robur* and *F. excelsior* but also faster in the core than in the margins (in the LE for *P. abies*, *A. alba*, *A. glutinosa*, and in the TE *F. sylvatica*, *P. abies*) (Figure 4.3c). Similarly, when conspecific basal area increases, recruitment abundance mu decreases more strongly in the margins than in the core (in the LE for *P. pineae* and in the TE for *C. sativa*, *F. sylvatica*, *P. nigra*, *P. pinea*, *P. pinaster*, *Q. pyreneica*) although decreasing more strongly in the core than in the margins in several species (in the LE for *Q. robur* in the TE for *A. glutinosa*, *P. halepensis*, *P. sylvestris* and *Q. robur*) (Figure 4.3d).

For both recruitment components, the interaction between marginality and conspecific basal area was important for more species than the interaction between marginality and

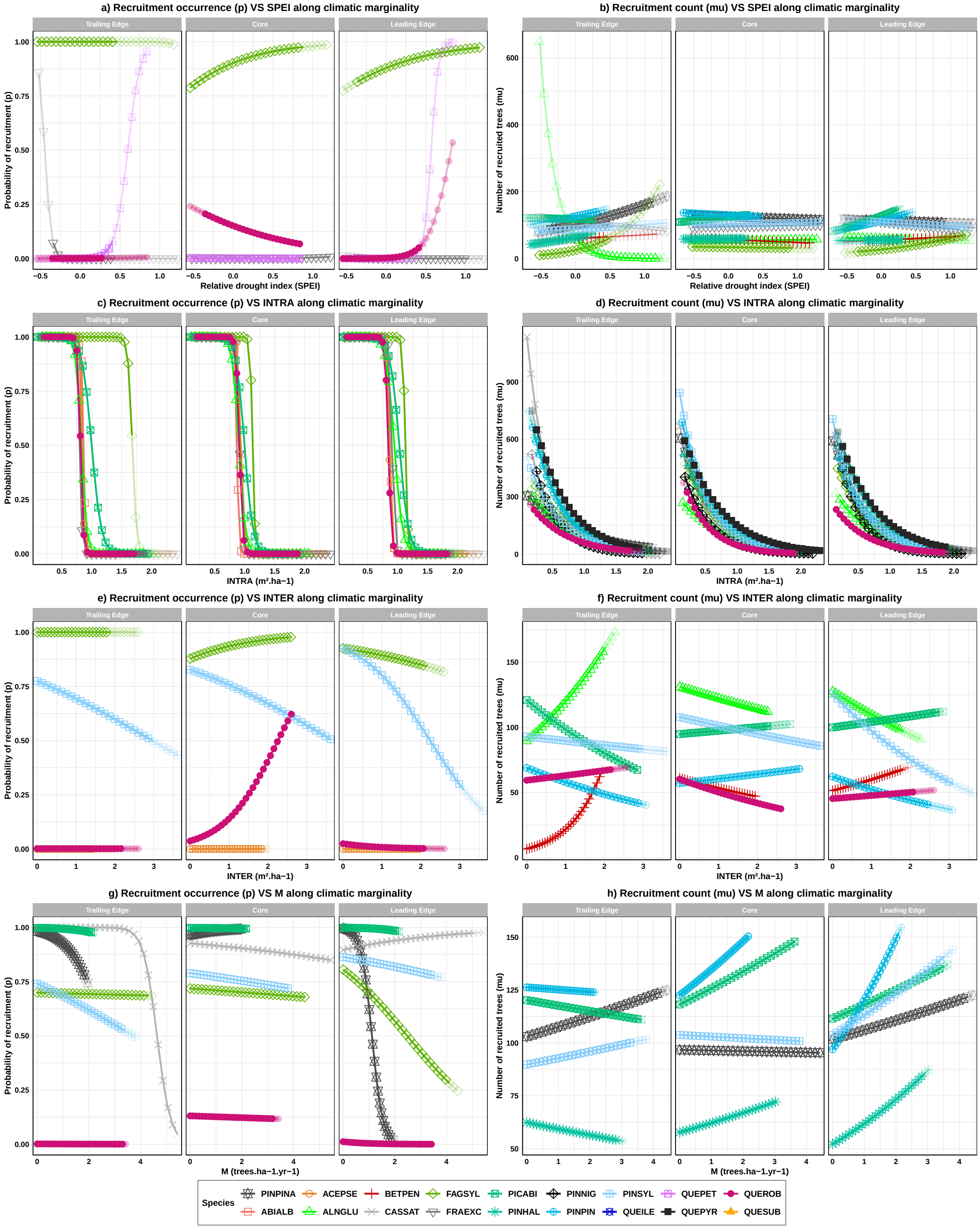


Figure 4.3: Predicted recruitment occurrence (expressed as a probability, y-axis, left panels a, c, e, g) and abundance (expressed as a count, y-axis, right panels b, d, f, h) by climatic marginality (trailing, core and leading edge) with (a, b) drought index (x-axis, negative values indicates drier conditions than during the reference period); (c, d) Intraspecific competition (m^2ha-1); (e, f) Interspecific competition (m^2ha-1); (g, h) Mortality (tree ha-1.year). Predictions were only made for those species where the interaction was found to be important. Predictions are shown in the ranges of the environmental gradients covered by each species (solid colors) and extrapolations outside the environmental gradients covered by the species are shown in light colors.

heterospecific basal area, that was significant in two species at the TE and three at the LE for recruitment occurrence (Figure 4.1a) and five species at the TE and two at the LE for recruitment abundance (Figure 4.1b). The effect of heterospecific basal area on recruitment varied according to climate marginality in fewer species than conspecific basal area, both on p (significant effect in two species at the TE, three at the LE; Figure 4.1a) and μ (significant in five of the species at the TE, two at the LE; Figure 4.1b).When heterospecific basal area increases, recruitment occurrence strongly decreases at the LE of *F. sylvatica*, *P. sylvestris*, *Q. robur* and slowly decreases at the TE of *A. pseudoplatanus* and *Q. robur* while increasing at the core (or slightly decreasing in *P. sylvestris*) (Figure 3e). Besides, when heterospecific basal area increases, recruitment abundance strongly decreases at the LE of *P. pinea* and *P. sylvestris* and at the TE of *P. pinea* and *P. abies* while slightly increasing or decreasing in the core. On the contrary, under increasing heterospecific basal area, recruitment abundance increases at the TE of *A. glutinosa*, *B. pendula* and *Q. robur* while decreasing at the core (Figure 4.3f).
The interaction between mortality rate and climatic marginality was important in eight species, both on recruitment occurrence (three species at the TE, four at the LE; Figure 4.1a) and abundance (significant in five species at the TE, one at the LE; Figure 4.1b). When M increases, recruitment occurrence decreases faster at the LE of *P. abies*, *P. pinaster*, *Q. robur* and at the TE of *C. sativa*, *F. sylvatica*, *P. sylvestris* than in their core but also increases at the LE of *F. sylvatica* while decreasing in its core (Figure 4.3g). Similarly, when mortality increases, recruitment abundance decreases in the TE while increasing in the core (*P. halepensis*, *P. pinea*, *P. pinaster*) but also increases in the TE while decreasing in the core (*P. abies*, *P. sylvestris*; Figure 4.3h).

4.3.5 Interaction of competition with drought and plot structure on recruitment

The effects of SPEI varied with con- and heterospecific basal area both for recruitment occurrence (significant in four species for conspecific basal area; two for heterospecific basal area; Figure 4.1a and Supplementary Table S9a) and abundance (significant in six species for conspecific basal area and six for heterospecific basal area; Figure 1b and supplementary Table S9b). With increasing relative drought (i.e. decreasing SPEI), recruitment occurrence was constant at both low and high levels of conspecific basal area and it only varied at average conspecific basal area in four species (Figure 4.4a). At low levels of conspecific basal area, recruitment abundance was strongly negatively correlated with relative drought in four species and positively correlated in two species (Figure 4.4b). At both average and high levels of conspecific basal area, recruitment abundance was low and unaffected by relative drought (Figure 4.4b).

Recruitment occurrence was constant or negatively correlated with relative drought

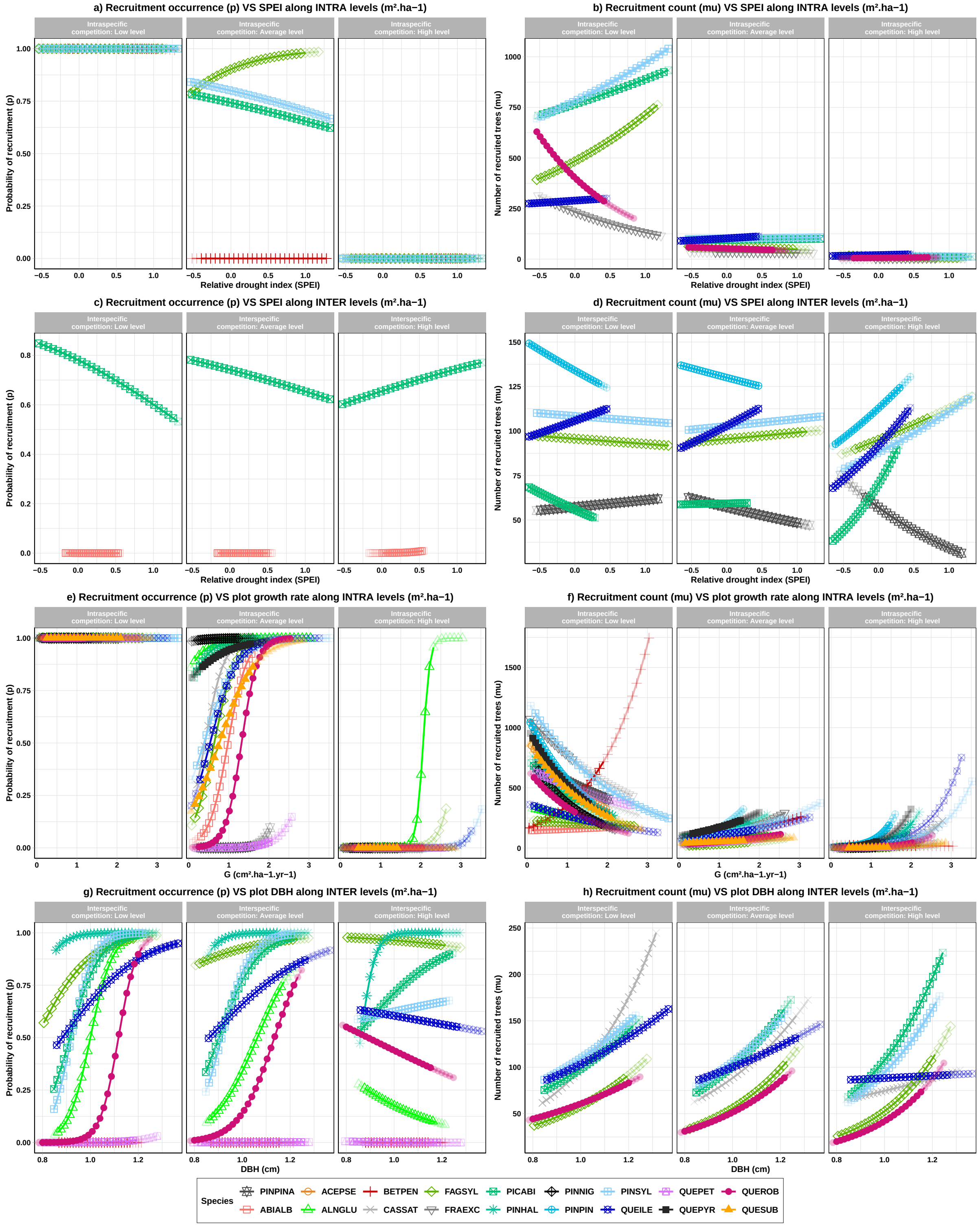


Figure 4.4: Predicted recruitment occurrence (expressed as a probability, y-axis, left panels a, c, e, g) and abundance (expressed as a count, y-axis, right panels b, d, f, h) by intra-specific competition (a,b,e,f; low, medium and high values) and inter-specific competition (c,d,g,h; low, medium and high values) with drought index (a, b, c ,d; x-axis, negative values indicates drier conditions than during the reference period); growth rate (e, f; x-axis; cm²ha-1.yr); mean DBH (g, h; x-axis, cm). Predictions were only made for those species where the interaction was found to be important. Predictions are shown in the ranges of the environmental gradients covered by each species (solid colors) and light colors indicate values not observed in the data. We used single species specific values to predict data for the three levels of competition (5th centile for low level, mean value for average level and 95th centile for high level).

increases at low and average level of heterospecific basal area but is positively correlated with relative drought at high levels of heterospecific basal area (Figure 4.4c). The predictions of recruitment abundance by increasing relative drought were similar in low, average and high levels of heterospecific basal area (Figure 4.4d). However, the correlations are stronger at high levels; five species strongly positively correlated and one species (*Pinus pinaster*) negatively correlated with relative drought (Figure 4.4d).
The effect of growth rate G on recruitment depends on the level of conspecific basal area in many species, both on recruitment occurrence (significant in 13 species; Figure 4.1a) and abundance (significant for all species; Figure 4.1b): When G increases, recruitment occurrence remains close to 1 for low level of conspecific basal area, remains close to 0 for high level of conspecific basal area and increases along with G for average level of conspecific basal area (Figure 4.4e). In addition, when G increases, recruitment abundance is high and decreases strongly at low levels of conspecific basal area, while remaining low but slightly increasing for medium and high levels of conspecific basal area(Figure 4.4f).

The importance of tree size on recruitment depends on the level of heterospecific basal area for several species, both on recruitment occurrence (nine species; Figure 4.1a) and abundance (significant in six species; Figure 4.1b). As tree size increases, the occurrence of recruitment increases and almost reaches 1 at low and medium levels of heterospecific basal area, while slightly increasing or decreasing but always remaining the lowest at high levels of heterospecific basal area (Figure 4.4g). In addition, as DBH increases, mu increases for any level of heterospecific basal area, being the fastest at high or low level of heterospecific basal area (4 and 2 species, Figure 4.4h).

4.4 Discussion

4.4.1 Spatial patterns of occurrence and amount of tree recruitment

Overall, our results did not show a decrease in recruitment towards the edge of the species ranges, which is in agreement with previous work analysing tree recruitment at large scales (Pironon et al., 2017; Purves, 2009). This absence of variation in recruitment across most species ranges could be the result of ontogenic thresholds or the importance of local conditions on tree recruitment. For instance, high seed germination and high seed survival could mitigate low seed deposition at high latitude/altitude while lower seed germination and seed survival could be mitigated by higher seed deposition at low latitude/altitude, resulting in similar recruitment of new trees (Merges et al., 2020).

We found lower recruitment count or probability at the trailing edge than in the core of 7 of 18 species, supporting the Center Periphery Hypothesis and suggesting a possible range contraction in the southern part of the range. Several of the species are drought sensitive temperate species (*F. sylvatica*, *P. sylvestris*, *A. glutinosa* and *B. pendula*) whose trailing edge is located in southern France and Spain and for which range contraction is expected at the southernmost part of their distribution (Durrant et al., 2016a; Durrant et al., 2016b; Beck et al., 2016; Durrant et al., 2016c). Our results are consistent with other studies demonstrating that Scots pine and beech are being progressively replaced by oak species in the Pyrenees (Galiano et al., 2010; Peñuelas et al., 2007) and suggests that similar range contraction could occur in other species, such as *Q. robur* for which range contraction as a response to climate change has not yet been described.

Our results indicate lower recruitment in the climatic leading edge (located in the Alps) of temperate species from eastern-central europe such as *A. alba* and *A. pseudoplatanus*, both known to be drought sensitive. Lower recruitment could indicate a possible range contraction in these two species, despite the ongoing debate concerning their possible range contraction or expansion as a response to climate change (Pasta et al., 2016; Mauri et al., 2016). Vanderwel et al. (2013) also observed a decrease in recruitment in temperate plant functional types, whereas Ettinger et al. (2017) also observed a decrease in recruitment and a decrease in growth at the leading edge of coniferous species. The decrease of summer precipitation and drought frequency are likely to increase in the future (IPCC, 2014) with direct consequences on boreo-alpine species for which summer precipitation is an important driver of recruitment (Matías et al., 2012). Therefore, drought-sensitive species at their trailing edge in the Pyrenees or at their leading edge in the Alps could be progressively replaced by more drought-tolerant species, as is observed in the tropics (Esquivel-Muelbert et al., 2019).

We found little support for the CPH in Mediteranean species such as *Q. suber* and *P. halepensis*, displaying lower recruitment in their leading edge than in the core, while *P. pinea* and *Q. ilex* displayed higher recruitment in their trailing edge. All of these species also display high recruitment rates all across their range (Figure 4.2), which is mostly restricted to Spain in our data. As these species are mostly resistant to drought but are strongly affected by wildfires, the patchy and sometimes opposite patterns in recruitment exhibited for all of them could be post-fire patterns driven by multiple environmental and human drivers (Baeza et al., 2007; Karavani et al., 2018). Furthermore, some Mediterranean species reach the southernmost part of their ranges in North Africa, preventing us from properly assessing recruitment at the trailing edge when using the European NFIs.

4.4.2 Recruitment response to drought and competition does not vary with climatic marginality

In a large majority of species, we found that drought and basal area effects on recruitment did not depend on climatic marginality although we hypothesized that recruitment would be driven mostly by climate at the leading edge and by competitive interactions at the trailing edge of the species range (HilleRisLambers et al., 2013; Louthan et al., 2015). Contrary to our expectations, the effect of drought at the leading and core was similar, which suggests that climate is likely not the only driver setting the northern range limit. In addition, we found the strongest effect of drought on recruitment in the trailing edge part of the range in a few species (5 of 18) and, according to our expectations, we found the strongest effect of conspecific basal area on recruitment in that part of the range in some species too. We therefore suggest that both factors could be equally important in setting the trailing edge of species.

Moreover, heterospecific basal area effect on recruitment was not different in climatic marginal areas than in the core, similarly to the results shown by Kunstler et al. (2020), who showed that competition effect on tree demography did not vary strongly with climatic marginality. Hence, heterospecific basal area was not the most important driver of tree recruitment in marginal populations as it has been previously suggested (Alexander et al., 2016). Besides, our results even suggest a facilitative effect with conspecific species in the core of the range in some species. These results agree with Ettinger et al. (2017), who found competitive interactions to be important at all range positions.

4.4.3 Tree recruitment depends more on stand-related variables than drought-related ones

Stand variables were the strongest predictors of recruitment. We found recruitment increases with stand density, which confirms that recruitment is higher in young forest with many small trees than older forest with few larger trees (Li et al., 2011). This is also supported by recent studies that have found increased recruitment associated with increased stand density (Yang et al., 2015; Zell et al., 2019). Moreover, our results show that recruitment tends to be higher in plots with large mean tree size and with low growth rate, which suggests that more mature stands can produce more offspring than younger stands. This is supported by other studies stating that mean tree size reflects maturity and the ability to produce offspring rather than competition for light (Kolo et al., 2017; Muledi et al., 2020). In addition, we argue that this trend could be amplified by the small threshold of inclusion we used during the census (10 cm of DBH), some of the smallest trees of our dataset being therefore likely not able to produce offspring yet.

We also found a positive association between mortality rate and average recruitment, as it was found in previous studies (Galiano et al., 2010; Klopcic et al., 2012). We suggest that this increase of recruitment could be explained by a reduction of plot density and increased light availability through increased mortality. Nonetheless, we also found a negative association between recruitment probability and mortality. We suggest this negative association could be related to extreme events of mortality in plots with many small trees, not yet mature enough to produce offspring.

We showed that drought had rarely a significant effect on tree recruitment occurrence and rate and it is therefore not the strongest driver of tree recruitment. Likewise, no effect of drought on Mediteranean species such as *Q.ilex* recruitment was found by Matías et al. (2012) and Adame et al. (2010), who did not report climate effects on *Q. pyreneica* recruitment either. Similarly, Zell et al. (2019) demonstrated a small effect of climate on tree recruitment in comparison with species dominating the plot or stand variables in numerous species. Nonetheless, we found a strong effect of SPEI on *F. sylvatica* and *P. sylvestris* recruitment rate suggesting that both species could benefit from relatively wetter conditions but suffer from increased relative drought. This result is confirmed by Klopcic et al. (2012) who showed a negative effect of decreased precipitation and increased temperatures on the recruitment probability of *F. sylvatica* or by Boulant et al. (2008) who demonstrated negative effects of drought duration in recruitment of *P. sylvestris* and *P. nigra.* The expected range contraction of these three species in the south could also occur all across their ranges as both survival and recruitment decline as a response to drought (Changenet et al., 2021; Galiano et al., 2010; Durrant et al., 2016b; Durrant et al., 2016a).

4.4.4 Recruitment response to competition is modified by change in stand characteristics

Our results showed that conspecific basal area was the main factor controlling recruitment, suggesting that recruitment is more competition- than drought-driven (Figure 4 and Supplementary Figure S8). This is in line with previous studies reporting the strongest effect of competition over drought, climatic variables or climate site index on many species in Europe, North America and Asia (Li et al., 2011; Xiang et al., 2016; Zell et al., 2019). Furthermore, we found that both recruitment occurrence and recruitment rates increase as plot maturity decreases, at medium and high levels of conspecific basal area. This result could reflect that the less mature plots tend to be the densest, therefore displaying larger recruitment rates and occurrence than more mature plots at similar levels of conspecific basal area (Lexerød et al., 2005; Li et al., 2011).

Our results showed that under low levels of conspecific basal area, the more mature plots

had the highest recruitment rates. We suggest that these mature plots with low levels of conspecific basal area could be those with few big trees, displaying low density and resulting in higher resource availability, seed production and recruitment than younger stands (Xiang et al., 2016). Unlike other studies (Xiang et al., 2016; Zell et al., 2019), we cannot relate our results to shade-tolerance or shade-intolerance ecologies as our results were similar across all our studied species regardless of their shade tolerance characteristics. Interestingly, heterospecific basal area was associated with both increased recruitment probability and decreased recruitment count in *F. sylvatica*, *P. abies*, *P. sylvestris*, *Q. petraea* and *Q. robur*. In addition, we found increasing probability of recruitment with decreasing tree size in *F. sylvatica*, *Q. ilex*, *Q. robur*, *A. glutinosa* and *Q. petraea* at high levels of heterospecific basal area whereas we found the opposite at low and medium levels suggesting that the smallest trees benefit the most from the increase presence of other species. Because most of these species are shade-intolerant (except *F. sylvatica*) but can tolerate shadow at early stage of life, these results suggest that recruitment is likely to occur under adult trees of dissimilar species, likely induce by the release of conspecific negative density dependence, or by facilitative mechanisms during the germination process such as decreasing seedling mortality though increase water availability (Granda et al., 2014; Jevon et al., 2020; Muledi et al., 2020). When seedlings become more shade-intolerant in the next stage of life, these facilitative mechanisms seem to be followed by competition for light as we observe a negative effect of heterospecific basal area on count of recruitment. Li et al. (2011) reported similar patterns (despite using the total basal area BA') with negative effect of increased BA on recruitment count but sometimes positive effect on probability of recruitment depending on the species type (shade tolerant, high light conditions).
We found increasing recruitment rate with increasing plot maturity at any level of heterospecific basal area in *P. sylvestris*, *F. sylvatica*, *Q. robur*, *P. abies*, *Q. ilex* and *C. sativa*, which suggest that plots containing few big trees benefit more than young dense plots of the presence of other tree species. This could be related to increased light penetration due to decreased density as suggested by Xiang et al. (2016) or niche complementarity between co-occurring neighborhood species (Jactel et al., 2017).

4.4.5 Recruitment response to competition is modified by change in drought conditions

Our results highlight the context dependency and the species specificity of climate-competitive interactions. In most species, we found no significant interaction of drought with either of the competition variables. However, we show that in a few species (*P. sylvestris*, *F. sylvatica*, *P. abies*, and *B. pendula*) the probability of recruitment depends strongly on the interaction between conspecific basal area, and drought. The drought effect is weak and visible at the intermediate level of conspecific basal area only (Figure 4.4a).

Similarly, effect of drought on recruitment rate was visible at low conspecific basal area only and was detrimental on *P. sylvestris*, *F. sylvatica*, *Q. ilex* and *P. abies* or beneficial on *Q. robur* and *F. excelsior* (Figure 4.4b). In addition, some of these species (*P. sylvestris*, *F. sylvatica*, *P. abies*, *Q. ilex*, *P. pinea*) were insensitive to drought at low and intermediate level of heterospecific basal area but at high level of heterospecific basal area, we show a positive effect of heterospecific basal area in low relative drought conditions that becomes a negative mechanism in high relative drought conditions and the opposite in *P. pinaster*.

These results first confirm that drought effect on recruitment is less important than intra-specific competition and hence conspecific negative density dependence (CNDD) as drought effect is visible only when CNDD is released, even-though most of these species are drought intolerant. Our result is supported by previous work showing that CNDD effect on recruitment is stronger in resource-rich environments because the activity of natural enemies such as species-specific pathogens and herbivores, is stronger under humid conditions (LaManna et al., 2016). Our results also suggest that in these species that experience CNDD effect on recruitment, the presence of other species induce positive effects on recruitment that could switch to negative effects with increasing drought, despite some of them not being particularly sensitive to competition (*P. abies* and *F. sylvatica*). Besides, *P. pinaster* is the only species that could benefit from the presence of other species with increasing drought, likely because of its better drought tolerance (Abad et al., 2016). Our results do not agree with the competition-environmental gradient hypothesis (CEGH), even suggesting the opposite pattern as the effect of drought was more limiting at the trailing edge than at the leading edge. Granda et al. (2012) found similar results as ours on *Q. ilex*, showing that positive interactions do not increase with increasing aridity as expected by the CEGH. Similar switch from facilitation to competition have also been reported along latitudinal gradient (Ettinger et al., 2017) in coniferous species. Our results confirm that the CEGH is species specific, likely because the relation between heterospecific basal area and climate can be dependent on resources or productivity gradients and follow a monotonic or hump-shaped relationships (Pugnaire et al., 2011).

Altogether, our results suggest that range limits in tree recruitment are mostly driven by conspecific basal area effects modulated by climate supporting thus Chen et al. (2018) results arguing that forest tree neighborhoods are more structured by CNDD than interactions with other species. Most importantly, our results suggest that the predicted increase in drought frequency and intensity in the next decades could affect *P. sylvestris*, *F. sylvatica*, *P. abies*, *Q. ilex* and *P. pinea* more strongly than expected (Trenberth et al., 2014).

4.4.6 Limitations

The use of National Forest Inventories (NFIs) data in recruitment studies has several problems: the size of the plot influences the estimation (Li et al., 2011) as well as the various plot radii across diameter classes (Fortin et al., 2007). The choice of subplot size to calculate recruitment can also induce clustered response when the variables used are not calculated on the same subplot (Adame et al., 2010). We used a random effect on the country and chose to calculate recruitment on all subplot sizes in order to overcome these problems. The fact that we used an offset on census time and variable plot size relies on the assumption of a linear increase of recruitment with these variables (Fortin et al., 2008) which is not always the case (Yang et al., 2015).
Recruitment may also be affected by other factors that are not considered in our models such as management (Kolo et al., 2017), grazing (Boulant et al., 2008), habitat type (Merges et al., 2020), soil characteristics (Adame et al., 2010; Muledi et al., 2020), snow (Hofgaard et al., 2009), wind (Batllori et al., 2009), species mixture and composition (Granda et al., 2014; Lexerød et al., 2005; Li et al., 2011; Yang et al., 2015), light requirements (Muledi et al., 2020), dispersal type (Muledi et al., 2020) and regeneration strategies (Adame et al., 2010).

Nevertheless, our models present better performance than most recruitment models (Adame et al., 2010; Klopcic et al., 2012; Yang et al., 2015). Hence, factors that may bias recruitment models such as the time lag between regeneration and establishment (Klopcic et al., 2012), or masting (Ribbens et al., 1994) are likely to play a limited role in our estimations as census interval in our data are large and climatic data (SPEI + climatic marginality) are based on the 30 years prior to the data collection date.

4.4.7 Synthesis and perspectives

Our study shows that recruitment in all species depends strongly on plot structure. Recruitment occurrence and rate did not exhibit strong spatial patterns in the climatic margins compared to the core populations in most species. However, we found some limited recruitment in a few common species (*F. sylvatica*, *P. sylvestris*, *Q. robur*, *A. glutinosa*, *A. alba*, *A. pseudoplatanus*) suggesting a possible range contraction. Despite interspecific interactions are supposed to be crucial in setting demographic limits when site productivity is high (Alexander et al., 2016), we found that heterospecific basal area effect (positive or negative) depends less on climatic marginality than on drought stress, and that conspecific basal area had a stronger effect than heterospecific basal area or drought in shaping tree recruitment. Recruitment occurrence and rate in a majority of species was not strongly affected by climate, contrary to other demographic rates such as mortality (Changenet et al., 2021).

Future work should assess regeneration but also other demographic traits in the dynamics of forest through better quantification of the contribution of the different drivers influencing it across the range and their interactions. The inclusion of information on the identity of the dominant species (Granda et al., 2014) is the next step after looking at differences between inter- and intra-specific competition. These steps could further help stakeholders to develop management strategies that mitigate climate change impact.

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CHAPTER 5

INCREASE OF INVASIVENESS OF QUERCUS RUBRA AND ROBINIA PSEUDOACACIA IN EUROPEAN FORESTS: AN APPROACH USING NATIONAL FOREST INVENTORIES

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Abstract

Quercus rubra L. and *Robinia pseudoacacia* were introduced in Europe from North America at the end of the 17th century as ornamental and forest trees. Since the end of the 20th century, forest managers question their invasive status. Our main goal was to evaluate whether these two species have expanded their ranges and relative dominance at the expense of native species and identify the underlying drivers of this expansion across European forests. We hypothesized i) that both species are expanding their ranges and have increased their occurrence and dominance at the expense of native species; and ii) that climate is triggering the increase in occurrence and dominance of these two species. We used data from six National Forest Inventories to i) perform a direct comparison between two surveys using 7 biotic indicators of expansion and ii) develop models of absolute and relative stand basal area growth to identify the underlying drivers of their expansion. Both species have significantly increased in presence, abundance, relative dominance and relative density between the two surveys, progressing considerably in conspecific- and dissimilar species- dominated plots. Human disturbances and climate (warmer and drier conditions) were respectively the main drivers of their absolute and relative growth, inducing a range expansion between the two surveys northwards and southwards in both species. In the context of increase in drought frequency and intensity, our results suggest a rapid change in species composition in the near future with concomitant negative ecological and economical outcome.

5.1 Introduction

As a response to changing climate, species are changing their distribution ranges and community structures (Parmesan et al., 2003; Parmesan, 2006). Range shifts are observed in tree species that cannot migrate fast enough to track climate change (Lindner et al., 2010; Milad et al., 2011). This is particularly evident at range boundaries between biomes (i.e. ecotones) such as the treeline in mountainous areas where species are shifting upwards and at the drier margin and colder margin of the distribution (i.e. the trailing edge and the leading edge) where species are moving northwards (Carnicer et al., 2014; Beckage et al., 2008; Evans et al., 2017; Lenoir et al., 2008).These shifts in species distributions and communities at the ecotones may leave empty spaces and pave the way to the invasion of opportunistic species, whose invasive success have increased in the last century (Fernandez-Manjarres et al., 2018). In these sensitive areas, the effects of climate are evident on tree demography, including growth, mortality and recruitment patterns that change along large geographical gradients (Benito-Garzón et al., 2013; Rigling et al., 2013; Benito-Garzón et al., 2018).

For instance, tree mortality can be particularly strong towards the climatic trailing edge of the species ranges (Changenet et al., 2021), likely leading to changes in forest composition (Ruiz-Benito et al., 2017) and carbon storage (Astigarraga et al., 2020). Similarly, in Spanish forests, the strong effect of drought limiting recruitment is pointed out (Carnicer et al., 2014), although together with an increase in tree growth, related to water availability and temperatures (Ruiz-Benito et al., 2014; Pretzsch et al., 2014). In turn, these changes in demography may induce changes in species composition (Vayreda et al., 2016). Therefore, while some species will likely suffer from the current climate change, others may benefit (Baxter et al., 2008), as for instance non-native species, potentially becoming invasive. This is already the case of Spanish forests for instance, where *Acacia dealbata* and *Acacia melanoxylon* have spread as a response to climate change (Hernández et al., 2014).

The capacity of non-native species to become invasive ones relies on having a habitat that favours their invasion (invasibility, Chytry et al. (2008)) and on the traits that help the invasive plant to outperform the local species (invasiveness; Rejmanek et al. (1996)). The vulnerability or resistance of native forest communities to invasion and the persistence of invasive species (i.e. invasibility) depends on the local conditions in the new habitats, including climate (Colautti et al., 2006; Richardson et al., 2006), competition intensity, maturity stage (Robertson et al., 1994), community diversity and functional group (Byun et al., 2013; Yang et al., 2017), stand structure (Hernández et al., 2014), with synergistic effects between them that may promote invasibility of the habitats and therefore fast invasive species expansion (Higgins et al., 1998). For instance, facilitation between native and non-native species can be triggered by environmental stress, thus promoting invasibility (Cavieres, 2021).

Deliberately introduced from the USA to Europe in the late 17th century and 18th century (GOEZE, 1916; Timbal, 1994; Magni Diaz, 2004), red oak (*Quercus rubra* L.) has been used both for ornamental and wood production purposes (Timbal, 1994; Woziwoda et al., 2014b). Since then, it has establised over the entire European continent (DAISIE, 2009) with published evidence mostly in central Europe (Riepsas et al., 2008; Major et al., 2013; Woziwoda et al., 2014a; Woziwoda et al., 2014b). In the 70-80s, it was considered as an interesting species for timber production, when forest managers asked for a tree breeding program to be undertaken in France (Kremer, 1986). Nowadays, the same foresters point out that its regeneration sometimes presents an invasive behaviour (CRPF-Normandie, 2001; CRPF-Lorraine-Alsace, 2005) even recommending to reduce its cultivation to avoid competition when local species are preferred. The ability of *Q. rubra* to spread at distance of original populations and establish new populations is still poorly documented in Europe. Acorns dispersal is mostly achieved by gravity and by animals: in the native range, acorns can be dispersed by jays and squirrels (Desmarais, 1998); in Europe, it was recently demonstrated that the spreading barriers can be overcome by native jays (Myczko et al., 2014) and by rodents (Bieberich, 2016; Merceron et al., 2017). Moreover, the ability of seeds to produce a new forest regeneration of *Q. rubra* showed a major contrast between its native area in North America and the invasive one in Europe. In recent decades, native populations in North America were marked by low regeneration levels (Crow, 1988; Fei et al., 2011) that could result from high competition from other plant species in forests where fire disturbance was reduced (Nowacki et al., 1990; Buckley et al., 1998). In Europe, on the contrary, introduced populations have sometimes demonstrated high levels of regeneration (Major et al., 2013), even higher than that of native oaks *Quercus robur* or *Quercus petraea* (Vansteenkiste et al., 2005). But these studies represent local cases do not allow us to understand the ability of *Q. rubra* to disperse over large distances.

Similarly, black locust (*Robinia pseudoacacia*) is native to North America and was introduced in Europe in the early 17th century for ornamental purposes. Later, in the 18th and early 19th century, its cultivation has been encouraged in Europe and extensive planting of black locust trees started in Central Europe, because of the its rot-resistant wood that is used for multiple purposes such as fire wood, for fences, construction and furniture (Sitzia et al., 2016). Since then, it occurs in 42 European countries and is naturalised in 32. It grows on a wide range of soil types, this tree species only avoids wet or compacted conditions. It is mainly distributed in sub-Mediterranean to warm continental climates and requires a rather high heat-sum (Sitzia et al., 2016). Its reproduction is mainly asexual through a high suckering capacity, exhibiting a strong capacity for clonal growth, up to 100 square meter (Chang et al., 1998) that is triggered by disturbances (Vitkova et al., 2015). In addition, several studies have shown dispersal distances of 1-2 m per year (Cierjacks et al., 2013; Crosti et al., 2016) but its seeds are dispersed over long distances in pods though wind, reaching distances up to several tens of metres (Morimoto et al., 2010) and by rivers with 25% of the seeds reaching at least 1200 m (Säumel et al., 2013). Thus its dispersal rate is quite high. Although it is considered invasive in most part of its range, only few countries have policies to tackle it (Sitzia et al., 2016).

Empirical studies have shown that both *Robinia pseudoacacia* and *Q. rubra* impact negatively the local species. The presence of Black locust (*Robinia pseudoacacia*) induces plant richness loss and shifts in species composition as well as reduction of diversity of birds (Sitzia et al., 2016) while the high regeneration of *Q. rubra* in Central Europe impede local tree species regeneration and the understory biodiversity (Chmura et al., 2013; Woziwoda et al., 2014a). Recent work suggests that climate warming might favour *Quercus rubra* L. and *Robinia pseudoacacia* L further expansion in Central and Northern Europe (Sitzia et al., 2016; Camenen et al., 2016) but whether climate is favouring these invasive species range expansion at the expense of native ones remains an opened question that have implications for ecosystem services, community composition, and would have important economic and societal consequences (Willis et al., 2010; Millar et al., 2007; Hoegh-Guldberg et al., 2008).

Our main goal is to assess the invasive status of *Q. rubra* and *R. pseudoacacia* at large geographical gradients using data from six National Forest Inventories in Europe. To this aim, we first compare directly two census surveys with census intervals (CI) ranging from 7 to 16 years of difference and developed species-specific linear models for absolute and relative stand basal area growth as proxy of invasive capacity (Daehler, 2003; Hernández et al., 2014) at the plot scale between surveys to evaluate the invasion capacity of these two exotic species in Europe. Our goals are to: i) Quantify the ability of exotic species to spread at the expense of native species; ii) Compare the occurrence, abundance and dominance of the invasive trees and native species; iii) Determine the main abiotic and biotic drivers underlying the spread of the invasive species; iv) Identify areas of high vulnerability to invasion (invasibility).
For these purposes we test two hypotheses. The first is that both species are expanding their ranges and have increased their occurrence and dominance at the expense of native species. If this hypothesis is fulfilled, the second one is that climate is triggering the increase in occurrence and dominance of these invasive species, implying that climate change may boost tree invasion in the coming years.

5.2 Materials and Methods

5.2.1 National Forest Inventories

We used National Forest Inventories (NFIs) from six countries (France, Finland, Germany, Spain, Sweden, Wallonia (Belgium)). They were initially harmonised in FunDivEUROPE (`http://project.fundiveurope.eu/`, except the French one that was harmonized later, (Archambeau et al., 2020) and are available for download through each NFI website (see Data Accessibility statement; (Baeten et al., 2013; Ratcliffe et al., 2020). NFIs from Finland, Germany, Spain, Sweden and Wallonia have permanent plots sampled several years apart, ranging from 1981 to 2011 (Supplementary Table S1). Data from the five NFIs cover a latitudinal gradient from 36° N (Spain) to 70.05° N (Finland). We used these NFIs (except the French one) for all our analyses. As the French National Forest Inventory do not have repetitive measurements, we only used it to model the relative stand basal area growth to identify the areas of high vulnerability to invasion.

5.2.2 Biotic indices from the NFIs

We used only those plots in which our target species (*Robinia pseudoacacia* and *Quercus robur*) were present in at least one census. For *Q. rubra* we have 1404 individuals (348 plots) varying from 100 mm to 1,310mm diameter at breast height (DBH; mm) and with census intervals (CI) ranging from 7 to 16 years (Supplementary Table S2). For *R.pseudoacacia* we had 933 individuals (234 plots) varying from 100 mm to 1,019mm diameter at breast height (DBH; mm) and with census intervals (CI) ranging from 7 to 15 years.

On each plot where either of the exotic species was present, we first calculated the species recruitment per plot R (trees. ha-1) as the number of trees (with DBH higher than 100mm) that appeared in the second survey but were not present in the first one; total plot basal area ($BA_{TOT}.HA$, cm2 ha-1) as a proxy of the total competition in the plot (Kunstler et al., 2016); Mean diameter at breast height of the plot (DBH, cm); tree total density as the number of trees of all species included in the plot ($N_TOT.HA$, No. trees ha-1); DBH and $N_{TOT}.HA$, are proxies of stand density and maturity (Muledi et al. (2020) and Yang et al. (2015); Table 5.1 and Supporting Information Table S3).

We then calculated seven indicators of species expansion (Hernández et al., 2014), that were calculated in each survey on each plot (Table 5.1): species absolute stand basal area ($BA_J.HA$, cm2 ha-1), species absolute density in the plot and species absolute density per hectare (N_J, No. trees and $N_J.HA$, No. trees ha-1), number and proportion of plots containing the species (N_{PLOT} and $PROP_{PLOT}$); species relative density per hectare ($Rel.N_J.HA$; %) as the ratio between the individuals of a given species $N_J.HA$ and the total number of individuals of all the species in a plot $N_{TOT}.HA$; species relative stand basal area ($Rel.BA_J.HA$) as the ratio between the absolute basal area of a given species $BA_J.HA$ and the total basal area of all species in the plot $BA_{TOT}.HA$. $Rel.N_J.HA$ and $Rel.BA_J.HA$ provide a good overview of invasive species dominance (Curtis, 1959).

From these indicators, we then calculated two proxy of species expansion: the absolute stand basal area growth 'G' (m^2.ha-1) as the difference of the species absolute stand basal area between the second ($BA_{J2}.HA$) and first ($BA_{J1}.HA$) surveys. A positive value of G indicates an increase in species coverage, whereas a negative G indicates a decrease in species coverage in the plot; the relative stand basal area growth '$Rel.G$' (%) as the difference between the species relative stand basal area in the second census $Rel.BA_{J2}.HA$ and relative stand basal area in the first census $Rel.BA_{J1}.HA$ (Daehler (2003) and Hernández et al. (2014), Table 5.1 and Supporting Information Table S3).

We identified the dominant species of the plot (*DOMIN.SP*) as the one presenting the highest species relative stand basal area ($Rel.BA_J.HA$) in the stand. Allometric relationships in trees indicate that basal area is proportional to crown leaf area (Davis et al., 2000) and thus canopy cover and basal areas can be considered equivalent proxies to get the stand dominant species. We then derived *DOMIN.SP8* from *DOMIN.SP* keeping the 8 most important species to avoid having to many levels and grouped the remaining species in the "Other species" level. In addition we retrieved the type of tree (i.e. conifer or broadleaf, *SP.GROUP*) of the dominant species in the plot. Shannon index of diversity ($H1$, unitless) was calculated using the species relative stand basal area of each species present in a plot rather than abundance (Table 5.1 and Supporting Information Table S3) and evenness index of Pieloud ($J1$, unitless) calculated as $H1/log(Richness)$ and constrained between 0 (not even communities dominated by few species) and 1 (totally even community). $H1$, $J1$, $DOMIN.SP8$, $DOMIN.SP$, *SP.GROUP* indicate structure of the plot.

Finally, we then calculated variables that indicate human disturbances: the total basal area removed ($BA_{HARVEST}$, cm2) as the sum of the basal area of each tree indicated as managed and Management which is a boolean variable indicating whether the plot has been managed or not before the second survey (Table 5.1 and Supporting Information Table S3).

Biotic indices abbreviation	Description (Unit)	Calculation	Survey	Country	Main use
R	Species recruitment count at the plot scale (trees. ha-1)	$\sum newtreesijk$	2	GE, SP, WA	Indicators of species expansion between surveys
DBH	Mean diameter at breast height of the species in the plot (cm)	$\frac{1}{N_{ij}} \times \sum DBH_{ijk}$	1	FR, GE, SP, WA	Model driver
$BA_{TOT}.HA$	Total basal area of the plot (cm^2 ha.1)	$\sum BA_1 HA_{ik}$	1	FR, GE, SP, WA	Model driver
$N_{TOT}.HA$	Total number of trees in the plot (trees.ha-1)	$N_J.HA$	1	FR, GE, SP, WA	Model driver
$BA_J.HA$	Mean species absolute basal area (cm^2/ha)	$BA_J.HA$	1 & 2	GE, SP, WA	Indicators of species expansion between surveys
N_J	Mean species absolute density per plot	N_J	1 & 2	GE, SP, WA	Indicators of species expansion between surveys
$N_J.HA$	Mean species absolute density per ha	$N_J.HA$	1 & 2	GE, SP, WA	Indicators of species expansion between surveys
$N_{PLOT.J}$	Number of plots with the species	$N_{PLOT.J}$	1 & 2	GE, SP, WA	Indicators of species expansion between surveys

Biotic indices abbreviation	Description (Unit)	Calculation	Survey	Country	Main use
$PROP_{PLOT.J}$ (%)	Proportion of plots with the species	$\frac{N_{PLOT.J}}{N_{PLOT.TOT}}$	1 & 2	GE, SP, WA	Indicators of species expansion between surveys
$Rel.N_J.HA$	Mean species relative density: % of total tree per ha	$\frac{N_J.HA}{N_{TOT}.HA}$	1 & 2	GE, SP, WA	Indicators of species expansion between surveys
$Rel.BA_J.HA$	Mean relative stand basal area of a given species in a given plot (%)	$\frac{BA_J.HA}{BA_{TOT}.HA}$	1 & 2	GE, SP, WA	Indicators of species expansion between surveys
G	Stand absolute basal area growth	$BA_{J2}.HA_i - BA_{J1}.HA_i$	Diff (2; 1)	GE, SP, WA	Model response
$Rel.G$ (%)	Relative stand basal area growth	$Rel.BA_{J2}.HA - Rel.BA_{J1}.HA$	Diff (2 ; 1)	GE, SP, WA	Model response
$BIO1$	Annual mean temperature (C°)	-	1	FR, GE, SP, WA	Model driver
$BIO12$	Annual precipitation (mm)	-	1	FR, GE, SP, WA	Model driver
CI	Census interval (years)	-	Diff (2; 1)	GE, SP, WA	Model offset
$DOMINSP$	Species with the highest basal area in the plot	$Max(Rel.G).plot$	1 & 2	FR, GE, SP, WA	Indicators of species expansion between surveys

Biotic indices abbreviation	Description (Unit)	Calculation	Survey	Country	Main use
$DOMINSP8$	Eight most frequent species with the highest basal area in the plot	$Max(Rel.G).plot$	1	FR, GE, SP, WA	Model driver
$H1$	Diversity index (Shannon)	$-\sum_{i,=1}^{s=Richness} \frac{BA_J.HA_i}{N_i} log \frac{BA_J.HA_i}{N_i}$	1	FR, GE, SP, WA	Model driver
$BA_{HARVEST}$	Removed basal area (cm^2 ha1)	$\sum_{i,k=HARVEST} BA_1.HA_{ik}$	2	GE, SP, WA	Model driver
$J1$	Evenness index (Pieloud)	$\frac{H1}{log(s=Richness)}$	1	FR, GE, SP, WA	Model driver
$MANAGEMENT$	Presence or absence of management	Yes or No	2	GE, SP, WA	Model driver
$SP.GROUP$	Type of tree dominating the plot (broadleaf or conifer)	$Max(Rel.G).plot$	1 & 2	FR, GE, SP, WA	Indicators of species expansion between surveys & model driver
$SPEI$	Monthly Standardised Precipitation-Evapotranspiration Index of the last 12 months	Averaged on the time period elapsed between the two-sampling procedure	1	FR, GE, SP, WA	Model driver

Table 5.1: Biotic indices calculated from the NFI. Biotic indices abbreviation: abbreviated names of the variables as used in the manuscript. Description: variable description and unit. Calculation: equation used for variable calculation for the kth individual of the ith individual plot of the jth species. Survey: Survey from which the calculation was done (1, 2, both or difference of the two surveys); Country: NFI from which calculation was done (FR = France, GE = Germany, SP = Spain, WA = Wallonia). Main use: Main use of the variable (Model response, Model driver, or Indicators of species expansion).

5.2.3 Climatic data description

We characterized the long-term climate of each plot with annual temperature- and precipitation-related variables with a resolution of 1km x 1km (Fréjaville et al., 2018). To make the variables comparable between different survey dates and countries, we averaged them over the last 15 years before the first survey. We selected the mean annual temperature ($BIO1$) and the mean annual precipitation ($BIO12$), (Table 5.1 and Supporting Information Table S3).

In addition, we used the standardized precipitation evapotranspiration index [SPEI v.2.5 (2017); `http://hdl.handle.net/10261/104742`] to account for temporal variability in drought intensity over the study period. We used $SPEI$ from a gridded dataset at 0.5-degree resolution (Vicente-Serrano et al., 2010) based on potential evapotranspiration and precipitation over a short-term, relative to median values for a long-term reference period, thus reflecting the average climate during this long period. Negative $SPEI$ values indicate lower water availability in the specific period of time than for the reference period (Vicente-Serrano et al., 2010). Here we selected a 12-month time-scale to consider water shortage of both current and previous year to the measurements and we used 1901–2015 as a reference period. For each plot, we calculated the mean $SPEI$ for the time interval between the first and the second inventory campaigns (hereafter, $SPEI$ variables; see Table 1 and Supporting Information Table S3)

5.2.4 Direct comparison between NFI censuses

We first assessed the ability of exotic species to spread at the expense of native species by comparing stand basal area growth between the two surveys according to the dominating species ($DOMIN.SP$) or dominating group ($SP.GROUP$) of the plot. Also, R and $Rel.G$ where spatially represented to investigate change in spatial distribution of both species between the two surveys. We then used the 7 following biotic indicators of species expansion ($BA_J.HA$, N_J, $N_J.HA$, N_{PLOT}, $PROP_{PROP}$, $Rel.N_J.HA$, $Rel.BA_J.HA$) to compare species spread between the two surveys. Because the variables used were not normally distributed, we assessed the median difference through Wilcoxon tests for all these indexes to show the overall patterns of expansion of the two species. Despite the time lag between the two surveys is not accounted for in these analyses, we assume the period of time between surveys is long enough for both species (7-16 years for *Q.rubra* and 7-15 years for *R.pseudoacia*) to identify a stagnation, expansion or diminution in presence, abundance, density and dominance, which could be otherwise hidden by an over-representation of short-time period.

5.2.5 Statistical model of absolute and relative stand basal area growth

To analyse the relative importance of biotic and abiotic factors driving the absolute stand basal area growth (G) and relative stand basal area growth ($Rel.G$) of the species, we calibrated a linear and linear mixed-effects model for each species, using the lm() and lme4() functions from lme4 package (Bates et al., 2015), respectively, in R version 4.0.4 (R Core Team, 2021). We specified normal distribution (Supplementary Figure S1) to model G and $Rel.G$. Each model relates the response Y_i (G or Rel.G) to the covariates following a normal distribution as follow:

$$Y_i = \alpha_0 i + \sum_{h=1}^{10} \beta_h x_{h.i} + \sum_{n=1}^{m} \gamma_n x_{n.i} z_{n.i} + \alpha_{\text{country}.k} + log(CI_i) + \epsilon_i$$

Where $\alpha_0 i$ is an intercept term, $\alpha_{\text{country}.k}$ is the random country intercept that account for sampling differences between each NFI (this effect follows a Gaussian distribution $\alpha_{\text{country}.k} \sim \mathcal{N}(0, \sigma^2_{\alpha_{\text{country}.k}})$); ϵ_i is the residual error following a Gaussian distribution $\epsilon_i \sim \mathcal{N}(0, \sigma^2_{\epsilon_i})$. β_h is the regression coefficient for the hth of 13 fixed effect predictors x_h (including DBH, $N_{TOT}.HA$, N_{J1}, $BA_{TOT}.HA$, $H1$, $J1$, $DOMIN.SP8$, $SP.GROUP$, $MANAGEMENT$,$BA_{HARVEST}$, $BIO1$, $BIO12$, $SPEI$ that were all standardised before the inclusion in the models; see Supplementary tables S3 for summary statistics and VIF in Supplementary table S4; Dormann et al. (2013)) and γ_n the regression coefficient of the nth interaction between fixed effect predictors $x_n.i$ and $z_n.i$ (including several interactions between climatic variables and stand structure or human disturbance variables, see supplementary Table S5a-d). To avoid the potential bias caused by the different years of NFIs campaigns (See Supplementary Table S1), we used an offset on census time (CI). We therefore assumed a proportional increase of the response variable along elapsed time.

5.2.6 Model selection

For G and $Rel.G.$ models, we used a stepwise regression approach using a forward selection. We started with a null model and added variables and interactions until none improves the model significantly. We compared models using the BIC criteria (Supplementary Table S5a-d) and retained the most parsimonious one. Finally, we calculated the Variance Inflation Factor (VIF) for the most parsimonious model to ensure the absence of collinearity between our predictors (i.e. removal of combinations with VIF > 10; Dormann et al. (2013)).

5.2.7 Model performance and validation

To control for the linearity, homogeneity of variance, collinearity, outliers, and normality of residuals of the models assumptions, we used the check_model() function of the performance package (Supplementary information Figure S1-S4). The goodness-of-fit was evaluated with a 10-fold cross validation using lmvar package (Partners, 2019). It allowed us to calculate the Mean Squared Error (MSE), Mean Absolute Error (MAE) and the Root Mean Squared Error (RMSE) to assess the model accuracy (Table 5.2). We also plotted observed versus predicted distribution of G and $Rel.G$ (Supplementary Figure S5). The proportion of variance explained was estimated with marginal and conditional r-squared, using R 4.0.4 (R Core Team, 2021) and the package Performance (Lüdecke et al. (2020); Table 5.2).

5.2.8 Model spatial predictions

For both species, we predicted $Rel.G$ across the NFI plots in plots where *Quercus rubra* and *Robinia pseudoacacia* were recorded at least once (including France). As the density ($N_{TOT}.HA$), the total basal area removed ($BA_{HARVEST}$) and (CI) were not present in the French inventory, we fixed their value at the mean value observed in the other inventories. For density ($N_{TOT}.HA$) and the total basal area removed ($BA_{HARVEST}$) we fixed the mean value according to the management status (managed and not managed).

5.3 Results and discussion

5.3.1 Direct comparison between NFI censuses

Quercus rubra **and** ***R.pseudoacacia*** **presence relative to native species**

Quercus rubra and *R.pseudoacacia* have increased their presence between the two surveys in broadleaved-, coniferous- and conspecific dominated stands. The number of *Q.rubra* and *R.pseudoacacia* dominated stands has increased drastically between the two surveys (+41 plots and +12 plots respectively) (Figure 5.1a and b) although their presence was higher under non-similar trees rather than conspecific: at the second survey time for instance, *Q.rubra* was present in 136 conspecific-dominated stands whereas it was present in 189 non-similar species-dominated stands (122 broadleaved and 67 coniferous dominated stands; Figure 5.1a). Similarly, at the second survey, *R.pseudoacacia* was present in 77 conspecific-dominated stands whereas it was present in 131 non-similar species-dominated stands (94 broadleaved and 37 coniferous dominated stands; Figure 5.1b). In both species, occurrence was higher under broadleaf than coniferous species.

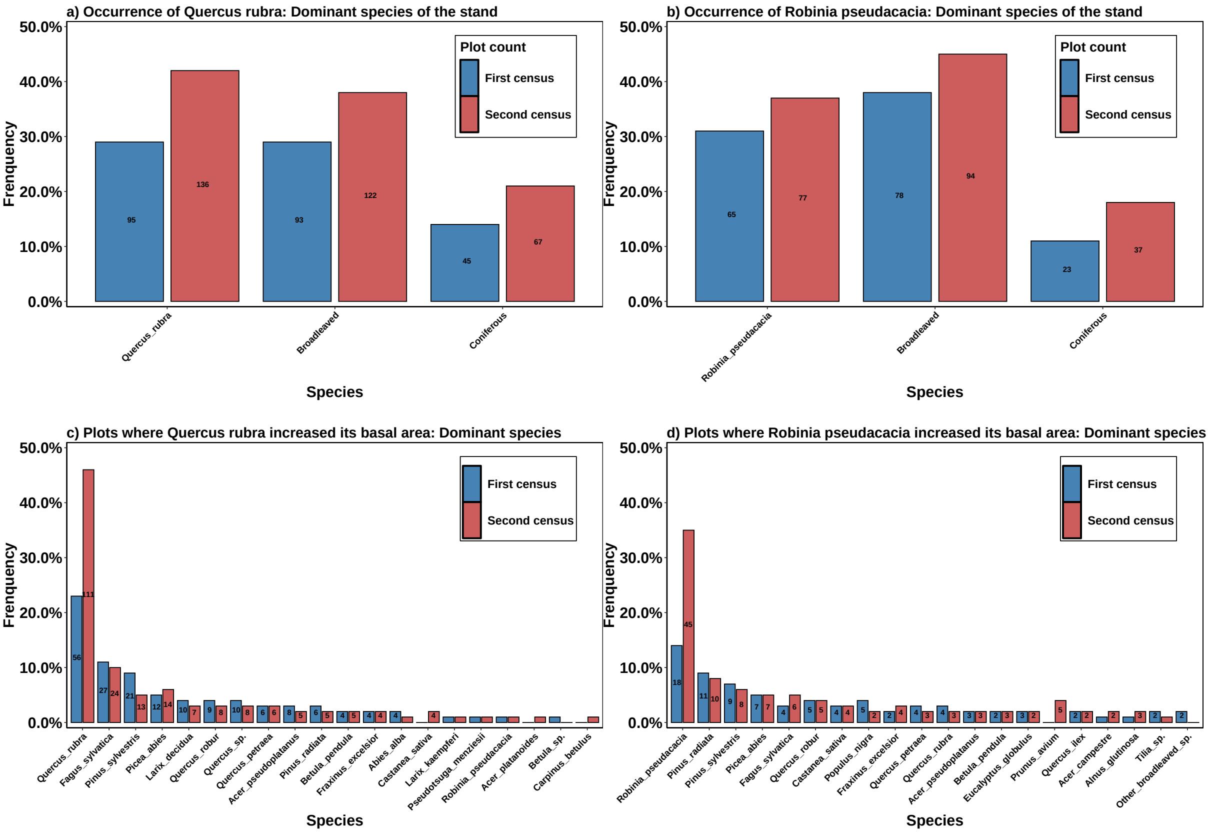

Figure 5.1: Barplots representing the occurrence of the species according to the dominated group of species for a) *Quercus rubra* and b) *Robinia pseudoacacia*. And representing the dominant species of the plots in plots where c) *Quercus rubra* cover has increased and d) *Robinia pseudoacacia* cover has increased.

Moreover, both invasive species co-occur and increased their coverage in plots dominated by many different species. *Q. rubra* co-occurs more with *Fagus sylvatica* (27 and 24 plots at first 'T1' and second survey 'T2', respectively), *Pinus sylvestris* (21 plots at T1 and 13 plots at T2) and Picea abies (12 plots at T1 and 14 plots at T2) while *Robina pseudoacacia* co-occurs more with *Pinus radiata* (11 plots at T1 and 10 plots at T2), *Pinus sylvestris* (9 plots at T1 and 8 plots at T2) and *Picea abies* (7 plots at T1 and 7 plots at T2). Many of the plots where either of *Q.rubra* or *R.pseudoacacia* were present but that were dominated (in terms of coverage) by any other species at the first survey, have become dominated by a different species at the second survey. Furthermore, most of the plots where either *Q.rubra* or *R.pseudoacacia* cover increased have become dominated by either of these two species (56 plots at T1 and 111 at T2 for *Q.rubra*; 18 plots at T1 and 45 at T2 for *R.pseudoacacia*, Figure 5.1c-d).

Our results show that *Q.rubra* progressed considerably under conspecific individuals although *R.pseudoacacia* seems to progress more under dissimilar neighbors, especially under broadleaf species, suggesting a direct competitive effect and potential species replacement in several plots. However, several confounding effects could also explain the loss of coverage of several species at the benefit of *Q. rubra* and *R. pseudoacaica*. Drought, for instance, strongly affects *Pinus sylvestris* and *Fagus sylvatica* in Europe (Durrant et al., 2016a; Durrant et al., 2016b). In addition, the identity of the dominant species under which *Q. rubra* and *R.pseudoacacia* could be found in Europe are those that are most commonly found in in the national forests of our studied country. In Germany for instance, forests are mainly spruce (25%), pines (22%) and beech (15%) plantations, with only 10% of oak forests (Federal-Ministry-of-Food-Agriculture-and-Consumer-Protection, 2021); this could largely explain that *Q. rubra* and *R.pseudoacacia* were most commonly distributed in *P. abies*-, *P. sylvestris*- and *F. sylvatica*- dominated stands, with relatively less plots dominated by oak trees. However, indications about forest management practices comfort our analysis that the distribution patterns evidence a natural spread of the species. *Q.rubra* is found in mono-specific plantations in Spain (Galicia, Navarra; Santana et al. (2015)) and either mono-specific plantations or mixtures with *F. sylvatica* in Germany (Ruhm, 2013). Similarly, *R. pseudoacacia* is usually planted as a monoculture, despite having mixed plantations with pines (*Pinus spp.*), oaks or maples (*Acer spp.*) in Germany (Nicolescu et al., 2020) and its traditional forest management in Spain includes a combination of silvopastoralism, coppicing, and short-rotation forestry that are mostly regularly managed pure *Robinia* stands (Vıtková et al., 2020). Thus, these monoculture and mixed plantations are mostly represented by the conspecifi-dominated plots in our data, and a part of the plots dominated by *F. sylvatica* (for *Q.rubra*) and *Pinus spp* (for *R.pseudoacacia*) but does not explain the presence of either species (*Q.rubra* or *R.pseudoacacia*) in other-species-dominated stands. Overall, *Q. rubra R.pseudoacacia* individuals present under other stands would be issued from natural regeneration after spreading of the species. Nonetheless, we cannot exclude that plots with new occurrence of either of the two species might always had contained *Q rubra* or *R.pseudoacacia* tree in the surroundings that had not been counted at the first survey.

***Quercus rubra* and *R.pseudoacacia* occurrence, abundance and relative dominance increased all across the latitudinal gradient**

In the first survey, *Q.rubra* and *R.pseudoacacia* were present in 0.25% (233 plots) and 0.17% (166 plots), respectively, of the total plots recorded in the NFI. By the second survey (on average 12 years later) they appeared in new plots where they were not in the first survey in 0.34% (325 plots) and 0.22% (208 plots), respectively (Table 5.2). When analysing NFI plots in which both species were present, we found that the number of trees per plot and per hectare, basal area, and relative density of both species significantly increased during this period. The number of trees per hectare and the relative density having almost doubled for *Q.rubra*, going from 126 to 219 and from 0.19 to 0.39, respectively (Table 5.2).

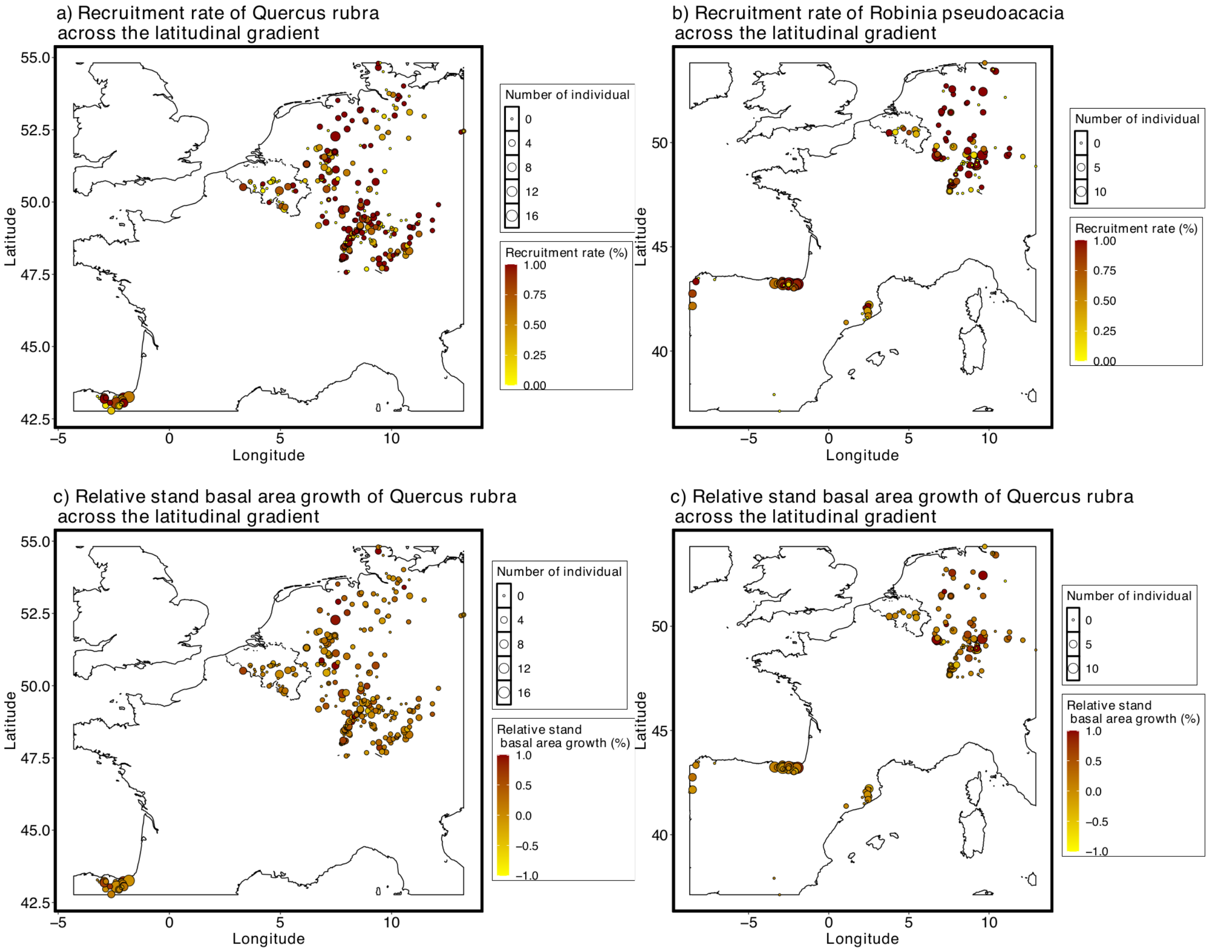

Figure 5.2: Maps representing (a,b) the recruitment rate with highest values in red, and lowest in yellow. The number of trees recruited by plot is represented by the size of the point. For instance: Big red dots means there is high proportion of recruitment made of many new individuals. a) *Q.rubra* and b) *R.pseudoacacia*. And (c,d) maps representing the relative stand basal area growth by plot with highest values in red and lowest in yellow. The number of trees recruited by plot is represented by the size of the point. For instance: Big red dots means there is high proportion of recruitment made of many new individuals. c) *Q.rubra* and d) *R.pseudoacacia*

Although all indicators displayed significant differences for both species, the increase has been larger for *Q.rubra* than *R.pseudoacacia*. In addition, our results show that both recruitment rates and relative stand basal area growth were high all across the species ranges, even though Germany displays the highest recruitment rates, for both *Q.rubra* and *R.pseudoacacia* (Figure 5.2 a-d).

Species	*Quercus rubra*					*Robinia pseudoacacia*				
Indicators	First inventory	Second inventory	Difference	Yearly difference	p.value	First inventory	Second inventory	Difference	Yearly difference	p.value
Absolute density $N_J.HA$	126.325	219.203	92.878	7	0.000	129.217	181.525	52.308	4,43	0.000
Absolute basal area $BA_J.HA$ (m2/ha)	7.302	10.526	3.224	0,25	0.000	5.547	8.060	2.513	0,2	0.000
Relative basal area $Rel.BA_J.HA$: % of total basal area	0.346	0.400	0.054	0	0.001	0.311	0.320	0.009	0	0.153
Relative density $Rel.N_J.HA$: % of total tree per ha	0.196	0.393	0.197	0,01	0.000	0.285	0.363	0.078	0	0.095
Number of trees per plot N_J	1.704	3.270	1.566	0,13	0.000	1.786	3.034	1.248	0,11	0.000
Number of plots with the species $N_{PLOT.J}$	233.000	325.000	92.000	7,08	NA	166.000	208.000	42.000	3,41	NA
Proportion of plots with the species $PROP_{PLOT.J}$	0,25	0,34	0,11	0,01	NA	0,17	0,22	0,05	0	NA

Table 5.2: Comparison of several invasive characteristics in the first and second campaign, all country confounded

The significant increase in presence, abundance, relative dominance and relative density of *Q. rubra* and *R.pseudoacacia* in the European forests are signs of their ability to disperse and establish in European forests. This recruitment in new plots could result from dispersal by animals such as jays and rodents for *Quercus rubra* (Myczko et al., 2014; Bieberich, 2016; Merceron et al., 2017) that are both capable of distant dispersal of seeds, displacing acorns at distance from the original stands. Besides the strong capacity for clonal growth of *R.pseudoacacia* (Chang et al., 1998) in addition to its deliberate cultivation in open landscapes and large-scale afforestation campaigns could explain its increased presence between the two inventories (Vıtková et al., 2020).
Overall, the presence of juvenile and mature trees (DBH $>$ 10cm) of *Q.rubra* and *R.pseudoacacia* mostly occurred under non similar canopies in the first survey and both have increased their presence of juvenile and adults in the second survey, even under stands presenting no mature tree of either species in the first survey. These results confirm our first hypothesis: These two species are able to disperse, develop new populations and have increased their presence and dominance relatively to the native species.

5.3.2 Modelling species absolute and relative stand basal area growth

Drivers of exotic species absolute stand basal area growth

The root mean squared error (RMSE) and the mean absolute error (MAE) of absolute stand basal area growth (G) models were respectively 5.57 and 4.14 for *Quercus rubra* and 4.59 and 3.38 for *Robinia pseudoacacia.* The marginal r-squared ranged from 40% in *Quercus rubra* to 22% for *Robinia pseudoacacia* and the BIC criteria ranged from 1980.85 in *Quercus rubra* to 1239.57 for *Robinia pseudoacacia* (Table 5.3).

In both species, absolute stand basal area growth (G) was significantly lower in managed plots than unmanaged plots (Figure 5.3a and b, Supplementary information figure S6). In addition, decreased G was associated with increase in the total removed basal area of the plot ($BA_{HARVEST}$), increase in the total basal area of the plot ($BA_{TOT}.HA$, Supplementary information figure S7a-b) and increasing mean temperatures ($BIO1$; Figure 5.4a and b). We also found decreased G associated with increasing evenness of the community ($J1$, Supplementary information figure S8a) only for *Robinia pseudoacacia*, but no diversity ($H1$) effect.
In *Quercus rubra* we found an increase in G associated with an increase in precipitation ($BIO12$), density ($N_{TOT}.HA$), and increase in $SPEI$ (relatively less dry conditions, Supplementary information figure S9a). G was significantly lower in conspecific dominated plots than by other broadleaved species (Supplementary information figure S6b). In addition, when removed basal area of the plot ($BA_{HARVEST}$) was increasing, G was

	Coefficient (Std. Error) Pr(>|t|)			
Species	*Quercus rubra*		*Robinia pseudoacacia*	
Model	Growth G	Relative Growth $Rel.G$	Growth G	Relative Growth $Rel.G$
Predictor				
$BA_{TOT}.HA$	-1.81 (0.36) 0	-0.04 (0.02) 0.01	-0.98 (0.35) 0.01	-
$BIO1$	-0.84 (0.42) 0.04	0.04 (0.02) 0.01	-0.9 (0.34) 0.01	0.05 (0.02) 0.03
$BIO12$	0.84 (0.41) 0.04	0.04 (0.02) 0.03	-	-
$BA_{HARVEST}$	-20.92 (2.45) 0	-0.15 (0.05) 0	-6.36 (2.38) 0.01	-
$J1$	-	-	-3.12 (0.97) 0	-
$Management$	-2.21 (0.78) 0	-	-2.12 (0.78) 0.01	-
$SPEI$	4.41 (2.08) 0.04	-0.22 (0.08) 0.01	-	-0.4 (0.09) 0
N_{HA}	1.04 (0.42) 0.02	-0.05 (0.02) 0	-	-0.04 (0.02) 0.03
SPGROUP:BLEAVED	-1.8 (0.85) 0.03	0.19 (0.04) 0	-	0.13 (0.04) 0
SPGROUP:BLEAVED *$BA_{HARVEST}$	15.77 (3.04) 0	-	-	-
SPGROUP:CONIF	0.1 (0.99) 0.92	0.26 (0.04) 0	-	0.21 (0.05) 0
SPGROUP:CONIF *$BA_{HARVEST}$	18.81 (3.08) 0	-	-	-
N_{J1}	-	0.01 (0) 0.03	-	-
MAE	4.13 (0.88)	0.13 (0.02)	3.53 (0.89)	0.14 (0.02)
MAE (scaled)	1.93 (0.41)	4 (0.66)	2.96 (0.75)	-8.86 (-1.48)
R2 (adj)	0.4	0.3	0.22	0.25
RMSE	5.47 (1.36)	0.19 (0.04)	4.74 (1.43)	0.21 (0.04)
RMSE (scaled)	2.56 (0.64)	5.58 (1.08)	3.97 (1.2)	-12.91 (-2.69)

Table 5.3: Significant variables in each model with their respective coefficient, standard error (in parenthesis) and p-value for G and $Rel.G$ models for both species. Species: Species name; Model: which model; Predictor: Variable name. '-' indicates that the variable has not been included in the most parsimonious model. The last five rows are the statistical evaluation of the models. AIC: Akaike information criterion; R2adj: Adjustedl r-squared; RMSE normalized: The RMSE is the square root of the variance of the residuals. The normalized RMSE is the proportion of the RMSE related to the range of the response variable. MAE: Mean absolute error. MAE (scaled) is the proportion of the MAE related to the range of the response variable.

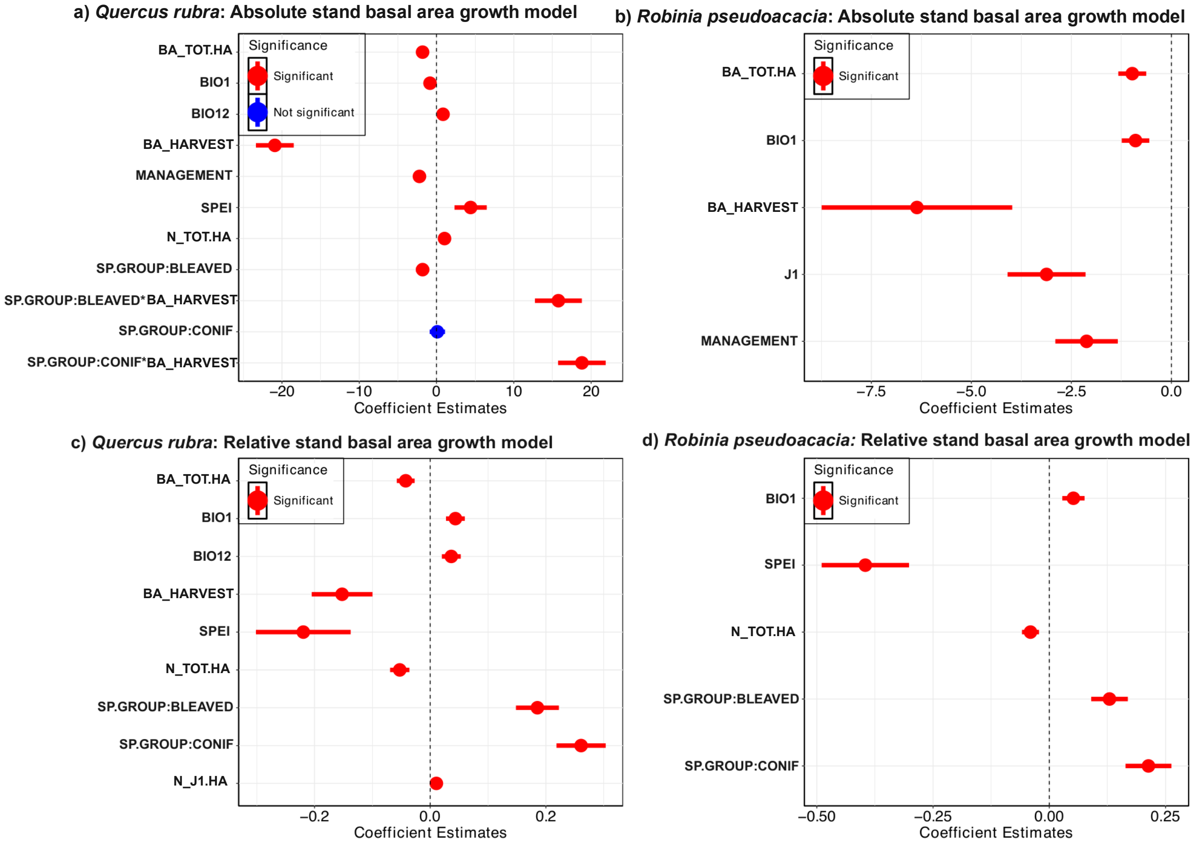

Figure 5.3: Model coefficient and standard errors for stand basal area growth model for a) *Quercus rubra* and b) *Robinia pseudoacacia*. Model coefficients and standard errors for relative stand basal area growth model for c) *Quercus rubra* and d) *Robinia pseudoacacia*.

strongly decreasing in *Quercus rubra* dominated plots while remaining stable or slightly increasing in the coniferous and broadleaved dominated plots (Figure 5.3a and b).

Drivers of exotic species relative stand basal area growth

The root mean squared error (RMSE) and the mean absolute error (MAE) of relative stand basal area growth ($Rel.G$) models were respectively 0.18 and 0.13 for *Quercus rubra* and 0.21 and 0.14 for *Robinia pseudoacacia*. The marginal r-squared in relative stand basal area growth ranged from 30% in *Quercus rubra* to 25% for *Robinia pseudoacacia* and the BIC criteria ranged from -13.20 in *Quercus rubra* to 33.78 for *Robinia pseudoacacia* (Table 5.3). In both species, relative dominance progression ($Rel.Domin$) was significantly lower in conspecific dominated plots than in coniferous and broadleaved dominated plots (Figure 5.3c and d and Supplementary information figure S6c-d). In addition, increased $Rel.G$ was associated with an increase in relative drought (decreasing $SPEI$, Supplementary information figure S9b-c) and increasing temperature ($BIO1$, Figure 5.4c and d). Increase in $Rel.G$ was also associated with decreasing density ($N_{TOT}.HA$). In *Quercus rubra* we also found increase in $Rel.G$ associated with increase in precipitation ($BIO12$) and the number of conspecific trees at the first survey (N_{J1}, Supplementary

Information Figure S8b). Increased $Rel.G$ in this species was also associated with a decrease in both the total basal area of the plot ($BA_{TOT}.HA$, Supplementary information figure S7c) and the total removed basal area of the plot ($BA_{HARVEST}$). In addition, we found no significant association between $Rel.G$ and evenness ($J1$) or diversity ($H1$) in any of the species (Figure 5.3c,d).

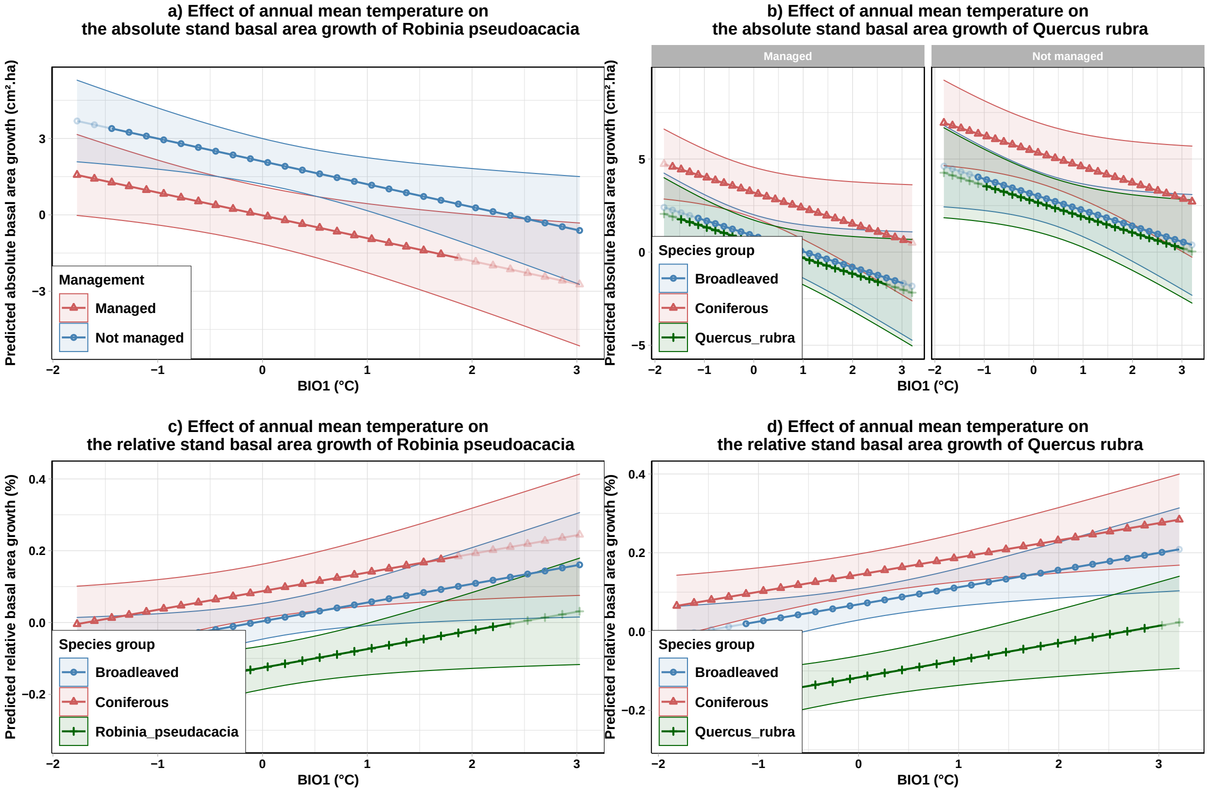

Figure 5.4: a) *Quercus rubra* and b) *Robinia pseudoacacia* stand basal area response to increased temperature. c) *Quercus rubra* and d) *Robinia pseudoacacia* relative stand basal area response to increased temperature.

The drivers of invasibility change along large climate gradients

Our predictions show changes in relative stand basal area growth could occur all across the latitudinal gradients range for *Quercus rubra* with the highest $Rel.G$ located in southern France and Spain, central France and Germany (Figure 5.5a). Conversely, only the southern part of the range of *Robinia pseudoacacia* displayed high values of increased $Rel.G$ while the northern part of its range indicate decreased $Rel.G$ (Figure 5.5b).

Human disturbances and climate are main drivers of species invasion

Our results confirm that human disturbances is one of the main drivers of species invasion. *R.pseudoacacia* absolute stand basal area was decreasing in plots that were denser ($N_{TOT}.HA$), containing more diverse communities ($J1$) and that displayed evidence of management. Together, these results confirm that *R.pseudoacacia* is more likely to spread in open area (following land abandonment for instance) and that its plantation should be mixed with other species favouring more diverse communities, boosting the resilience of the local ecosystems to invasion. This is in line with other studies suggesting that regularly managed buffer zones surrounding *R.pseudoacacia* plantations should be established and could act as a biological barrier against its natural regeneration by root suckers (Vıtková et al., 2020). Similarly, *Quercus rubra* absolute stand basal area was increasing in sparse ($N_{TOT}.HA$) plots that were managed and dominated by dissimilar species, suggesting that intensive management strategies in plots where it occurs could boost its invasion capacity.

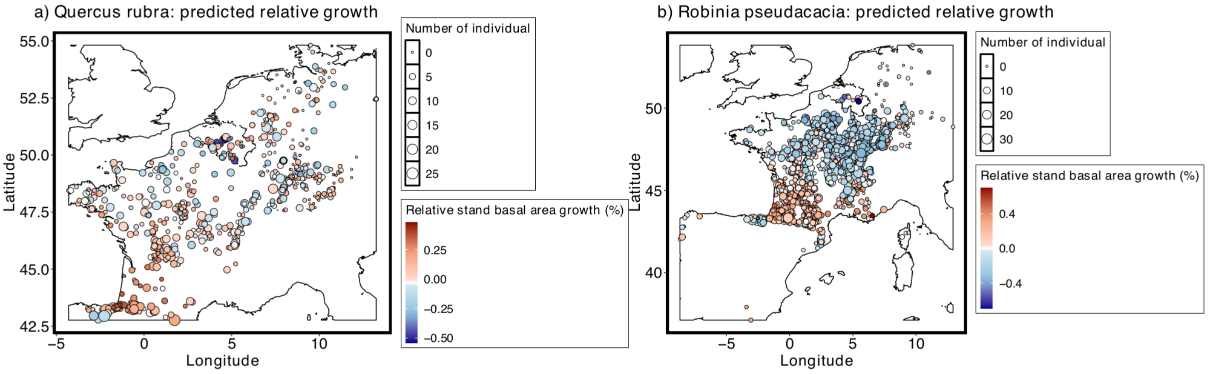

Figure 5.5: Predicted maps of relative stand basal area growth for a) *Quercus rubra* and b) *Robinia pseudoacacia* with highest values in red, and lowest in yellow.

Our results also confirm that temperature and drought are boosting *Q.rubra* and *R.pseudoacacia* growth at the expense of other species. Despite both species absolute stand basal area growth (G) are negatively affected by an increase in temperature (Figure 5.3a-b and Figure 5.4a-b) and relative drought (Figure 5.3a-b and Supplementary information figure S9a), our results show that drier and warmer conditions also trigger their growth relatively to other species ($Rel.G$) (Figure 5.3c-d and Figure 5.4c-d and Supplementary information figure S9b-c). This response in relative growth to climate confirm the better drought tolerance of *Q. rubra* and *R. pseudoacacia* relatively to other species. *R. pseudoacia* is relatively more drought tolerant in comparison with other native deciduous tree species because of its ecophysiological adaptations (Xu et al., 2009; Minucci et al., 2017) and fast recovery after drought stress (Moser et al., 2016). Similarly, several studies have shown a better resistance to drought of *Q.rubra* than native *Q. petraea* and *Q. robur* ((Lorent et al., 2000; Dressel et al., 2002) which is largely explained by its lower water consumption as well as its growth, less affected by water deficit than other species (Nicolescu et al., 2020).

This is further confirmed by our predictions, showing that both *Quercus rubra* and *Robinia pseudoacacia* are likely to grow more than other species in drought-prone areas (Figure 5.5a-b) with *Quercus rubra* benefiting from increased drought and warmer conditions in Germany, Wallony, France and Spain whereas *Robinia pseudoacacia* increases its growth in southern France and Spain following drought gradient.

Overall, drier conditions could enhance spread of *Q.rubra* and *R.pseudoacia* relatively to other species, less adapted or more sensitive to dry conditions which confirm our second hypothesis: climate is triggering exotic species expansions. Furthermore, these results suggest that stress tolerance is a key trait to invasion success (Dukes et al., 1999). These findings could indicate a rapid change in species composition to come with the incoming increase in drought frequency and intensity in the area we have studied (Astigarraga et al., 2020; Buras et al., 2020; Trenberth et al., 2014), with potential negative ecological and economical outcome.

5.3.3 Limitations and perspectives

The data analysed throughout this study concern trees that were already established at the first survey. Hence, the patterns of expansion or colonization we inferred should be taken with caution and could represent the fast growth of young individuals that were already presents in the first survey but too small to be accounted for. To assess the dispersal capacity of *Q. rubra* and *R.pseudoacaica*, a spatial landscape analysis should be performed to take into account propagule pressure, through evaluation of the distance to the closest planted mono-specific *Q. rubra* and *R.pseudoacacia* stands. Alternatively, a conjoint analyses of their growth, recruitment and mortality would help quantify the population and expansion dynamics. Further work should compare drought related traits in invasive and native species, both within native and non-native habitats to compare spreading capacity and better characterize species invasiveness.

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"What men want is not knowledge, but certainty" Bertrand Russell

Chapter 6

General discussion and conclusion

In this thesis I studied the main demographic processes of the major native and exotic tree species inhabiting European forests from National Forest Inventory records measured along large latitudinal gradients. In particular, I analysed mortality and recruitment of the major native tree forests and the relative growth of two invasive trees. My results can be used to evaluate the future of forests in Europe, the potential impact of climate change on demography and ecosystem dynamics and guide forest management practices. My main results were i) Mortality in European forests is highest toward the climatic trailing edge and it is mostly driven by drought whereas the intensity of mortality is triggered by competition, drought and high temperatures and was uniformly scattered across species ranges; ii) Recruitment of European forests is more limited by competition than by drought and it does not differ across species ranges; iii) The risk of invasion by exotic tree species is higher in southern European forests and is triggered by drought and warmer temperatures.

6.1 Tree mortality in Europe

In the third chapter of this thesis, I investigated the drivers of tree mortality across the distribution range of 20 European tree species. I found that competition is the most important driver of tree mortality across species ranges, whereas average climatic conditions are strongly affecting mortality at the species range margins. These results confirm the previously described association between large mortality rates and increased competition (Dietze et al., 2011; Lutz et al., 2006; Das et al., 2016; Taccoen et al., 2019; Luo et al., 2011). I found that the effect of competition on mortality was more pronounced than that of average climatic variables all across species distribution ranges and regardless of the environmental conditions, which is confirmed by previous studies (Condés et al., 2015; Luo et al., 2013; Ruiz-Benito et al., 2013). Furthermore, our results suggested that inter-specific competition could have a buffering role during drought events. This is in agreement with previous studies showing that the change from facilitation to competition across species ranges is mainly driven by environmental conditions (drought in our case) that can modulate tree relationships in mixed forests (Pretzsch et al., 2013). In a broader context, these results confirm the key role of competition for stabilizing ecosystems (Kunstler et al., 2016) and coexistence through mechanisms such as conspecific density dependence (intra-specific competition) and niche complementarity between species (Rio et al., 2017).

Although some studies attributed tree mortality solely to competition intensity (Thorpe et al., 2012), many others, including those that I showed in my thesis, showed that temperature and drought are major drivers of tree mortality. For instance, tree mortality increases with warmer and drier summer conditions, as well as with high seasonal variability in precipitation (Neumann et al., 2017). In France, a recent study pinpointed the importance of competition and management in explaining high mortality rates, with 18 species out of the 43 studied also showing a strong response to climate, especially temperature (Taccoen et al., 2019).

My results showed that it is possible to dissociate intense mortality events from background mortality using National Forest Inventories. On one hand, background mortality is higher at the climatic trailing edge than in other parts of the range for *Abies alba*, *Picea abies*, *Pinus sylvestris*, *Castanea sativa*, *Pinus pinea* and *Pinus nigra* and it is mostly driven by drought, suggesting that mortality plays a critical role in delimiting the driest part of the species ranges (Gaston, 2009; Benito-Garzón et al., 2013b; Ruiz-Benito et al., 2017; Benito-Garzón et al., 2018), in both temperate and Mediterranean species. Previous studies identified similar patterns in *Fagus Sylvatica* and *Pinus sylvetris* (Archambeau et al., 2020; Anderegg et al., 2019). These increased mortality at trailing edge suggested species may contract their ranges in the near future as drought induced mortality is rising in Europe (Senf et al., 2020) exponentially (Greenwood et al., 2017). In addition, drought increased have caused approximately 500,000 ha of excess forest mortality between 1987 and 2016 in Europe (Senf et al., 2020) and has already caused considerable damage in 2018 and 2019 (Buras et al., 2020; Schuldt et al., 2020), which likely induce disastrous effects in these areas.
On the other hand, I showed that the intensity of mortality is scattered across the distribution range of most species and it is triggered by increasing temperature at the climatic leading edge for *A. alba*, *Fraxinus excelsior*, *Pinus halepensis*, *Pinus nigra*, *Pinus pinea*, *Q. ilex*, *Q. petraea* and *Q. robur*. It suggests that the climatic leading edge is likely to be threatened by incoming change in temperature, via release of winter pathogens for instance (Kliejunas, 2010). My results on intensity of mortality were similar to previous European studies showing increased background mortality associated with warmer temperatures at the northern margin of the species ranges (Neumann et al., 2017; Ruiz-Benito et al., 2013). The absence of correlation between the intensity of mortality and drought that I found was surprising, as we could expect larger events of mortality in dry areas (Young et al., 2017). Both my results on the intensity of mortality and those of background (Neumann et al., 2017; Ruiz-Benito et al., 2013) showed high mortality at the leading edge of species range, suggesting that these species could experience temperature-induced range contraction. These observations could be worse than depicted as France, Germany, Sweden, Finland

and Belgium appear as hotspot of drought induced mortality after 2018 drought (Buras et al., 2020).

Overall, my results on tree mortality at large climatic gradients have several implications in forestry management in European forests. Most of the species I studied are valuable and economically important. For instance *Pinus sylvestris* whose forests now exceed 28 million hectares in Europe or *Quercus robur*, both of which are amongst the most economically important trees in Europe. As competition is an important component of both die-off and background mortality, reduced competition through management practices such as basal area reduction could be used to mitigate high mortality rates (Bradford et al., 2017). In addition, the increased pathogen and insect outbreaks to come in response to temperature augmentation could be mitigated by the presence of other species in comparison to monospecific stands (Jactel et al., 2017). Therefore, my results suggest that management practices that favor tree diversity over monoculture would be beneficial in a global change context.

6.2 Recruitment of trees in Europe

In the fourth chapter of my thesis, I investigated the drivers of tree recruitment across the range of 18 European tree species. I showed that recruitment was strongly limited by competition and often depended on age, or growth rate of the plot, whereas the role of drought in tree recruitment was only evident in interaction with tree competition. My results showed that the characteristics of the existing forest such as competition, density and tree size are the most important drivers of tree recruitment over the entire geographic range regardless of the environmental conditions, for any species. These results were in agreement with previous studies, suggesting that younger and denser forest areas containing many small individuals produce more offspring because of a reduced competition for light (Klopcic et al., 2012; Yang et al., 2015; Kolo et al., 2017). My results also confirmed that the effect of competition on tree demography does not vary with climatic marginality, as previously evidenced (Kunstler et al., 2020).
Moreover, I showed that conspecific basal area is the strongest driver of recruitment, with high conspecific basal area inducing strong decrease in recruitment, as shown in several other studies based on National Forest Inventories across Europe (Zell et al., 2019; Klopcic et al., 2012). This result suggests that conspecific negative density dependence (CNDD) is a major driver of species recruitment and forest dynamics, as it was largely evidenced in tropical forests and more recently in temperate ones (LaManna et al., 2017; Zhu et al., 2015; Johnson et al., 2014; Jevon et al., 2020; Lines et al., 2020).

I also showed that some species such as *P. sylvestris*, *F. sylvatica*, *P. abies*, *Q. ilex*, and *P. pinea* may benefit from other species presence, especially under favorable climatic conditions when facilitation process occur, either during the germination process by decreasing seedling mortality though increase water availability (Granda et al., 2014; Muledi et al., 2020) or through nursing effect of vegetation that enhance seedling survival and growth (Batllori et al., 2009). It could also indicate niche complementarity between co-occurring neighborhood species (Ruiz-Benito et al., 2014; Jactel et al., 2017). However, contrarily to our results on mortality where we showed that interspecific competition might buffer from harsh climatic conditions, in tree recruitment, this positive effect can turn into a negative one under less favorable conditions. For instance, at high level of interspecific competition, we evidenced increased recruitment in relative low drought conditions but strongly decreasing recruitment at relative high drought conditions. These results demonstrated the strong direct effects of competition on recruitment and the interactions between competition and climate, as it was previously evidenced on both growth and survival (Kunstler et al., 2020). In the context of climate change, all these results suggested that increase drought frequency and intensity could increase the negative effect of interspecific competition, boosting the negative effect of drought in denser forests, favoring more competitive species such as broadleaf species (Vayreda et al., 2016) or maybe invasive ones (Vıtková et al., 2020; Nicolescu et al., 2020b). Similar results have already been observed on recruitment (Carnicer et al., 2014) but also on other demographic traits such as mortality, which is disproportionally impacted by drought in dense areas (Young et al., 2017).

Although I found that intra-specific competition influences recruitment under certain environmental conditions, I also showed that for most species, climate in itself is not the most important driver of tree recruitment, in agreement with previous studies (Zell et al., 2019). Yet, there is controversy on the role of climate in recruitment, with some authors claiming a strong effect of climate: for instance, spring temperatures and heterogeneity in soil moisture were found to be key drivers of recruitment in a 10 years monitoring of 5 species (Ibáñez et al., 2007). Similarly, drought is suggested to be a threat for the recruitment of several species in the Mediterranean region. For instance, an observational study showed that several species, including *Pinus sylvestris* and *Pinus nigra* were strongly recruitment limited by rainfall variability, with recruitment completely collapsing in very dry year (Mendoza et al., 2009). Similarly, an experimental study showed that the reduction in frequency of wet summer was a strong driver of tree recruitment, more important than drought, except in *Q.ilex* that was able to recruit new individuals even in the driest years (Matías et al., 2012). These studies demonstrated the importance of extreme climatic events on species recruitment. It is likely that the average drought index we used does not adequately represent these climatic extremes. Furthermore, several authors reported stronger effect of competition over drought and climate on many species in Europe, North

America and Asia (Li et al., 2011; Xiang et al., 2016; Zell et al., 2019). In agreement with these studies, our results showed that recent climatic change (represented by relative drought in our study) plays a secondary role in driving tree recruitment, as previously suggested for other demographic traits such as mortality or growth (Astigarraga et al., 2020).

Contrary to the mortality processes, recruitment did not indicate a generalized stronger response to drought in the warm margin of the species ranges, nor did it highlight any difference between the cold margin, the warm margin and the core area. Nevertheless, several drought sensitive species such as *F. sylvatica*, *P. sylvestris*, *A. glutinosa* and *B. pendula* displayed lower recruitment at their the trailing edge while *A. alba* and *A. pseudoplatanus* displayed lower recruitment at their leading edge, suggesting an uncertain future for these species at their range margins. By contrast, *P. pinea* and *Q.ilex* displayed higher recruitment in their trailing edge. My results are consistent with other studies demonstrating that Scots pine and beech are being progressively replaced by oak species in the Pyrenees (Galiano et al., 2010; Peñuelas et al., 2007) while Mediterranean oaks such as *Q.ilex* are expanding their range and replace *Pinus sp.* in the Mediterranean region, promoted a combination of climate change, fires and the management legacies (Carnicer et al., 2014).
Altogether, these results suggested a potential upward shift of the treeline, both in the Alps and in the Pyrenees as a response to extreme climatic events in interaction with competition. In addition, as competition strongly drives recruitment interaction negatively with climate, these results suggest that management strategy such as selective thinning could be an efficient way to mitigate climate change (Astigarraga et al., 2020).

6.3 Invasive species in Europe

In the fifth chapter of this thesis, I evaluated whether two exotic species, *Q.rubra* and *R.pseudoacia*, have expanded their ranges and relative dominance at the expense of native species and identified the underlying drivers of this expansion across European forests. I showed that both species have increased their presence and relative dominance between the survey periods, and that human disturbances (management) and both warmer and drier climate were the main drivers of their growth, likely inducing their range expansion northwards and southward. My results showed that *Q.rubra* and *R.pseudoacacia* progressed considerably in conspecific- and dissimilar species- dominated plots. In addition, we found a significant increase in presence, abundance, relative dominance and relative density of *Q. rubra* and *R.pseudoacacia* in several country confirming their ability to disperse and establish in European forests, as previously evidenced (Major et al., 2013;

Sitzia et al., 2016). These results suggested a direct competitive effect and potential species replacement in several European countries confirmed by their fast growing and good competitive abilities (Enescu et al., 2013; Nicolescu et al., 2020b).

My results also highlighted that management is one of the main drivers of their growth as both species displayed lower growth in managed than unmanaged areas. Hence, the relatively sparse forests in which they are found, resulting from either intensive management of dissimilar species, either from land abandonment are the most susceptible environment to be invaded. This is confirmed by several studies showing that they are spreading fast in European forests, colonize abandoned fields and may become more common in the transitional zones between Mediterranean and temperate areas, together with other exotic species such as *Ailanthus altissima*, *Prunus serotina*, and *Acer negundo* (Camenen et al., 2016; Vıtková et al., 2020). Therefore, a management strategy that favours mixed plantations with more diverse community for *R. pseudoacacia* while dynamic management including heavy thinning to maintain intermediate forest density for *Q.rubra* would boost ecosystem resilience and act as a biological barrier against invasions (Vıtková et al., 2020; Nicolescu et al., 2020b) and in fine, prevent against their expansion. However, *Q. rubra* and *R. pseudoacacia*, are regarded as interesting alternatives in managed temperate forests to replace several other native species affected by extreme climatic events such as *F. sylvatica* and *P. abies* (Thurm et al., 2018) which requires further investigations considering their high invasive potential and my results.

In addition, I showed that their relative growth, a key element of invasive success (Daehler, 2003; Hernández et al., 2014) increased as a response to drier and warmer climate. This result suggest that drier and warmer conditions induce larger growth in *Q.rubra* and *R.pseudoacia* relatively to other species with which they co-occur with in Europe, thus confirming that they have better drought tolerance ability than native tree species (Minucci et al., 2017; Nicolescu et al., 2020a). These results suggested that stress tolerance is a key trait to invasion success (Dukes et al., 1999) and that climate change would increase the invasibility of many habitats in which they already occur in southern and central Europe (Camenen et al., 2016; Fernandez-Manjarres et al., 2018; Vıtková et al., 2020).

These findings, considered together with the incoming increase in drought frequency and intensity in Europe (Astigarraga et al., 2020; Buras et al., 2020; Trenberth et al., 2014), the growing interest for *Q. rubra* and *R.pseudoacacia* for large-scale cultivation (Thurm et al., 2018), and the likely increased risk of propagation induced by fires in unmanaged areas (Fernandez-Manjarres et al., 2018) suggest that new opportunities for the establishment of exotic species and rapid change in species composition might arise in the coming decades with concomitant negative ecological and economical outcome.

6.4 Limitations

6.4.1 National Forest Inventories

The interval of time between surveys varies between and within species. The time lag between inventories is in some cases long, which makes difficult retrieving a mortality or recruitment event. I partially solved this problem by including an offset in the models, allowing me to estimate rates instead of counts. This offset relies on the assumption of a linear increase in demographic processes over time (i.e. recruitment, growth and mortality, Fortin et al. (2008)). In other words, no estimation is performed on the coefficient for the time between census, it is rather assumed to be equal to 1. This hypothesis is not always true and longer intervals usually result in lower rate estimates (Sheil et al., 1996). One alternative to the use of an offset is to estimate the census interval- associated biases first and to use it as a correction (Kohyama et al., 2018). Another alternative that is less time consuming is the inclusion of the log of the time in the model as another covariate. The associated coefficient that is estimated can be thus significantly different from 1 (linear increase). If > 1, then the demographic rate would increase faster over time than linearly whereas < 1 would imply that the increase is slower over time than a linear relationship (Fortin et al., 2008). When using this latter approach, Yang et al. (2015) found that recruitment did not increase proportionally over time but slower than expected, confirming the work of (Sheil et al., 1996). It is thus likely that I slightly underestimated recruitment, mortality and growth throughout this work. Similarly, big trees, that are the most strongly affected by die-off (Bennett et al., 2015; Stovall et al., 2019) and extreme responses are usually under-represented in the NFI's which has also contributed to underestimate the extend of background and die-off mortality in the chapter 3 (Ruiz-Benito et al., 2020).

In addition, I used data coming from 6 NFI in Europe, which represented a large climatic gradient. However, for the case of many Mediterranean species such as *Pinus halepensis*, *Pinus pinea*, *Quercus suber*, *Quercus ilex* etc, the southernmost and likely the climatic trailing edge of the distribution ranges was in Africa, where no NFI were available. Similarly, the full range of widely distributed species as *Pinus sylvetris* was not entirely covered by the 6 NFI used, which has likely biased our analyses for these species towards Mediterranean climate, especially at the southern climatic margins.

6.4.2 Biotic factors affecting mortality and recruitment

The distinction between background and intensity of mortality events in our results should be interpreted with caution because die-off events are generally related to extreme events such as wind, insect outbreaks, fires (Csilléry et al., 2013), heatwaves and drought (Allen et al., 2010; Allen et al., 2015). While drought events are likely to be well represented by the relative drought variables that I used (SPEI, Vicente-Serrano et al. (2010)), drought may weakens trees and make them more vulnerable to insect and pathogen attacks, that are not accounted for in my thesis. For example, increased minimum temperatures increase the winter survival rates of pathogens and pests, and decrease the length of their generation cycles, boosting mortality in boreal species. Climate warming can hence help pathogens survival and progression to new environments (Pureswaran et al., 2018). This is the case of some geometrids associated with mountain birch, the autumnal moth, *Epirrita autumnata*, and the winter moth, *Operophtera brumata*, in the boreal areas of northern Europe, where eggs now encounter more favourable conditions during winter than years ago. Likewise, in the Mediterranean region *Thaumetopoea pityocampa* have shifted upward into high elevation stands of mountain pine as a response to climate change (Netherer et al., 2010). Another recent study found that the probability of mortality of *Pinus sylvestris* in northeast Spain was correlated with climatic conditions favourable to four bark beetle species that matched the optimal climatic conditions of *Pinus Sylvestris* (Jaime et al., 2019).

The "ink disease" (*Phytophtora cinamonni*) is a widespread root fungus affecting *Quercus ilex*, *Quercus suber* and *Castanea sativa* in the Mediterranean area, boosted by the increase of winter temperatures (Burgess et al., 2017). This is also the case of *Diplodia sapinea*, mainly affecting *Pinus pinea*, *Pinus sylvestris*, *Pinus nigra* and *Pinus halepensis*, whose upward shift in altitude in response to rising temperatures by 2050-2070 is predicted (Bosso et al., 2017). Similarly, *Acer pseudoplatanus* is threatened by several pathogens spreading rapidly in Europe including *Cryptostroma corticale*, that is also harmful for humans and whose attacks are triggered by high summer temperatures and drought (Pasta et al., 2016).

More importantly, the effects of these pathogens and insect pests interact strongly with those of drought and are responsible for massive dieback in many forest species (Jactel et al., 2012; Anderegg et al., 2015; Wood et al., 2018). Pathogens and insects are also of major importance for recruitment as host-specific pathogens can make the areas near a parent tree inhospitable for those younger trees in the surroundings, causing negative density dependence at recruitment (Wright, 2002; Chen et al., 2018). Similarly, in the case of invasive species, the absence or reduction of pathogens in the environment of introduction is thought to favour the success of the invasion by non-native species (Keane et al., 2002). A systematic survey of pathogens, pests and extreme events in plots is needed to refine our understanding of demographic processes and biological invasions.

6.5 The future of forests in Europe

In many species, I found that drought induces both higher mortality rates and lower recruitment rates. *Abies alba* and *Quercus robur*, for instance, showed both higher mortality rates and lower recruitment rates at their leading edge in response to increase in temperature which indicates a very probable range contraction at their cold margin. While the debate about the expansion or contraction of the range of *Abies alba* is still ongoing (Mauri et al., 2016a), there is little evidence in the literature that can confirm our results in *Quercus robur* (But see Sáenz-Romero et al. (2017)).

Similarly *Pinus sylvestris* and *Alnus glutinosa* could expand their ranges at their leading edge as both species show lower mortality rates in this part of the range, consistent with the range expansion suggested by other studies (Durrant et al., 2016c; Durrant et al., 2016b). However, we did not evidenced higher recruitment rates in this part of their range. Moreover several studies in the Swiss Alps have found an increase in recruitment in many coniferous and broadleaved species (including *Acer pseudoplatanus*, *Abies alba*, *Fraxinus excelsior*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Quercus petrae*), promoted by climate warming (Gehrig-Fasel et al., 2007; Hofgaard et al., 2009; Vitasse et al., 2012). Their results, together with ours advocate for an upward shifts of the treeline in the Alps.

However, it is worth noting that evidence for climate induce range-shift at the leading edge of species range are scarce, mainly because many other factors such as soil conditions, nutrients availability, land use history and species-specific traits are likely to compensate climatic effect (Cudlin et al., 2017). In their review, Evans et al. (2017) showed that only 33% of the studies provided evidence of a distributional shift of the boreal-temperate ecotone in the direction predicted by climate change, highlighting that biotic factors are an important component of species range shift in this part of the range. This is also confirmed by our results as we found competition to be a major driver of both mortality and recruitment in most species (Chapter 3 and 4).

Conversely, evidence for drought-induced range-shifts in southern Europe is accumulating rapidly (Fernandez-Manjarres et al., 2018). This trend is largely confirmed by our results as we evidenced both lower recruitment rates (Chapter 4) and higher mortality rates (Chapter 3) at the trailing edge of numerous species including *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica*, *Pinus sylvestris*, *Quercus robur* and *Quercus petrae*, suggesting a high probability of range contraction at their dry margin.

Several authors have already highlighted trailing edge contraction for *Fagus sylvatica*, *Pinus sylvestris*, *Alnus glutinosa* and *Betula pendula* (Durrant et al., 2016c; Durrant et al., 2016b; Durrant et al., 2016a; Beck et al., 2016), even suggesting a replacement of beech trees (Peñuelas et al., 2007) and Scots pine by oak species in altitude in the Pyrenees. In the case of Scots pine this is related to high mortality and low recruitment rate (Galiano et al., 2010; Vilà-Cabrera et al., 2013), which is in line with our results. In addition, several oak species such as the temperate *Quercus petraea* and the sub-Mediterranean *Q. faginea* (Urli et al., 2014) are moving northwards as a response to climate change. However, no studies have highlighted similar patterns of mortality in *Quercus robur* to our knowledge (But see (Sáenz-Romero et al., 2017)).

Our results are more ambiguous for a number of other species likely suggesting demographic trait-offs. This is the case of *Pinus halepensis* and *Fraxinus excelsior* for which we observed increased mortality rates at the leading edge but also lower recruitment rates at the trailing edge (linked to high relative droughts in *F. excelsior*). These results could suggest a contraction of their range both at their leading and trailing edge, which is contradiction with studies suggesting a range expansion for *Pinus halepensis* (Mauri et al., 2016b). Likewise, *Abies alba* displayed high mortality rates in response to drought at its warm trailing edge, but its recruitment was not affected, which makes any conclusion difficult regarding its possible range contraction, which is still under debate (Mauri et al., 2016a). These results should be taken with caution in the absence of trend for recruitment, which could have disproportional importance for the species dynamics at the edge (Clark et al., 2014; Defossez et al., 2016). Similarly, *Picea abies*, *Pinus pinea* and *Quercus ilex* appear to be highly affected by mortality at their trailing edge due to increased drought, whereas their recruitment rates seem to benefit from drier conditions. Holm oak (*Quercus ilex*) and other evergreen oak range expansions at the expense of deciduous broadleaved species and conifers in the Mediterranean region are frequently reported in the literature (Fernandez-Manjarres et al., 2018; Galiano et al., 2010). For instance it was shown that *Quercus ilex* is progressively expanding northwards in the Mediterranean region limiting the recruitment of major Mediterranean pines, including *Pinus nigra*, *Pinus sylvestris*, *Pinus pinaster*, *Pinus halepensis* and *Pinus pinea* (Carnicer et al., 2014).
Similarly, some studies have suggested the replacement of drought resistant conifers by evergreen, fire-resistant, and slow-growing broadleaved trees (e.g., *Quercus suber*, *Quercus ilex*) in the Mediterranean region which is not consistent with climate warming but rather influenced by forest structure due to past land use change (Vayreda et al., 2016).

Overall, our results, considered together with the current literature confirm that the Mediterranean-temperate ecotone is strongly affected by climate change (Fernandez-Manjarres et al., 2018) and that shifts in species ranges are likely occurring as a response to climate, particularly at the drier margin of the distribution (Kunstler et al., 2016), boosted by the competition effect on recruitment and mortality.

Another important result is that none of the species that I studied, in response to climate, showed both higher recruitment and lower mortality at any of their margins. This result suggest that rather than being replaced by species extending their range, the species that contract their ranges would rather leave empty spaces. In addition land abandonment has been particularly high in the Mediterranean region and is particularly marked in marginal and less productive areas in Europe including several mountainous areas (Fernandez-Manjarres et al., 2018). These newly available spaces (through non replacement of species or land abandonment) are an opportunity for invasive species usually establishing in these type of open areas (Vıtková et al., 2020; Nicolescu et al., 2020b) that benefit from drier and warmer climates at the southern margin for *Quercus rubra* and *Robinia pseudoacacia* and even at the northern margin for *Quercus rubra*, according to our results (Chapter 5).

Furthermore, our results of Chapter 5 indicate that *Pinus sylvestris*, *Fagus sylvatica* and *Quercus petrae* are the species that co-occur the most with *Quercus rubra* and *Robinia pseudoacacia*, and that they are losing their dominance in favour of an increase in the cover of either of the invasive species. Similarly, *Quercus rubra* also appears to be increasing its distribution range at the expense of *Abies alba* and *Quercus robur*, both of which are contracting their range, at the leading edge for *Abies alba*, and at both margins for *Quercus robur* (Chapter 3 and 4).

Altogether, these results suggest that range-contracting species such as *Pinus sylvestris*, *Fagus sylvatica* (at their trailing edge) and *Abies alba* (at its leading edge) would not only be replaced by more drought resistant broadleaved species (Durrant et al., 2016b; Durrant et al., 2016a; Mauri et al., 2016a; Vayreda et al., 2016) but also by invasive ones. Similarly, oak species such as *Q. robur* and *Q. petraea* that are both contracting their range at the dry margin but are supposed to be shifting upward (Vayreda et al., 2016) will likely compete and be replaced by the more drought tolerant *Q.rubra* and *R.pseudoacacia* (Minucci et al., 2017; Nicolescu et al., 2020b; Nicolescu et al., 2020a).

Based on NFI data from 1981 to 2014, our results suggest that major shifts in species distribution are already occurring. In addition, drought induced mortality is rising in Europe (Senf et al., 2020) and several observational studies confirmed that it has already caused considerable damage in 2018 and 2019 (Buras et al., 2020; Schuldt et al., 2020), specially in France, Germany, Sweden, Finland and Belgium that were described as hotspot of drought induced mortality after 2018 drought (Buras et al., 2020).
Furthermore, several studies predict that a strong increase mean temperatures, in the intensity and frequency of drought events in the future, particularly in the Mediterranean

area, Western Europe, and Northern Scandinavia, (Drobinski et al., 2016; Spinoni et al., 2018). Thus, drylands in the Mediterranean Basin are expected to expand (Huang et al., 2016), and the average climatic conditions of the European forest, currently mainly adapted to deciduous species, are expected to evolve towards climatic conditions mainly adapted to more xeric Mediterranean species (Hanewinkel et al., 2013; Schueler et al., 2014). According to our results, an expansion of drylands in the Mediterranean regions would not only boost xeric Mediterranean species, but also invasive species that would benefit from these drier conditions to invade new empty spaces. Together with these predictions, my results suggest that mortality rates will keep on increasing as a response to changing climate, suggesting important shift in future tree species composition to come, if they not already have.

In chapter 3 we found that intensity of mortality was higher in slow-growing trees than in fast-growing trees in seven species, suggesting that plots containing bigger trees are more likely to experience intense events of mortality. This result is in line with several studies showing that large trees, that have lower resistance to drought are the most affected by die offs events (Bennett et al., 2015; Stovall et al., 2019), which has serious implication for the carbon cycle as large trees hold half of all mature-forest carbon, globally (Lutz et al., 2018). By dying more and recruiting less, forest are becoming on average younger and might release more carbon than what they uptake. In addition, while recruitment decreases with increasing aridity, warming is affecting the forest carbon balance of Spanish forests by reducing forest growth (Vayreda et al., 2012). Similarly, despite increasing productivity over time, aggravation of the negative effects of climate change on forest demography are observed, reducing recruitment and increasing mortality but also decreasing growth (Astigarraga et al., 2020). This change in productivity is also driven by initial forest structure and increased competition. Furthermore, several authors suggested that legacies from past land use might significantly contribute increase trees mortality (Senf et al., 2018), in addition to boost exotic species range expansion (Vıtková et al., 2020; Nicolescu et al., 2020b), as we also evidenced (Chapter 5).
The above mentioned studies together with my results show that competition, forest structure and management are playing an important role on mortality (Chapter 3), recruitment (Chapter4), triggering biological invasion (Chapter 5) and decreasing forest productivity (Astigarraga et al., 2020). Yet, recent developments in forest management towards natural climate solutions silviculture might alleviate impacts from land use, competition and climate on forest (Brang et al., 2014).

6.6 Management practices to mitigate the negative impact of climate

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We evidenced a strong effect of competition on mortality in Chapter 3. This competitive effect induces increase in competition for resources enhancing species vulnerability to drier climate (Linares et al., 2010; Young et al., 2017). In this regard, several authors have suggested to reduce competition by thinning as an adaptation measure that could counteract the negative effects of climate warming on tree mortality (Gracia et al., 1999; Martın-Benito et al., 2010; Bradford et al., 2017). Therefore, reducing competition in forest would leverage drought effects on the populations at risk. Neighborhoods of species that are the most sensitive to competition and climate such as conifers at their southernmost limit, such as *P. sylvestris* should be prioritized (GÓMEZ-APARICIO et al., 2011).

In chapter 4, I showed that conspecific negative density dependence (CNDD) is a major driver of species recruitment that can interact with drought in several sensitive species such as *F. sylvatica* or *P. sylvestris*. CNDD can act through species-specific pathogens. As a response to increasing temperature, these pathogens and insects are expected to be release and increase their presence and abundance (Anderegg et al., 2015; Wood et al., 2018). Their presence can be mitigated by mixed forests in comparison to monospecific stands (Jactel et al., 2017). In addition, mixed forests have lower fire risks compared to conifer plantations in the Mediterranean (Fernandez-Manjarres et al., 2018), have a positive effect on diversity, carbon storage and tree productivity (Ruiz-Benito et al., 2014). In addition, high diversity forests would boost ecosystem resilience and act as a biological barrier against invasions (Vıtková et al., 2020; Nicolescu et al., 2020b; Nicolescu et al., 2020a).

Finally, natural regeneration should be preferred over management intensive strategies (Fernandez-Manjarres et al., 2018). These could be essential to mitigate the negative effects of climate change on tree mortality (Di Sacco et al., 2021) because the new trees could offset our carbon sins more effectively than old forest (Pugh et al., 2019; Bastin et al., 2019). In European forests, Fernandez-Manjarres et al. (2018) suggest that reforestation and natural regeneration should be adopted in areas where dry conditions would favour the establishment of stable evergreen populations, such as the Mediterranean-temperate ecotone where they would be more adapted to the drier climate and the incoming change in intensity of fire regimes. However, our results suggest that while these evergreen broadleaved such as *Q.ilex* would spread through natural regeneration in the Mediterranean Basin, it is likely that *Robinia pseudoacacia* and *Q.rubra* would also spread rapidly in southern Europe as they are both fast growing and good competitive species (Enescu et al., 2013; Nicolescu et al., 2020b). Furthermore, these two species are regarded as interesting alternatives in managed temperate forests to replace several other native species affected by extreme climatic events such as *F. sylvatica* and *P. abies* (Thurm et al., 2018) and are economically interesting and attractive for biomass production (Sitzia et al., 2012; Nicolescu et al., 2020b).

Although invasive species such as *Q.rubra* and *R.pseudoacacia* might present a very important economical interest, their large scale cultivation would likely induce negative impacts on native species, contributing to spread of diseases and pests and negatively alter biodiversity and the function, structure and dynamics of forest ecosystems if they are not maintained under silvicultural control (Thurm et al., 2018; FOREST-EUROPE, 2020).

6.7 Perspectives

The translocation of biological material to compensate for climate change generally enclosed in the term assisted migration (Hoegh-Guldberg et al., 2008; Schwartz et al., 2012) encompasses different options that would lead to different climate-related risks and need to be considered separately. In forestry, assisted gene flow has been the most studied option (Aitken et al., 2016). In Europe, examples of translocation of populations exist for commercial species (Benito-Garzón et al., 2013a; Isaac-Renton et al., 2014; Benito-Garzón et al., 2015), but no attention has been paid to other species that will help to maintain ecosystems services in the future. In the case of the shift between Mediterranean-temperate ecotone and invasive species shift, my work would help to identify the target sites and species susceptible to assisted migration programs. For instance, those regions where most species have high mortality combined with low recruitment and species like *Pinus sylvestris* or *Quercus robur*, that are also both ecologically and economically important.

Finally, the possible inclusion of spatialized variables accounting for the frequency, intensity and duration of other extreme events and to evaluate their relative importance in our models would provide considerable insight regarding tree mortality, recruitment and invasion potential. Indeed, the systematic recording of causes associated with tree death or the coupling of available databases with information concerning extreme events such as forest fires or storms could be beneficial to distinguish extreme mortality events from background mortality events. It would also help to refine our understanding of demographic processes and to determine the importance of such events in biological invasions. However, there is a considerable lack of geo-referenced data on pests and in European forests (Ruiz-Benito et al., 2020). The development and use of such databases (historical data on abiotic (i.e. wind, fire and snow damage) and biotic (pathogens and insects) disturbance) and their integration into demographic models is an interesting avenue for future large-scale demographic studies.

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Appendices

Annexes 1

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Similar patterns of background mortality across Europe are mostly driven by drought in European beech and a combination of drought and competition in Scots pine

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ABSTRACT

Background tree mortality is a complex demographic process that affects structure and long-term forest dynamics. Here we investigated how climatic drought intensity interacts with interspecific and intraspecific competition (or facilitation) in shaping mortality patterns across tree species ranges. To this aim, we used data from five European national forest inventories to perform logistic regression models based on individual tree mortality in Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.). We computed the relative importance of climatic drought intensity, basal area of conspecific and heterospecific trees (proxy of indirect intra- and interspecific competition or facilitation) and the effects of their interactions on mortality along the entire European latitudinal gradient of both species range. Increase in climatic drought intensity over the study period was associated with higher mortality rates in both species. Climatic drought intensity was the most important driver of beech mortality at almost all latitudes while Scots pine mortality was mainly driven by basal area. High conspecific basal area was associated with high mortality rates in both species while high heterospecific basal area was correlated with mortality rates that were high in Scots pine but low in beech. Overall, beech mortality was directly affected by climatic drought intensity while Scots pine mortality was indirectly affected by climatic drought intensity through interactions with basal area. Despite their different sensitivity to drought and basal area, the highest predicted mortality rates for both species were at the ecotone between the cool temperate and Mediterranean biomes, which can be explained by the combined effect of climatic drought intensity and competition. In the context of global warming, which is expected to be particularly strong in the Mediterranean biome, our results suggest that populations at the southern limit of species ranges may experience increased mortality rates in the near future.

1. Introduction

Tree mortality plays a major role in shaping forest dynamics, structure and composition (Franklin et al., 1987; Ruiz-Benito et al., 2017a), species range shifts (Benito Garzón et al., 2013), ecosystem functioning and services (Millar and Stephenson, 2015), carbon fluxes and feedback to the global climate system (Sitch et al., 2008). Therefore, understanding and predicting tree mortality is a key challenge in ecology, particularly in a changing climate.

Global change is exacerbating drought-induced tree mortality

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(Allen et al., 2015). Recent forest die-off events have occurred in all major biomes and on every wooded continent (Allen et al., 2015) and background tree mortality also appears to have increased in North America (Mantgem et al., 2009; Hember et al., 2017) and in Spain (Carnicer et al., 2011). Less conspicuous than die-offs events, minor large-scale changes in tree background mortality can have a huge impact on forest ecosystems and dynamic, including changes in productivity rates, functional composition and species turnover (Stephenson and Mantgen, 2005; Ruiz-Benito et al., 2017b). Yet, an empirical quantification of background tree mortality at continental scale is missing and whether or not forest mortality follows an increasing global trend that will keep rising under global change remains unclear (Hartmann et al., 2018). Moreover, mortality is a major process which delimits species range (Gaston, 2009), notably at the driest edge of their distribution (Benito Garzón et al., 2013). Therefore, large scale studies that capture the entire species distribution are essential to determine how climate change induced mortality might affect species distribution.

Understanding and predicting background tree mortality patterns at large scales remains challenging for several reasons (but see Das et al. (2016) and Neuman et al. (2017) for examples of large-scale studies). First of all, mortality is a stochastic phenomenon (Franklin et al., 1987), which is therefore difficult to predict. Secondly, it is often the result of a complex and gradual process with multiple interacting drivers (Manion, 1981), that act at different spatial and temporal scales (Dietze and Moorcroft, 2011). Thirdly, there may be a lag time between episodic stressful conditions and tree mortality responses (Cailleret et al., 2017; Jump et al., 2017). Lastly, background tree mortality rates are difficult to estimate due to the small sample size of dying trees in local studies, while large samples are needed to understand mortality patterns.

In European forests, background tree mortality is strongly driven by climate variability (Neumann et al., 2017). Among the climatic factors affecting tree mortality, drought plays a major role (McDowell et al., 2008; Benito Garzón et al., 2013; Ruiz-Benito et al., 2013; Allen et al., 2015) and particularly affects populations at the driest edge of species distributions (Benito Garzón et al., 2018). Among the biotic factors, competition for limited resources may be an important cause of tree mortality and may also interact with climate, notably through a higher increase in mortality rates in areas that are both dry and dense (Ruiz-Benito et al., 2013; Vilà-Cabrera et al., 2013; Young et al., 2017). Moreover, tree mortality responses can differ widely depending on whether we consider intra- or inter-specific competition (Condés and del Río, 2015). However, how intra- and interspecific competition interact with climatic drought to shape range-wide mortality patterns remains unknown.

Tree mortality sensitivity to biotic and abiotic factors vary along species' ecological strategies, from stress-tolerators to competitors and from angiosperms to gymnosperms (Choat et al., 2012; Ruiz-Benito et al., 2017a). European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) are two widely distributed European tree species with different life history strategies. Beech is a highly competitive, shade-tolerant and late-successional species while Scots pine is a weakly competitive and light demanding pioneer tree (San-Miguel-Ayanz et al., 2016). Scots pine is considered as a drought-avoiding species, which has narrow xylem vessels (tracheids) and withstands droughts by closing its stomata early and maintaining a reduced metabolism (isohydric response; McDowell et al., 2008). By contrast, beech is known to be sensitive to drought (van der Maaten, 2012; Chen et al., 2015), has wide vessels more prone to cavitation and maintains a more constant metabolism but a narrower margin of hydraulic safety under droughts (anisohydric response; McDowell et al., 2008). Regional scale studies suggested that both species are being progressively replaced by other species in the southern part of their distribution (Vilà-Cabrera et al., 2013; Galiano et al., 2010) and in some inner Alpine valleys in the case of *P. sylvestris* (Rigling et al., 2013).

Our main objective was to understand and predict range-wide patterns of background mortalities in Scots pine and European beech. To that end, we parameterised individual-level logistic regression models, as a function of climatic drought and basal area of heterospecific and conspecific trees (used as a proxy of inter and intra-competition or facilitation, at the plot level), using records from five National Forest Inventories covering the entire European latitudinal gradient, from Spain to Finland. We hypothesised that (i) mortality in both species is influenced by climatic drought, basal area and their interaction but with a higher influence of basal area in the case of Scots pine; and (ii) that despite these differences in their sensitivity to drought and basal area, both species display similar spatial patterns of mortality across their ranges: high mortality in the south resulting from increasingly dry climates, especially in the Mediterranean biome.

2. Material and methods

2.1. Forest inventory data

We used mortality data from five national forest inventories (NFIs) covering the entire European latitudinal gradient, from the Mediterranean to boreal biome. Data from four of the NFIs had been previously harmonised as part of FunDivEUROPE project (Spain, Germany, Sweden and Finland) and the French NFI was added to this study. In each NFI, trees were recorded in temporary or permanent plots depending on the country. Plots in the German, Finnish and Swedish inventories are gathered within clusters (see Appendix S1 for details of the survey design and sampling methods for each NFI). We selected plots in which at least one of our two target species (i.e. *F. sylvatica* or *P. sylvestris*) was recorded. These plots were classified into Mediterranean, cool temperate and boreal biomes (see the map of biome boundaries in Fig. S1.1) and were unevenly distributed along the latitudinal gradient (Fig. S1.2). The final datasets contained 57,191 beech trees and 161,720 Scots pine trees in 10,150 plots and 16,669 plots, respectively. From those trees, 1490 (2.6%) and 7649 (4.7%) were recorded as dead for beech and Scots pine, respectively.

As explanatory variables of tree mortality, we selected tree *DBH* (diameter at breast height) as *DBH* is known to influence individual tree mortality (Ruiz-Benito et al., 2013). We additionally calculated three proxies of indirect competition between trees (or facilitation) (Fig. S2.1): basal area of neighbouring trees considering all tree species (i.e. *BAall*, m^2 ha^{-1}), basal area of neighbouring conspecifics (i.e. *BAintra*, m^2 ha^{-1}) and basal area of neighbouring heterospecifics (i.e. *BAinter*, m^2 ha^{-1}).

2.2. Drought-related variables

Climatic drought intensity over the study period (Fig. S2.2) was characterised by a water availability index: $WAI = (MAP-PET) / PET$, where *MAP* is the mean annual precipitation (mm) and *PET* the mean potential evapotranspiration (mm). For each plot, *PET* was extracted from the CRU v3.24.01 monthly gridded dataset at 0.5-degree resolution (Harris et al., 2013) and *MAP* was calculated from a downscaled version of E-OBS at 1 km resolution (Moreno and Hasenauer, 2016). For each plot, *WAI* was averaged over the period between two years before the first survey date and the second survey date to include delayed effects of drought on mortality (Greenwood et al., 2017).

Changes in climatic drought intensity over the study period (i.e. temporal variability of drought intensity) were described by the Standardized Precipitation Evapotranspiration Index (*SPEI,* Fig. S2.2; Vicente-Serrano et al., 2009), obtained from a gridded dataset at 0.5-degree resolution (Beguería and Vicente Serrano, 2017). *SPEI* is a multi-scalar drought index whose variations have been shown to be highly correlated with tree response to climate (Greenwood et al., 2017). Its calculation considers both *PET* and *MAP*, with *PET* derived from the Penman–Monteith equation. *SPEI* compares drought intensity during a long-term reference period (i.e. from 1901 to 2015) to that of a given period from 3 to 48 months. In our study, we selected a 12-month period to consider both current and previous year water shortage. *SPEI* is expressed as a standardised index relative to each site, with a standard deviation of 1, where negative values indicate more intense drought over the timescale considered compared to reference conditions. For each plot, we calculated mean *SPEI* (hereafter *SPEI*) over the period from two years before the first survey date to the second survey date.

2.3. Model description

We parameterised two species-specific models, where P_i is the annual probability of mortality for each individual tree *i*. We used a logistic regression model with a link *cloglog* to allow the sigmoidal curve of the mortality probability to be asymmetrical and deal with zero inflated distributions (Zuur et al., 2009):

$$\mathrm{P}_i = 1 - \exp(-\exp(\alpha_0 + \alpha_{country} + k_{i,sp} + \log(t_i))) \tag{1}$$

where α_0 is an intercept term (set to zero); $\log(t_i)$ is an offset variable that takes into account the survey interval length t_i (years) for each tree *i*; $\alpha_{country}$ is the random country intercept to include the sampling differences between each NFI and $k_{i,sp}$ is a species-specific linear function that includes the relationship between the mortality of tree *i* of the species *sp* (i.e. *F. sylvatica* or *P. sylvestris*) and the explanatory fixed-effect variables. Although clusters and plots could be considered as a source of variation for each tree, we did not consider cluster and plot as random terms because most of the clusters contained only one plot and in many plots no trees died between the two survey dates. We used the function "glmer" of the "lme4" package to run the model described in Eq. (1) in R 3.3.3 (R Core Team 2017).

For both species, we explained mortality patterns using four fixed-effect predictors with low collinearity (i.e. Spearman correlation coefficient: $r < 0.59$, and Variance Inflection Factor: VIF < 2; Dormann et al., 2013), namely: *BAintra, BAinter, WAI* and *SPEI*. Conspecific and heterospecific basal area (i.e. *BAintra* and *BAinter*) were both included in the model as they can have different effects on tree mortality (Condés and del Río, 2015). To ensure a linear relationship between each explanatory variable and tree mortality, *BAinter, WAI* and *SPEI* were log transformed (see Appendix S3 for details).

Tree size (*DBH*) was included as a covariate in our model, as we were not directly interested in the importance of tree size on mortality. As we required a single parameter per predictor to estimate the relative importance of each predictor (see Section 2.5), we calculated a non-linear variable from *DBH*: $DBHnl_{sp} = DBH + r_{sp} \times \log(DBH)$ (see Appendix S3 for details).

To understand how tree mortality was affected by basal area and climatic drought, we included the main effect of each variable and first-order interaction terms between abiotic and biotic variables. Herewith, the function *k* from Eq. (1) took the form:

$$\begin{aligned} k_{i,sp} = {} & \beta_{1,sp} \times \log(WAI_i) + \beta_{2,sp} \times \log(SPEI_i) \\ & + DBHnl_{i,sp} \times (\beta_{3,sp} + \gamma_{1,sp} \times \log(WAI_i) + \gamma_{2,sp} \times \log(SPEI_i)) \\ & + BAintra_i \times (\beta_{4,sp} + \gamma_{3,sp} \times \log(WAI_i) + \gamma_{4,sp} \times \log(SPEI_i)) \\ & + \log(BAinter_i) \times (\beta_{5,sp} + \gamma_{5,sp} \times \log(WAI_i) + \gamma_{6,sp} \times \log(SPEI_i)) \end{aligned} \tag{2}$$

where β_x and γ_x are the estimated coefficients of the main and interaction effects, respectively (Table S3.1).

2.4. Model performance and evaluation

Binned residuals plots were used to ensure our final species-specific models were well-calibrated (Fig. S3.3–4). To evaluate the discrimination accuracy of our models, we computed the mean area under the curve (AUC) on 100 bootstrap samples among the predicted and observed values. AUC values of 0.6–0.7 show a fair discrimination accuracy, between 0.7 and 0.8 good and above 0.8 excellent (Hurst et al., 2011). We used independent cross-validation to measure the generalisation power of the model, for which we used 75% of the data to fit the model and the remaining 25% to independently validate our predictions.

2.5. Relative importance of climatic drought and basal area on mortality

Following Ratcliffe et al. (2016), we explored the relative importance of each predictor on individual tree mortality in relation to the other predictors by considering the predictors' main effects and their interactions. For doing so, we first computed the absolute importance of each predictor using our model coefficients. For instance, to compute $A_{BAintra,i}$ the absolute importance of *BAintra* on the probability of mortality of the tree *i*, we applied the following equation separately for each species:

$$A_{BAintra,i,sp} = \beta_{4,sp} + \gamma_{3,sp} \times \log(WAI_i) + \gamma_{4,sp} \times \log(SPEI_i) \tag{3}$$

where β_x and γ_x are the estimated coefficients of the single predictors and their interaction effects respectively; WAI_i and $SPEI_i$, are the plot values corresponding to these variables.

Secondly, the relative importance of each predictor was computed for each tree by dividing the absolute importance of the focal predictor by the maximum absolute importance between all predictors of the target tree. For instance, to estimate the relative importance of *BAintra* for the tree *i*, we calculated for each species: $|A_{BAintra,i,sp}|$ / max $(|A_{BAintra,i,sp}|, |A_{SPEI,i,sp}|, |A_{WAI,i,sp}|, |A_{BAinter,i,sp}|)$; where $A_{SPEI,i}$, $A_{WAI,i}$ and $A_{BAinter,i}$ are the absolute importance of *SPEI, WAI* and *BAinter* for tree *i*, respectively. For each tree *i*, the predictor that had the greatest influence on individual tree mortality probability had a relative importance of one.

3. Results

3.1. Model performance and validation

Scots pine and beech models showed good agreement between observed and predicted values (AUC = 0.73 and 0.71, respectively). The Scots pine model performed well in predicting annual tree mortality probability across the European latitudinal gradient as predicted and observed values exhibited similar patterns (Fig. 1a). Nevertheless, caution is needed to interpret the results at the southern part of the latitudinal gradient where Scots pine mortality probability was slightly underestimated. In the beech model, mortality probability was accurately predicted in the southern half of the latitudinal gradient but was overestimated between 48° and 54° latitude, which corresponds mainly to northern Germany (Fig. 1b). Model and partial residual plots for each predictor showed no strong spatial patterns, thus supporting the validity of the models (Fig. S3.3–4).

3.2. Relative importance of climatic drought and basal area across latitude

In the case of Scots pine, basal area variables (i.e. *BAintra* and *BAinter*) were more important than drought-related variables (i.e. *WAI* and *SPEI*) in explaining the probability of mortality across the latitudinal gradient (Fig. 2a and Table 1). The conspecific basal area was the most important driver from south to north with a mean relative importance of 0.96 (Table 1). The order of importance of the four predictors was stable across latitude, except from 43° to 45° latitude (corresponding to the French part of the Mediterranean biome) where drought-related variables (mainly *SPEI*) were nearly as important as basal area variables (Fig. 2a). From south to north, high levels of both conspecific and heterospecific basal area and increases in drought intensity (i.e. low *SPEI*) were correlated with higher probability of

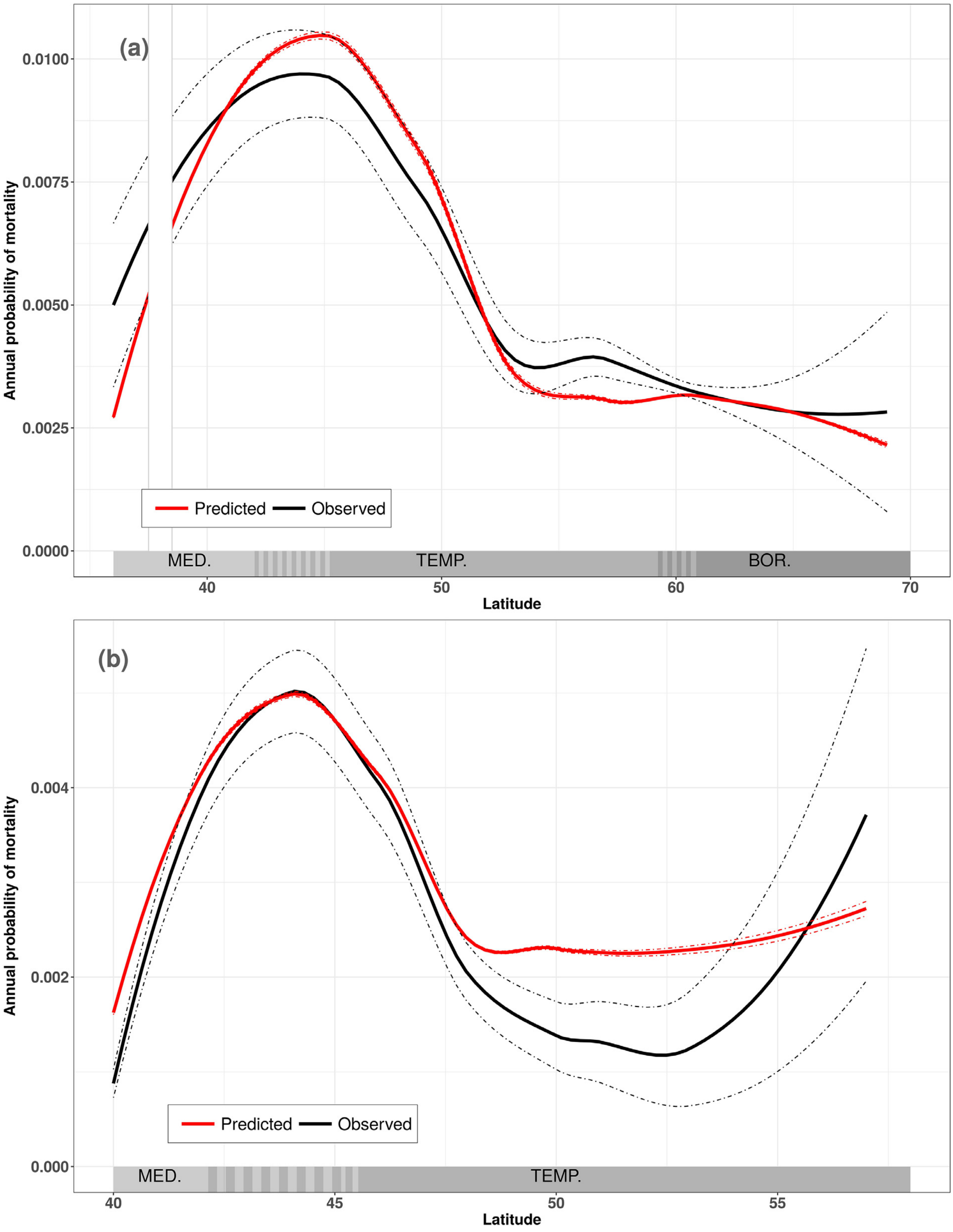

Fig. 1. Predicted and observed annual probability of mortality along the latitudinal gradient covered by the NFIs plots (a) for *P. sylvestris* and (b) for *F. sylvatica*. Predicted and observed values were estimated at the individual-level and were clustered at 1° latitude resolution. A locally weighted regression was used to obtain the smooth solid lines ("loess" method of the geom_smooth function in "ggplot2" R package). Dotted lines indicate 95% confidence intervals. The acronyms MED., TEMP. and BOR. in grey bars refer to the Mediterranean, cool temperate and boreal biome, respectively. The white section for *P. sylvestris* in the Mediterranean biome represents missing data (due to its distribution in Spain).

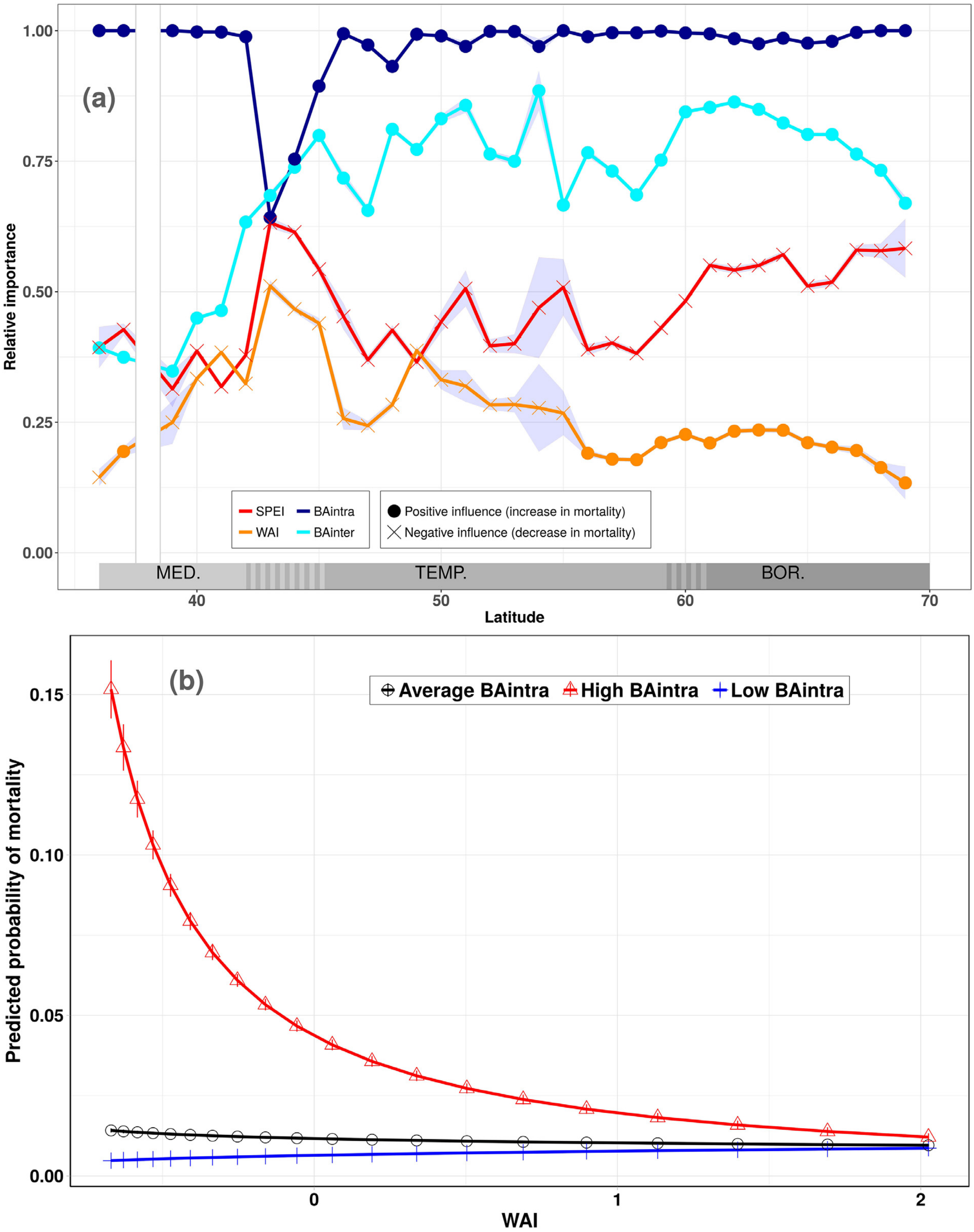

Fig. 2. Effects of drought-related variables and basal area on Scots pine mortality. (a) Relative importance of the changes in climatic drought intensity over the study period (i.e. *SPEI*), climatic drought intensity (i.e. *WAI*), conspecific basal area (i.e. *BAintra*) and heterospecific basal area (i.e. *BAinter*) on Scots pine predicted probability of mortality. The relative importance of each variable was computed for each tree from the logistic regression model (see Section 2.5), by giving a value of one to the most influencing variable and scaling the remaining variables accordingly. For each variable, the relative importance values were aggregated by 1° latitude resolution and the points of the graph correspond to the average values. The grey areas around the curves correspond to the 95% confidence intervals. The acronyms MED., TEMP. and BOR. in grey bars refer to the Mediterranean, cool temperate and boreal biome, respectively. The white section corresponds to missing data at that latitude (due to Scots pine distribution in Spain). (b) Interactions between conspecific basal area (i.e. *BAintra*) and climatic drought intensity (i.e. *WAI*) on Scots pine probability of mortality. This interaction was considered significant if its z value was lower than -2 or higher than 2 and was the most important interaction influencing Scots pine mortality (Table S3.1). Scots pine mortality was predicted at three different levels of conspecific basal area (mean value, 99.5th percentile and 0.005th percentile; proxies of average, high and low competition, respectively) along a drought gradient while the other predictors were fixed at their mean value.

Table 1

Mean relative importance of each predictor and mean annual predicted probability of both species mortality per biome. See Fig. S1.1 for biome boundaries. The relative importance of each variable was first computed for each tree from the logistic regression model (see Section 2.5), by giving a value of one to the most influencing variable and scaling the remaining variables accordingly. Secondly, the relative importance and the annual predicted probabilities of mortality (P_i in the Eq. (1)) were average for each biome. Numbers in brackets refer to 95% confidence intervals. *BAintra*: conspecific basal area (m^2 ha^{-1}), *BAinter*: heterospecific basal area (m^2 ha^{-1}), *WAI*: water availability index (adimensional), *SPEI*: Standardised Precipitation-Evapotranspiration Index (adimensional).

		P. sylvestris				*F. sylvatica*		
		All biomes	Mediterranean biome	Cool temperate biome	Boreal biome	All biomes	Mediterranean biome	Cool temperate biome
Relative importance	***BAintra***	0.96 (0.9616; 0.9630)	0.95 (0.9455; 0.9482)	0.96 (0.9625; 0.9644)	0.99 (0.9860; 0.9870)	0.61 (0.6134; 0.6162)	0.64 (0.6411; 0.6465)	0.61 (0.6076; 0.6107)
	BAinter	0.67 (0.6755; 0.6737)	0.52 (0.5235; 0.5258)	0.73 (0.7308; 0.7331)	0.83 (0.8293; 0.8314)	0.54 (0.5377; 0.5426)	0.80 (0.7915; 0.8010)	0.49 (0.4878; 0.4928)
	WAI	0.31 (0.3089; 0.3114)	0.35 (0.3509; 0.3552)	0.32 (0.3191; 0.3233)	0.22 (0.2169; 0.2201)	0.74 (0.7390; 0.7442)	0.71 (0.6997; 0.7130)	0.75 (0.7456; 0.7513)
	SPEI	0.44 (0.4370; 0.4397)	0.40 (0.3976; 0.4017)	0.42 (0.4218; 0.4258)	0.53 (0.5265; 0.5311)	0.70 (0.7018; 0.7066)	0.61 (0.6055; 0.6168)	0.72 (0.7196; 0.7249)
Annual predicted mortality		0.0061 (0.00611; 0.00618)	0.0077 (0.00763; 0.00775)	0.0063 (0.00619; 0.00631)	0.0033 (0.00332; 0.00337)	0.0038 (0.00374; 0.00382)	0.0052 (0.00506; 0.00530)	0.0035 (0.00347; 0.00354)

mortality (Fig. 2a). In contrast, low *WAI* was associated with high mortality probabilities in the Mediterranean biome and with low mortality probabilities in the boreal biome (see changes from negative to positive influence in Fig. 2a).

For beech trees, drought-related variables were more important than basal area variables in explaining mortality probability across the major part of the latitudinal gradient (except in the south) with a mean relative importance of 0.74 and 0.70 for *WAI* and *SPEI*, respectively (Fig. 3a and Table 1). Low *WAI* and *SPEI* were associated with higher mortality rates (see negative influence in Fig. 3a). The relative importance of conspecific basal area remained stable across latitude whereas that of heterospecifics varied from being the most important variable explaining beech mortality in the Mediterranean biome to being the least important one in the cool temperate biome (Fig. 3a and Table 1). Beech mortality probability increased with conspecific basal area and decreased with heterospecific basal area (Fig. 3A and Table 1).

3.3. Interactions between climatic drought and basal area

In the Scots pine model, all interactions between drought-related variables (i.e. *WAI* and *SPEI*) and basal area variables (i.e. *BAintra* and *BAinter*) were significant (Table S3.1). The strongest interaction was between climatic drought intensity and conspecific basal area (i.e. *WAI* and *BAintra*; Fig. 3b and Table S3.1): regardless of drought intensity, the probability of mortality remained weak when the conspecific basal area was low or intermediate, whereas it strongly increased in dry areas where the conspecific basal area was high (Fig. 2b; see Fig. S4 for the other interactions that affected mortality weakly, albeit significantly).

In the beech model, the only significant interaction was that between climatic drought and heterospecific basal area (*WAI* and *BAinter*; Table S3.1): the probability of mortality increased in dry areas where heterospecific basal area was low or intermediate, while the probability of mortality remained stable (and always low) in dry areas where heterospecific basal area was high (Fig. 3b).

3.4. Spatial patterns of predicted tree mortality across Europe

Across their range, the predicted annual probability of Scots pine mortality was on average higher than that of beech (0.0061 and 0.0038, respectively; Table 1) but followed the same trend across the latitudinal gradient (Fig. 4). The highest predicted mortality rates for both species were in south-eastern France, at the ecotone between the Mediterranean and cool temperate biomes (Fig. 4).

The predicted rates of Scots pine mortality were highest in the Mediterranean biome (mean value of 0.0077 for 62,165 trees), intermediate in the cool temperate biome (mean value of 0.0063 for 62,914 trees) and lowest in the boreal biome (mean value of 0.0033 for 36,641 trees) (Table 1). Similarly, the predicted individual probability of beech mortality was higher in the Mediterranean biome (mean value of 0.0052 for 9315 trees) than in the cool temperate biome (mean 0.0035 for 47,876 trees) (Table 1). However, the gap between mortality rates in the Mediterranean biome and the more northern biomes is likely to be higher than predicted as the Scots pine model slightly underestimated mortality probability in the Mediterranean biome (Fig. 1a) and the beech model overestimated mortality probability in the cool temperate biome (Fig. 1b).

4. Discussion

Exploring the drivers of background tree mortality at a continental scale opens a new perspective for understanding tree mortality patterns across species' ranges, including some demographic events observed at a smaller scale (Carnicer et al., 2011). Although considerable attention has been paid to the effects of drought and basal area on tree mortality (Mantgem et al., 2009; Greenwood et al., 2017; Hember et al., 2017; Ruiz-Benito et al., 2013), our results demonstrate that the combination

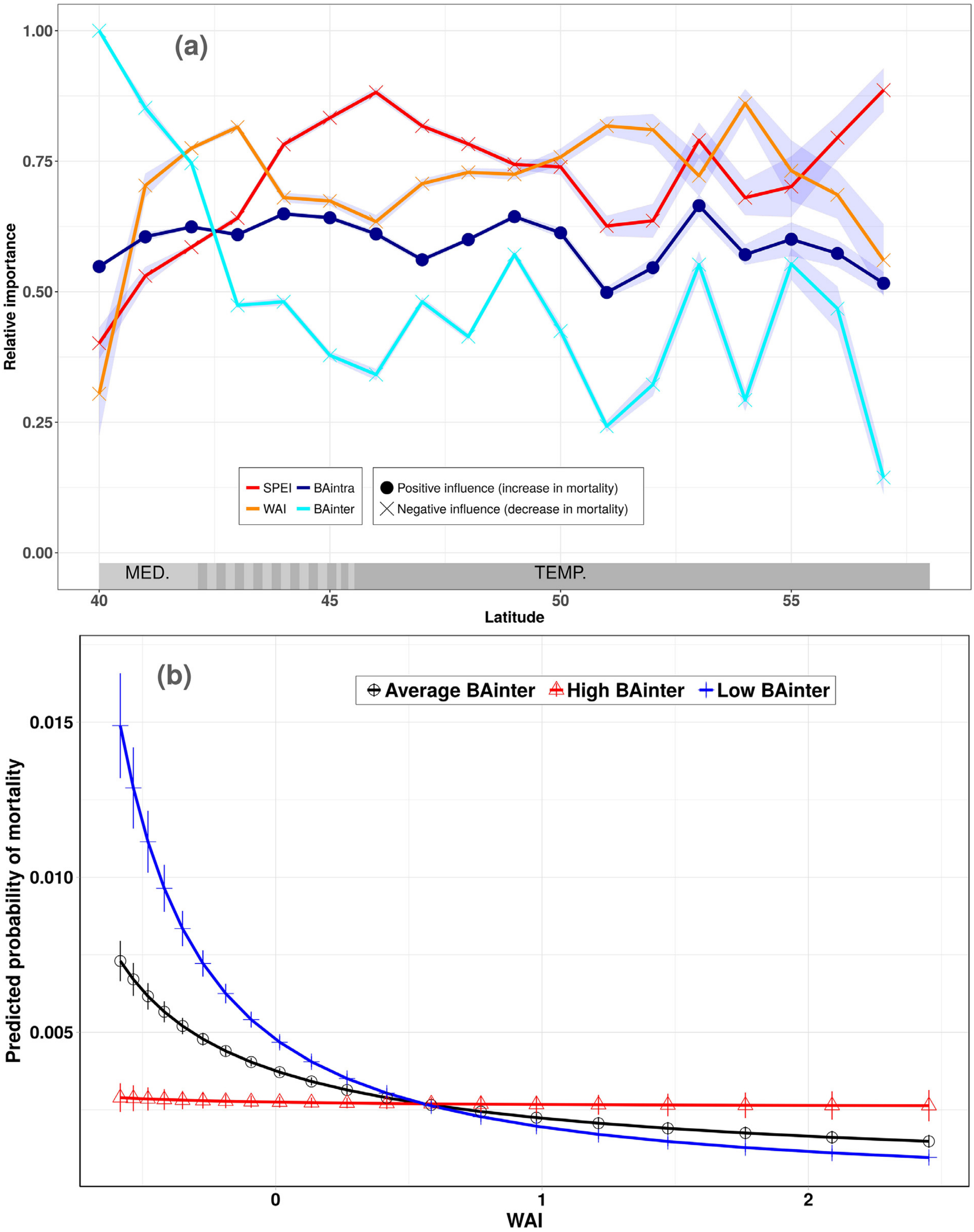

Fig. 3. Effects of drought-related variables and basal area on beech mortality. (a) Relative importance of the changes in climatic drought intensity over the study period (i.e. *SPEI*), climatic drought intensity (i.e. *WAI*), conspecific basal area (i.e. *BAintra*) and heterospecific basal area (i.e. *BAinter*) on beech predicted probability of mortality. The relative importance of each variable was computed for each tree from the logistic regression model (see Section 2.5), by giving a value of one to the most influencing variable and scaling the remaining variables accordingly. For each variable, the relative importance values were aggregated by 1° latitude resolution and the points of the graph correspond to the average values. The grey areas around the curve correspond to the 95% confidence intervals. The acronyms MED. and TEMP. in grey bars refer to the Mediterranean and cool temperate biome, respectively. (b) Interaction between heterospecific basal area (i.e. *BAinter*) and climatic drought intensity (i.e. *WAI*) on beech probability of mortality. This interaction was considered significant as its z value was higher than 2 (see Table S3.1). Beech mortality was predicted at three different levels of heterospecific basal area (mean value, 99.5th percentile and 0.005th percentile; proxies of average, high and low competition, respectively) along a drought gradient while the other predictors were fixed at their mean value.

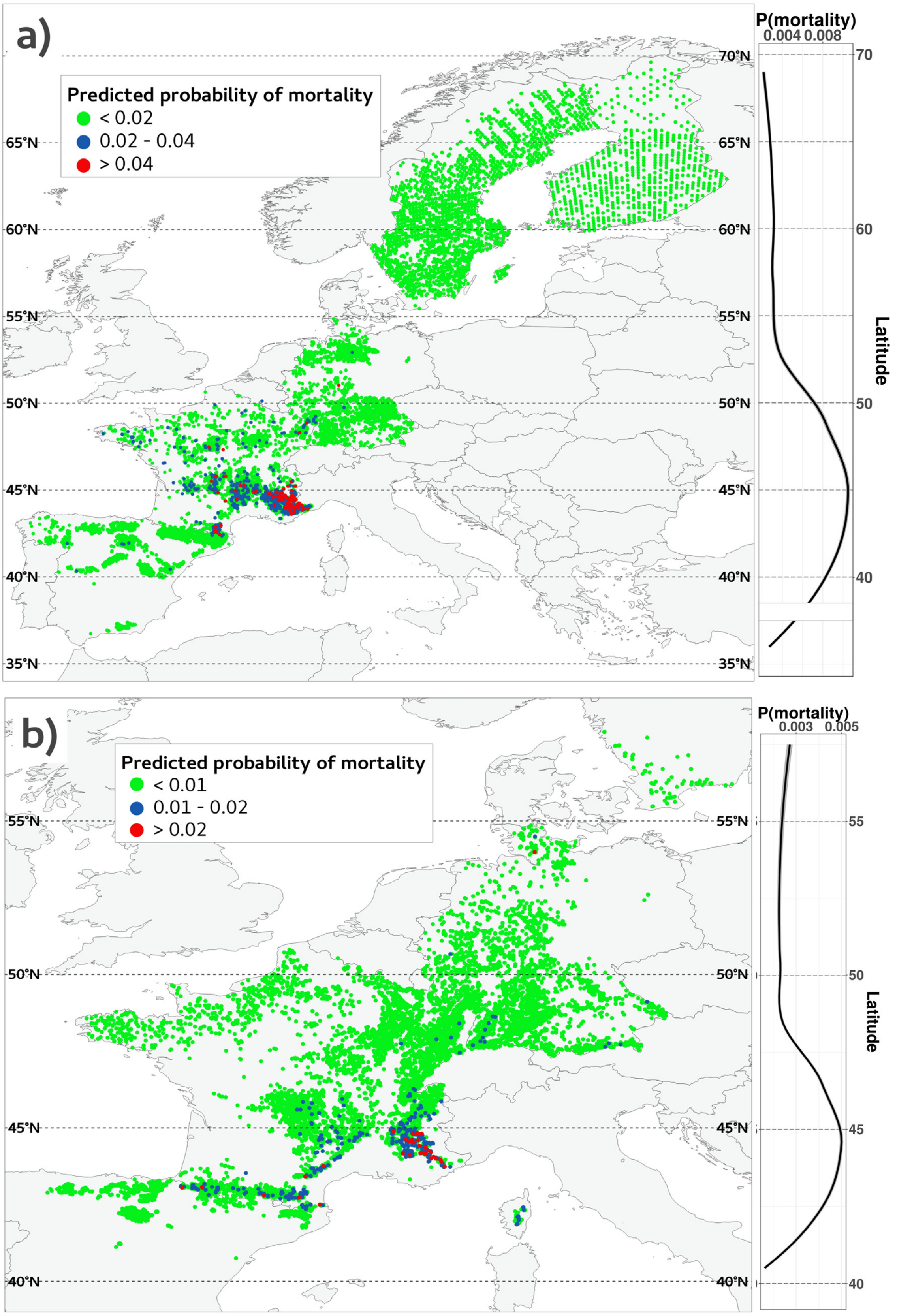

Fig. 4. Spatial projection of the annual predicted probability of mortality at the individual-level across Europe for (a) *P. sylvestris* and (b) *F. sylvatica*. Graphs in the right panels display predictions (noted as *P(mortality)*) across latitude. For both species, predictions were calculated for all trees from the logistic regression model and were clustered at 1° latitude resolution. A locally weighted regression was used to obtain the smooth solid lines ("loess" method of the geom_smooth function in "ggplot2" R package). Grey areas indicate 95% confidence intervals (almost confused with the curves). The white section for *P. sylvestris* in the Mediterranean biome represents missing data at that latitude (due to its distribution in Spain).

of the two, through direct and indirect effects that vary along geographical gradients and between the two species (Figs. 2 and 3), is shaping background mortality across species' ranges (see also Ruiz-Benito et al., 2013; Jump et al., 2017; Young et al., 2017). Interestingly, both species had similar patterns of predicted mortality, with the highest mortality rates in the southern French part of the Mediterranean biome (Fig. 4).

4.1. Increase in climatic drought intensity associated with higher mortality rates

Drought-related variables were more important for beech mortality than Scots pine (Figs. 2 and 3), probably reflecting functional differences in species responses to drought (Choat et al., 2018). Scots pine is a drought-avoiding species (e.g. a species which rapidly closes its stomata to maintain high water status; McDowell et al., 2008), that can survive from wet to dry environments (San-Miguel-Ayanz et al., 2016), whereas beech is a drought-sensitive species (van der Maaten, 2012; Chen et al., 2015) with an anisohydric response to drought (e.g. a species that keeps its stomata open until late during droughts to maintain carbon uptake; McDowell et al., 2008). Nevertheless, both beech (i.e. an angiosperm and broad-leaved species) and Scots pine (i.e. a gymnosperm and evergreen species) exhibited higher mortality rates in areas that were subject to increasing droughts during the study period (negative *SPEI*; Figs. 2 and 3). This result suggests that major phylogenetic and functional groups could display a similar mortality response to increasing drought (Greenwood et al., 2017) and is consistent with the results of a multi-species study suggesting that climatic extremes (like extreme droughts) are affecting tree mortality in Europe (Neumann et al., 2017).

The increase in drought intensity that occurred at about 45° latitude during the study period (see the lowest *SPEI* values in Fig. S2.1 and S2.3b) could be responsible for the higher tree mortality rates in the Mediterranean biome (Fig. 4), which is also supported by the high relative importance of the increase in drought intensity at this latitude (see the highest values of *SPEI* in Figs. 2 and 3). Moreover, we observed higher mortality rates in the driest areas (i.e. low *WAI*), as already reported for Scots pine in some inner Alpine valleys (Rigling et al., 2013) and in the Iberian Peninsula (Vilà-Cabrera et al., 2011; Galiano et al., 2011). Nevertheless, the stronger effect of increasing droughts over the study period (i.e. *SPEI*) than that of drought intensity (i.e. *WAI*) on Scots pine mortality could mean that mortality events tend to occur when drought conditions exceed the average in a given area, suggesting a certain degree of Scots pine adaptation to local conditions (Savolainen et al., 2007).

Drought-related variables were key drivers of beech mortality and were comparatively more important than heterospecific and conspecific basal area. A regional study of tree mortality suggested that competition between trees is more important than climate (Ruiz-Benito et al., 2013), but that study did not cover a climatic gradient as large as our study. Drought-induced mortality could also be studied under the assumption that mortality events follow a period of reduced growth (Caillleret et al., 2016). This assumption needs to be used with caution for beech, which can survive long periods of reduced growth before death (Hülsmann et al., 2018). In addition, beech growth-based studies produced contradictory results, showing both drought-induced reduction in growth (Jump et al., 2006) and drought-associated increase in growth (Tegel et al., 2014). Contrarily, Scots pine growth variations (i.e. and those of gymnosperms in general; Cailleret et al., 2017) can be used to predict upcoming drought-induced mortality events because, although more drought-resistant, Scots pine does not support long periods of reduced growth (Hülsmann et al., 2018).

4.2. Conspecific and heterospecific neighbours can affect individual tree mortality differently

Competition is a critical driver of forest structure (Kunstler et al., 2016), which strongly influences tree mortality and is comparatively more important for shade-intolerant than shade-tolerant species (Ruiz-Benito et al., 2013). High mortality rates were associated with high conspecific basal area in both species and high heterospecific basal area in Scots pine. However, high heterospecific basal area was correlated with low mortality rates in beech (Figs. 2 and 3). Scots pine is a shade-intolerant tree which is highly sensitive to competition for light (Ruiz-Benito et al., 2013), which might explain why both intra and inter-specific competition strongly and positively influenced its mortality rate (Condés and del Río, 2015). In contrast, beech is a late successional and shade-tolerant species (Hülsmann et al., 2018) that outcompetes other species in fertile sites (Condés and del Río, 2015). This is consistent with our observation of high mortality rates with high conspecific basal area but also with low heterospecific basal area: beech mainly suffers from the presence of conspecific neighbours, but not from heterospecific neighbours, which are necessarily less competitive species. This result is supported by growth studies showing that beech benefits from admixture with other species but is highly sensitive to intra-specific competition (Pretzsch et al., 2013a; Ratcliffe et al., 2015).

The heterospecific basal area affected the mortality rates of both species less than the conspecific basal area (Table S3.1, Figs. 2 and 3). The dominant nature of both Scots pine and beech in European forests may partly explain this difference as the basal area of heterospecifics was much lower than that of conspecifics all along the latitudinal gradient (Fig. S2.1). Nevertheless, the overdominance of intra-specific competition, a key process for stabilising ecosystems, is a globally-observed pattern (Kunstler et al., 2016), which could be linked to how interspecific differences determine complementarity mechanisms and, consequently, individual resource-use and coexistence mechanisms (Ruiz-Benito et al., 2017b).

4.3. The effects of climatic drought and basal area should be considered jointly in mortality studies

Competition with neighbours can be expressed as asymmetric competition for light on small suppressed trees (Ruiz-Benito et al., 2013) but also as symmetric competition for limited resources, like water or nutrients (Franklin et al., 1987; Gessler et al., 2017). Drought-induced mortality may be strong in areas with high levels of competition, because plants are more stressed and small changes in water availability could result in massive mortality events (Bradford and Bell, 2017; Ruiz-Benito et al., 2013; Young et al., 2017). In the case of Scots pine, the strong interaction between drought intensity and conspecific basal area reinforces this assumption (Table S3.1). Indeed, mortality rates were high in dry areas with high conspecific basal area whereas in areas with lower conspecific basal area, trees had still sufficient resources to survive despite reduced water availability (Fig. 2b). This result suggests that Scots pine suffers from the presence of neighbouring trees only when resources are scarce (Young et al., 2017).

In the case of beech, the influence of conspecific basal area on mortality was not modulated by drought (Table S3.1), suggesting that resource depletion does not exacerbate competitive pressure among beech trees. However, the probability of beech mortality in the driest areas was considerably higher when heterospecific basal area, the most important predictor in the Mediterranean biome (Fig. 3a and Table 1), was low (Fig. 3b). These findings suggest that beech survival in the driest part of its range is positively influenced by its neighbours (facilitation), which are mainly *Q. pyrenaica, P. sylvestris* and *C. sativa* (Table S5.1). Our results can only be compared to those of growth studies because the effect of mixing species has been more investigated in growth than mortality studies. Beech trees were shown to be more resilient and resistant to drought in mixed stands with oaks

(Pretzsch et al., 2013b). By contrast, Bosela et al. (2018) found that the growth of beeches mixed with fir trees or in pure stands was equally negatively affected by long-term droughts but they didn't explore the south-western part of beech distribution. Overall, these results suggest that beech growth and mortality are influenced by interspecific interactions that vary along the European drought gradient: from neutral interactions in wet areas where beech co-occurs mainly with *Abies alba* and *Picea abies*, to facilitation in dry areas where beech co-occurs with more Mediterranean species (Fig. 3b and Table S5.1). However, the mechanisms behind these interspecific interactions, particularly in dry areas, are still largely unknown. Identifying associations of species that can survive droughts could help to better understand drought-related mortality patterns in the coming years.

In the case of Scots pine, previous regional studies reported contradictory interaction effects between competition and drought: higher rate of decline in dry areas but only at low competition levels (Vilà-Cabrera et al., 2013), low mortality rates related to high heterospecific basal area in wet areas (Condés and del Río, 2015) and only additive effects of competition and drought on mortality with no interaction effects (Galiano et al., 2010). Our study is the first to describe interaction patterns between drought and basal area at the scale of the distribution of each species (Figs. 2, 3 and S4). As we found four significant interactions (albeit three of which only slightly affect mortality) influencing Scots pine mortality and only one in the case of beech (Table S3.1), we can assume that Scots pine mortality is affected directly and indirectly by drought through interactions with basal area while beech mortality was more directly affected by drought.

4.4. *Tree mortality patterns along latitude and potential associated range shifts*

Predicted probability of mortality in both beech and Scots pine was higher in the southern part of their distribution, mainly corresponding to the French part of the Mediterranean biome and the Pyrenees in the case of beech (Fig. 4). In these areas, beech and Scots pine mortality rates were accurately predicted (Fig. 1), except at the southern end of Scots pine range where mortality rates are likely to be slightly higher than predicted (Fig. 1a). These accurate predictions in the southern part of species ranges were expected as we chose climatic variables related to droughts, generally more important in the Mediterranean biome (Fig. S2.3). Surprisingly, the association of drought and competition-related variables alone explained Scots pine mortality patterns in the northern part of its distribution (Fig. 1a) but overestimated the probability of beech mortality in northern Germany (Fig. 1b) suggesting that other factors come into play in these areas to explain beech mortality patterns (see 4.3 Limitations).

An unexpected result was that French Mediterranean Scots pines and beech trees suffered even more from climatic drought than those in Spain, where several studies reported high mortality or defoliation rates in the Iberian Peninsula in both species (Carnicer et al., 2011; Vilà-Cabrera et al., 2011, 2013; Benito Garzón et al., 2013). Nevertheless, this pattern may be explained by the high altitudes at which both species occur in Spain, and the calcareous soils of southeastern France, which do not retain water and are consequently very dry. In the case of Scots pine, we also hypothesise that local adaptation to temperature explains our underestimated mortality predictions in the southernmost part of the gradient (Savolainen et al., 2007): populations in these areas may be highly locally-adapted to drought conditions and therefore less resistant to changing climate (Benito Garzón et al., 2011).

The high mortality rates predicted in the French part of the Mediterranean biome could be explained by the increase in drought intensity during the study period in that region (Fig. S2.3b), suggesting that mortality plays a critical role in delimiting the driest part of the species ranges (Gaston, 2009; Benito Garzón et al., 2013; Ruiz-Benito et al., 2017a), in particular in the Mediterranean biome, which is expected to face drier conditions in the coming decades. In addition to direct effects of climate change, Scots pine and beech are exposed to more intense fires in the driest parts of their range (Fréjaville et al., 2018) and these should increase the likelihood of range contraction at the ecotone between Mediterranean and cool temperate biomes.

4.5. *Limitations*

Until recently, European forests have been extensively exploited and forest management is still widespread, particularly in the Scandinavian countries (Schelhaas et al., 2018). Although we removed the direct effects of management in our study (i.e. by removing plots in which trees were noted as harvested), management may still result in both an overestimation (e.g. by reducing competition pressure in thinned plots) and an underestimation of natural mortality rates through salvage loggings (i.e. the harvest of dead trees after a natural disaster) or sanitation fellings (i.e. the harvest of diseased trees).

Other factors also affect tree mortality, either directly, indirectly or through interactions, such as: changes in disturbance regimes (Seidl et al., 2017), insect outbreaks (Anderegg et al., 2015), mistletoe (Dobbertin and Rigling, 2006), atmospheric pollutants (Dietze and Moorcroft, 2011), populations genetic differentiation and plasticity (Benito Garzón et al., 2011), soil characteristics (Dietze and Moorcroft, 2011). However, given our concern to limit the model complexity and the lack of large-scale data, we decided not to include them in our study and to focus on comparing the effects of drought and competition on mortality.

5. Conclusions

Mortality of Scots pine and beech was affected by climatic drought intensity and indirect competition from neighbouring trees, but in different ways. Drought directly affected beech mortality rates and beech trees benefited from mixing with other species, particularly in the Mediterranean biome. Scots pine mortality suffered mostly from competition and was indirectly affected by drought through interactions with competitors, especially in southeastern France. In this area, which experienced a marked increase in drought intensity during the study period, high mortality rates were predicted for both species, as expected for temperate trees for which the Mediterranean biome corresponds to the southernmost part of the distribution. In a warming climate, our study is a step further in understanding geographical patterns of tree mortality in Europe and shed light on the high mortality risks faced by European tree species, regardless of their different life-history strategies, especially at the ecotone between the Mediterranean and cool temperate biomes. In this priority area, beech could benefit from mixing with other species and pine from reduced competition.

Data accessibility

The data are available upon request to the co-authors.

Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2019.107772.

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Annexes 2: harmonized species list in the national forest inventories

Sp ID	Final code	FUNDIV code	Initial names	Final name	Rank	Origin
1	ABIALB	61	Abies alba Mill.	Abies alba	species	native
8	ABICEP	70SC	SAPIN DE CEPHALONIE	Abies cephalonica	species	native
2	ABICON	68SC	Abies concolor (Gordon) Lindl. ex Hildebr.	Abies concolor	species	exotic
3	ABIGRA	72V	Abies grandis (D.Don) Lindl.	Abies grandis	species	exotic
8	ABINOR	71	SAPIN DE NORDMANN	Abies nordmanniana	species	native
8	ABIBOR	70SB	SAPIN DE TURQUIE	Abies nordmanniana bornmulleriana	subspecies	native
6	ABIPIN	70SE	Abies pinsapo Boiss.	Abies pinsapo	species	exotic
7	ABIPRO	72N	Abies procera Rehder	Abies procera	species	exotic
8	ABI	NA	Abies spp.	Abies sp.	genus	NA
10	ACADEA	NA	Acacia dealbata Link	Acacia dealbata	species	NA
12	ACA	29MI	MIMOSA	Acacia farnesiana	NA	exotic
11	ACAMEL	NA	Acacia melanoxylon R.Br.	Acacia melanoxylon	species	NA
12	ACA	NA	Acacia spp.	Acacia sp.	genus	NA
14	ACECAM	21C	Acer campestre L.	Acer campestre	species	native
15	ACEMON	21M	Acer monspessulanum L.	Acer monspessulanum	species	native
16	ACENEG	29EN	Acer negundo L.	Acer negundo	species	native
17	ACEOPA	21O	Acer opalus Mill.	Acer opalus	species	native
18	ACEPLA	15P	Acer platanoides L.	Acer platanoides	species	native
19	ACEPSE	15S	Acer pseudoplatanus L.	Acer pseudoplatanus	species	native
24	AESHIP	29MA	Aesculus hippocastanum L.	Aesculus hippocastanum	species	native

25	AILALT	29AI	Ailanthus altissima (Mill.) Swingle	Ailanthus altissima	species	native
26	ALNCOR	13C	AULNE DE CORSE	Alnus cordata	species	native
27	ALNGLU	13G	Alnus glutinosa (L.) Gaertn.	Alnus glutinosa	species	native
28	ALNINC	13B	Alnus incana (L.) Moench	Alnus incana	species	native
26	ALN	NA	Alnus spp.	Alnus sp.	genus	NA
29	ALNVIR	37	Alnus viridis (Chaix) DC.	Alnus viridis	species	native
33	APOBAR	NA	Apollonias barbujana (Cav.) A.Br.	Apollonias barbujana	species	NA
34	ARBCAN	NA	Arbutus canariensis Veill.	Arbutus canariensis	species	NA
35	ARBUNE	40	Arbutus unedo L.	Arbutus unedo	species	native
46	BETPEN	12V	Betula pendula Roth	Betula pendula	species	native
47	BETPUB	12P	Betula pubescens Ehrh.	Betula pubescens	species	native
48	BET	NA	Betula spp.	Betula sp.	genus	NA
54	BUXSEM	49BS	Buxus sempervirens L.	Buxus sempervirens	species	undetermined
57	CARBET	11	Carpinus betulus L.	Carpinus betulus	species	native
58	CASSAT	10	Castanea sativa Mill.	Castanea sativa	species	native
516	CASEQU	29fi	Filao	Casuarina equisetifolia	species	exotic
59	CEDATL	65	Cedrus atlantica (Endl.) Carrire	Cedrus atlantica	species	exotic
60	CEDDEO	NA	Cedrus deodara (D.Don) G.Don	Cedrus deodara	species	NA
61	CEDLIB	76	Cedrus libani A.Rich.	Cedrus libani	species	exotic
62	CELAUS	16	Celtis australis L.	Celtis australis	species	native
63	CERSIL	NA	Ceratonia siliqua L.	Ceratonia siliqua	species	NA
394	CERCSIL	49CS	ARBRE DE JUDEE	Cercis siliquastrum	species	undetermined
64	CHALAW	68CL	Chamaecyparis lawsoniana (A.Murray bis) Parl.	Chamaecyparis lawsoniana	species	exotic

508	CIT	49CA	ORANGER	Citrus xsinensis	genus	undetermined
396	CORMAS	39	CORNOUILLER MALE	Cornus mas	species	native
85	CORSAN	NA	Cornus sanguinea L.	Cornus sanguinea	species	NA
91	CORAVE	31	Corylus avellana L.	Corylus avellana	species	native
92	CORCOL	NA	Corylus colurna L.	Corylus colurna	species	NA
98	CRAAZA	49AA	AUBEPINE AZEROLIER	Crataegus azarolus	species	undetermined
95	CRALAC	NA	Crataegus laciniata Ucria	Crataegus laciniata	species	NA
98	CRALAE	49AE	AUBEPINE EPINEUSE	Crataegus laevigata	species	undetermined
97	CRAMON	49AM	Crataegus monogyna Jacq.	Crataegus monogyna	species	undetermined
98	CRA	NA	Crataegus spp.	Crataegus sp.	genus	NA
451	CRYJAP	68CJ	CRYPTOMERIA DU JAPON	Cryptomeria japonica	species	exotic
99	CUPARI	NA	Cupressus arizonica Greene	Cupressus arizonica	species	NA
100	CUPLUS	NA	Cupressus lusitanica Mill.	Cupressus lusitanica	species	NA
101	CUPMAC	68CM	Cupressus macrocarpa Hartw.	Cupressus macrocarpa	species	exotic
102	CUPSEM	66	Cupressus sempervirens L.	Cupressus sempervirens	species	native
398	CYDOBL	49C	COGNASSIER	Cydonia oblonga	species	undetermined
120	ERIARB	49EA	Erica arborea L.	Erica arborea	species	undetermined
124	ERISCO	NA	Erica scoparia L.	Erica scoparia	species	NA
129	EUCCAM	NA	Eucalyptus camaldulensis Dehnh.	Eucalyptus camaldulensis	species	NA
130	EUCGLO	NA	Eucalyptus globulus Labill.	Eucalyptus globulus	species	NA
131	EUCGOM	NA	Eucalyptus gomphocephalus DC.	Eucalyptus gomphocephalus	species	NA
132	EUCNIT	NA	Eucalyptus nitens (H.Deane Maiden) Maiden	Eucalyptus nitens	species	NA
504	EUC	36	EUCALYPTUS (GENRE)	Eucalyptus sp.	genus	exotic

133	EUCVIM	NA	Eucalyptus viminalis Labill.	Eucalyptus viminalis	species	NA
134	EUOEUR	49EV	Euonymus europaeus L.	Euonymus europaeus	species	undetermined
139	FAGSYL	09	Fagus sylvatica L.	Fagus sylvatica	species	native
140	FICCAR	23F	Ficus carica L.	Ficus carica	species	exotic
142	FRAAME	NA	Fraxinus americana L.	Fraxinus americana	species	NA
143	FRAANG	17O	Fraxinus angustifolia Vahl	Fraxinus angustifolia	species	native
144	FRAEXC	17C	Fraxinus excelsior L.	Fraxinus excelsior	species	native
145	FRAORN	17F	Fraxinus ornus L.	Fraxinus ornus	species	native
158	HEBBAH	NA	Heberdenia bahamensis (Gaertn.) Sprague	Heberdenia bahamensis	species	NA
165	ILEAQU	49IA	Ilex aquifolium L.	Ilex aquifolium	species	undetermined
166	ILECAN	NA	Ilex canariensis Poir.	Ilex canariensis	species	NA
167	ILEPLA	NA	Ilex platyphylla Webb Berthel.	Ilex platyphylla	species	NA
169	JUGNIG	27N	NOYER NOIR	Juglans nigra	species	exotic
170	JUGREG	27C	Juglans regia L.	Juglans regia	species	native
171	JUNCED	NA	Juniperus cedrus Webb Berthel.	Juniperus cedrus	species	NA
172	JUNCOM	69JC	Juniperus communis L.	Juniperus communis	species	native
173	JUNOXY	69JO	Juniperus oxycedrus L.	Juniperus oxycedrus	species	native
174	JUNPHO	NA	Juniperus phoenicea L.	Juniperus phoenicea	species	NA
177	JUNTUR	NA	Juniperus phoenicea L. subsp. turbinata (Guss.) Nyman	Juniperus phoenicea turbinata	subsp	NA
381	"JUN"	NA	Juniperus spp.	Juniperus sp.	genus	NA
176	JUNTHU	69	Juniperus thurifera L.	Juniperus thurifera	species	native
498	LABALP	38AL	CYTISE DES ALPES	Laburnum alpinum	species	native

410	LABANA	38AU	CYTISE AUBOUR	Laburnum anagyroides	species	native
179	LARDEC	63	Larix decidua Mill.	Larix decidua	species	native
180	LARKAE	74J	Larix kaempferi (Lamb.) Carrire sec. Franco	Larix kaempferi	species	exotic
181	LAR	NA	Larix spp.	Larix sp.	genus	NA
181	LARXE	74H	MELEZE HYBRIDE	Larix xeurolepis	species	exotic
183	LAUAZO	NA	Laurus azorica (Seub.) Franco	Laurus azorica	species	NA
184	LAUNOB	49LN	Laurus nobilis L.	Laurus nobilis	species	undetermined
453	LIQSTY	29LI	LIQUIDAMBAR	Liquidambar styraciflua	species	exotic
411	LIRTUL	42	TULIPIER DE VIRGINIE	Liriodendron tulipifera	species	exotic
197	MALSYL	23PM	Malus sylvestris Mill.	Malus sylvestris	species	native
200	MORALB	49MB	Morus alba L.	Morus alba	species	undetermined
202	MOR	NA	Morus spp.	Morus sp.	genus	NA
203	MYRFAY	NA	Myrica faya Aiton	Myrica faya	species	NA
208	OLEEUR	28	Olea europaea L.	Olea europaea	species	native
473	OSTCAR	32	CHARME HOUBLON	Ostrya carpinifolia	species	native
371	OTHBRO	29AF	Other broadleaved	Other broadleaved sp.		NA
370	OTHCON	68CE	Other conifers	Other conifers sp.		exotic
376	OTHEUC	NA	Other eucalyptus	Other eucalyptus sp.		NA
372	OTHLAU	NA	Other Laurels	Other laurels sp.		NA
378	OTHOAK	NA	Other oaks	Other Oaks sp.		NA
377	OTHPIN	NA	Other pines	Other pines sp.		NA
375	OTHRIP	NA	Other riparian trees	Other riparian sp.		NA
213	PERIND	NA	Persea indica (L.) Spreng.	Persea indica	species	NA

215	PHILAT	49FL	Phillyrea latifolia L.	Phillyrea latifolia	species	undetermined
219	PHOCAN	NA	Phoenix canariensis hort. ex Chabaud	Phoenix canariensis	species	NA
220	PHO	NA	Phoenix spp.	Phoenix sp.	genus	NA
221	PICEXC	NA	Picconia excelsa (Aiton) DC.	Picconia excelsa	species	NA
223	PICABI	62	Picea abies (L.) H.Karst.	Picea abies	species	native
227	PICOMO	68EO	Picea omorika (Pancic) Purk.	Picea omorika	species	exotic
228	PICPUN	NA	Picea pungens Engelm.	Picea pungens	species	NA
229	PICSIT	73	Picea sitchensis (Bong.) Carrire	Picea sitchensis	species	exotic
222	PIC	NA	Picea spp.	Picea sp.	genus	NA
231	PINCAN	NA	Pinus canariensis Sweet ex Spreng.	Pinus canariensis	species	NA
232	PINCEM	59	Pinus cembra L.	Pinus cembra	species	native
233	PINCON	68PC	Pinus contorta Douglas ex Loudon	Pinus contorta	species	exotic
234	PINBRU	57B	PIN BRUTIA (OU) ELDARICA	Pinus halapensis brutia	subspecies	native
234	PINHAL	57A	Pinus halepensis Mill.	Pinus halepensis	species	native
235	PINMUG	NA	Pinus mugo Turra	Pinus mugo	species	NA
236	PINNIG	54	Pinus nigra J.F.Arnold	Pinus nigra	species	native
236	PINLAR	53CA	PIN LARICIO DE CALABRE	Pinus nigra laricio	subspecies	native
236	PINLAR	53CO	PIN LARICIO DE CORSE	Pinus nigra laricio	subspecies	native
236	PINNIG	53S	PIN DE SALZMANN	Pinus nigra salzmannii	species	native
238	PINPINA	51	Pinus pinaster Aiton	Pinus pinaster	species	native
239	PINPIN	55	Pinus pinea L.	Pinus pinea	species	native
240	PINPON	NA	Pinus ponderosa Douglas ex P.Lawson C.Lawson	Pinus ponderosa	species	NA
241	PINRAD	68PM	Pinus radiata D.Don	Pinus radiata	species	exotic

230	PIN	NA	Pinus spp.	Pinus sp.	genus	NA
242	PINSTR	56	Pinus strobus L.	Pinus strobus	species	native
243	PINSYL	52	Pinus sylvestris L.	Pinus sylvestris	species	native
520	PINTAE	77	PIN A L'ENCENS ET HYBRIDES	Pinus taeda	NA	exotic
244	PINUNC	58	Pinus uncinata Mill. ex Mirb.	Pinus uncinata	species	native
246	PISLEN	49PL	PISTACHIER LENTISQUE	Pistacia lentiscus	species	undetermined
247	PISTER	49PT	Pistacia terebinthus L.	Pistacia terebinthus	species	undetermined
248	PLAHIS	NA	Platanus hispanica Ten.	Platanus hispanica	species	NA
505	PLAOCC	26OC	PLATANE D'OCCIDENT	Platanus occidentalis	species	native
248	PLAACE	26E	PLATANE A FEUILLES D'ERABLE	Platanus xacerifolia	NA	native
252	POPALB	33B	Populus alba L.	Populus alba	species	native
382	POPBAL	NA	Populus balsamifera subsp. trichocarpa (Torr. Gray ex Hook.) Brayshaw	Populus balsamifera trichocarpa	subspecies	NA
458	POPCAN	33G	PEUPLIER GRISARD	Populus canescens	speceies	native
253	POPNIG	33N	Populus nigra L.	Populus nigra	species	native
251	POP	19	Populus spp.	Populus sp.	genus	native
254	POPTRE	24	Populus tremula L.	Populus tremula	species	exotic
255	POPXC	NA	Populus xcanadensis Moench	Populus xcanadensis	species	NA
256	PRUAVI	22M	Prunus avium L.	Prunus avium	species	native
419	PRUCER	49PC	PRUNE-CERISE	Prunus cerasifera	species	undetermined
263	PRU	22C	CERISIER	Prunus cerasus	species	native
420	PRUDOM	23PD	PRUNIER DOMESTIQUE	Prunus domestica	species	native
474	PRUDUL	23A	AMANDIER	Prunus dulcis	species	native

257	PRULUS	NA	Prunus lusitanica L.	Prunus lusitanica	species	NA
258	PRUMAH	49PM	CERISIER DE SAINTE-LUCIE	Prunus mahaleb	species	undetermined
259	PRUPAD	22G	Prunus padus L.	Prunus padus	species	native
261	PRUSER	22S	Prunus serotina Ehrh.	Prunus serotina	species	native
263	PRU	NA	Prunus spp.	Prunus sp.	genus	NA
262	PRUSPI	49PS	Prunus spinosa L.	Prunus spinosa	species	undetermined
264	PSEMEN	64	Pseudotsuga menziesii (Mirb.) Franco	Pseudotsuga menziesii	species	exotic
266	PYRCOR	23PF	POIRIER A FEUILLES EN COUR	Pyrus cordata	species	native
423	PYRPYR	23PC	Pyrus pyraster Burgsd.	Pyrus pyraster	species	native
266	PYR	NA	Pyrus spp.	Pyrus sp.	genus	NA
266	PYRAMY	23PA	POIRIER A FEUILLES D'AMANDIER Pyrus amygdaliforms	Pyrus spinosa	species	native
268	QUECAN	NA	Quercus canariensis Willd.	Quercus canariensis	species	NA
267	QUECER	34	CHENE CHEVELU	Quercus cerris	species	native
271	QUEFAG	NA	Quercus faginea Lam.	Quercus faginea	species	NA
273	QUEILE	6	Quercus ilex L.	Quercus ilex	species	native
275	QUEPAL	29CM	Quercus palustris Munchh.	Quercus palustris	species	native
276	QUEPET	3	Quercus petraea (Matt.) Liebl.	Quercus petraea	species	native
277	QUEPUB	5	Quercus pubescens Willd. (Q. Humilis)	Quercus pubescens	species	native
278	QUEPYR	7	Quercus pyrenaica Willd.	Quercus pyrenaica	species	native
279	QUEROB	2	Quercus robur L.	Quercus robur	species	native
280	QUERUB	4	Quercus rubra L.	Quercus rubra	species	exotic
267	QUE	NA	Quercus spp.	Quercus sp.	genus	NA

281	QUESUB	08S	Quercus suber L.	Quercus suber	species	native
282	RHAALA	49RA	Rhamnus alaternus L.	Rhamnus alaternus	species	undetermined
283	RHAALP	49RP	NERPRUN DES ALPES	Rhamnus alpina	species	undetermined
141	FRAALN	49BO	BOURDAINE rhamnus frangula	Frangula alnus	species	undetermined
426	RHACAT	49RC	NERPRUN PURGATIF	Rhamnus cathartica	species	undetermined
428	RHUTYP	49RT	SUMAC DE VIRGINIE	Rhus typhina	species	undetermined
296	ROBPSE	14	Robinia pseudacacia L.	Robinia pseudacacia	species	exotic
305	SALALB	25B	Salix alba L.	Salix alba	species	native
306	SALATR	25R	Salix atrocinerea Brot.	Salix atrocinerea	species	native
307	SALBAB	NA	Salix babylonica L.	Salix babylonica	species	NA
308	SALCAN	NA	Salix canariensis Chr.Sm. ex Link	Salix canariensis	species	NA
310	SALCAP	25M	Salix caprea L.	Salix caprea	species	native
462	SALCIN	25C	SAULE CENDRE	Salix cinerea	speces	native
501	SALDAP	25FD	SAULE FAUX DAPHNE	Salix daphnoides	species	native
311	SALELA	25D	Salix elaeagnos Scop.	Salix eleagnos	species	native
312	SALFRA	25FR	Salix fragilis L.	Salix fragilis	species	native
314	SAL	2500000	SAULE A CINQ ETAMINES	Salix pentandra	genus	native
314	SAL	NA	Salix spp.	Salix sp.	genus	NA
464	SALTRI	25000	SAULE A TROIS ETAMINES	Salix trianda	species	native
465	SALVIM	25V	SAULE DES VANNIERS	Salix viminalis	species	native
315	SAMNIG	49SN	Sambucus nigra L.	Sambucus nigra	species	undetermined
317	SAMRAC	49SR	Sambucus racemosa L.	Sambucus racemosa	species	undetermined
466	SEQSEM	68SV	SEQUOIA TOUJOURS VERT	Sequoia sempervirens	species	exotic
324	SORARI	23AB	Sorbus aria (L.) Crantz	Sorbus aria	species	native

325	SORAUC	23SO	Sorbus aucuparia L.	Sorbus aucuparia	species	native
327	SORDOM	23C	Sorbus domestica L.	Sorbus domestica	species	native
495	SORINT	NA	Sorbus intermedia (Ehrh.) Pers.	Sorbus intermedia	species	NA
329	SORLAT	23AF	ALISIER DE FONTAINEBLEAU	Sorbus latifolia	species	native
329	SORMOU	23AM	ALISIER DE MOUGEOT	Sorbus mougeoti	species	native
329	SOR	NA	Sorbus spp.	Sorbus sp.	genus	NA
330	SORTOR	41	Sorbus torminalis (L.) Crantz	Sorbus torminalis	species	native
335	TAMAFR	49TF	TAMARIS D'AFRIQUE	Tamarix africana	species	undetermined
335	TAMGAL	49TG	TAMARIS DE FRANCE	Tamarix gallica	species	undetermined
335	TAM	NA	Tamarix spp.	Tamarix sp.	genus	NA
434	TAXDIS	68CC	CYPRES CHAUVE	Taxodium distichum	species	exotic
336	TAXBAC	67	Taxus baccata L.	Taxus baccata	species	exotic
339	THUPLI	68TG	THUYA GEANT	Thuja plicata	genus	exotic
339	THU	NA	Thuja spp.	Thuja sp.	genus	NA
346	TILCOR	20P	Tilia cordata Mill.	Tilia cordata	species	native
347	TILPLA	20X	TILLEUL DE HOLANDE	Tilia platyphyllos	NA	native
347	TILPLA	20G	Tilia platyphyllos Scop.	Tilia platyphyllos	species	native
348	TIL	NA	Tilia spp.	Tilia sp.	genus	NA
349	TSUHET	68TH	TSUGA HETEROPHYLLE	Tsuga heterophylla	genus	exotic
349	TSU	NA	Tsuga spp.	Tsuga sp.	genus	NA
354	ULMGLA	18M	Ulmus glabra Huds.	Ulmus glabra	species	native
353	ULMLAE	18D	ORME LISSE	Ulmus laevis	NA	native
355	ULMMIN	18C	Ulmus minor Mill.	Ulmus minor	species	native

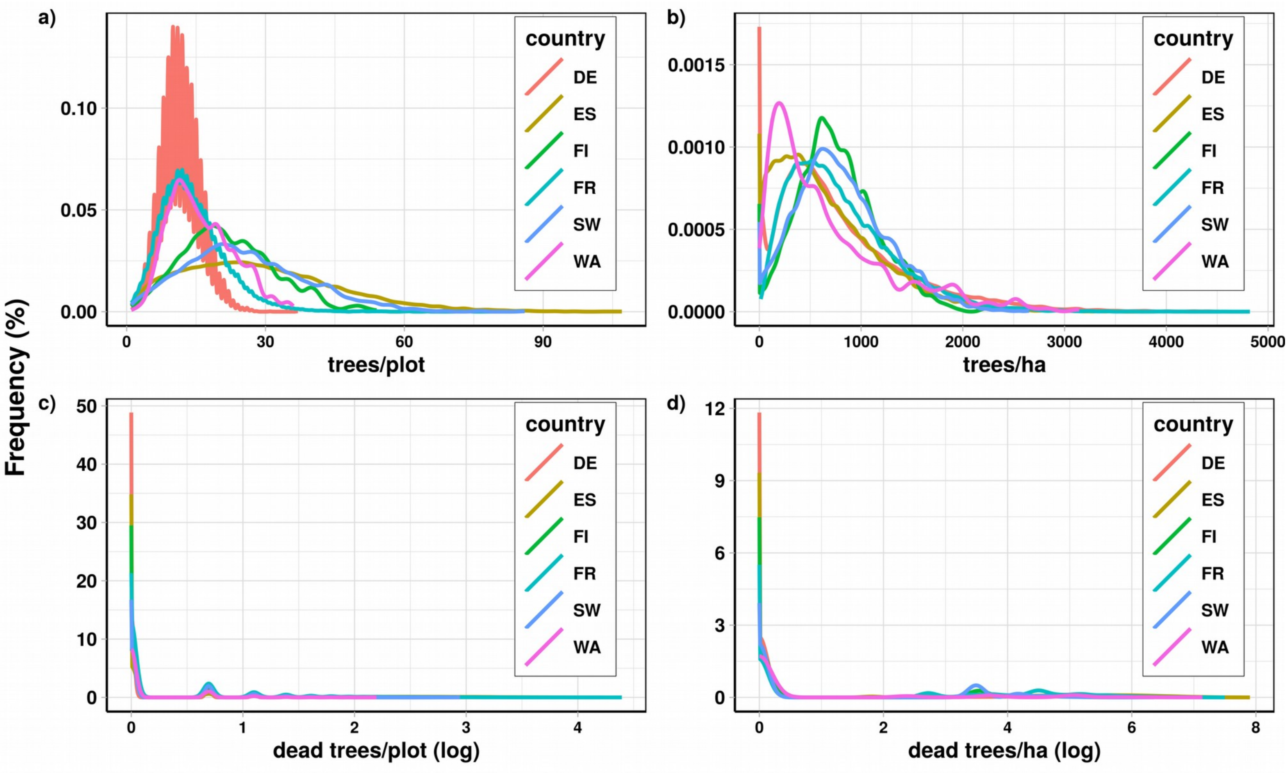
356	ULMPUM	NA	Ulmus pumila L.	Ulmus pumila	species	NA
353	ULM	NA	Ulmus spp.	Ulmus sp.	genus	NA

Annexes 3: Supplementary figures of chapter 3

Supplementary Information: Figures

Section 1: Plot descriptive statistics by country

Figure S1: Distribution of the number of trees/plot (a), number of trees/ha (b), number of dead trees/plot (c) and number of dead trees/ha (d) according to the different NFI's countries.



Section 2: Climatic marginality

Figure S2: Climatic characterization of the species distribution ranges into core, transition and marginal (leading or trailing) areas. We show an example for *Pinus sylvestris* from EUFORGEN including: a) Species distribution range; b) the climatic variables within the species range are analysed using a Weighted PCA to define three clusters including C = Core areas with C: the lowest weighted scores within the range calculated on the two first axis of the PCA (Core % thresholds (CT) are shown in Table S2 for each species range); M = Marginal areas with M: the largest weighted scores within the range (extremes individuals) calculated on the two first axis of the PCA (margin % thresholds (MT) are shown in Table S2); T = Transition areas with T: weighted scores that fall between the lowest values (core) and largest values (marginal areas); c) results of the Marginal climatic areas that were clustered into: TE trailing edge (TE) and (leading edge (LE) areas (Table S2) with a Discriminant Principal Component Analysis (DPCA).; d) map of the areas defined within the species range with their respective colors. (“Core” in yellow, “trailing edge” in blue, “leading edge” in red and “transition” zone in gray).

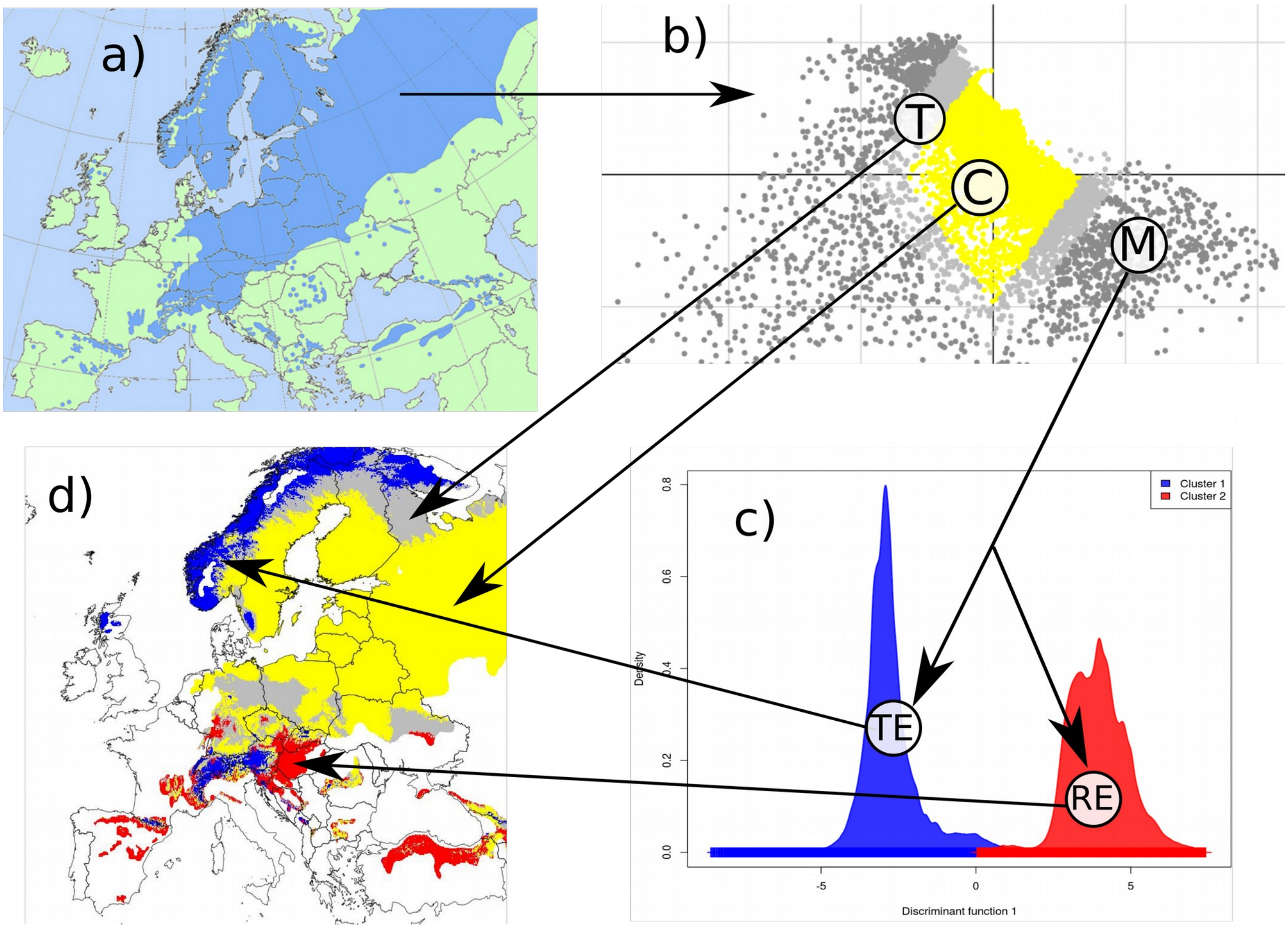
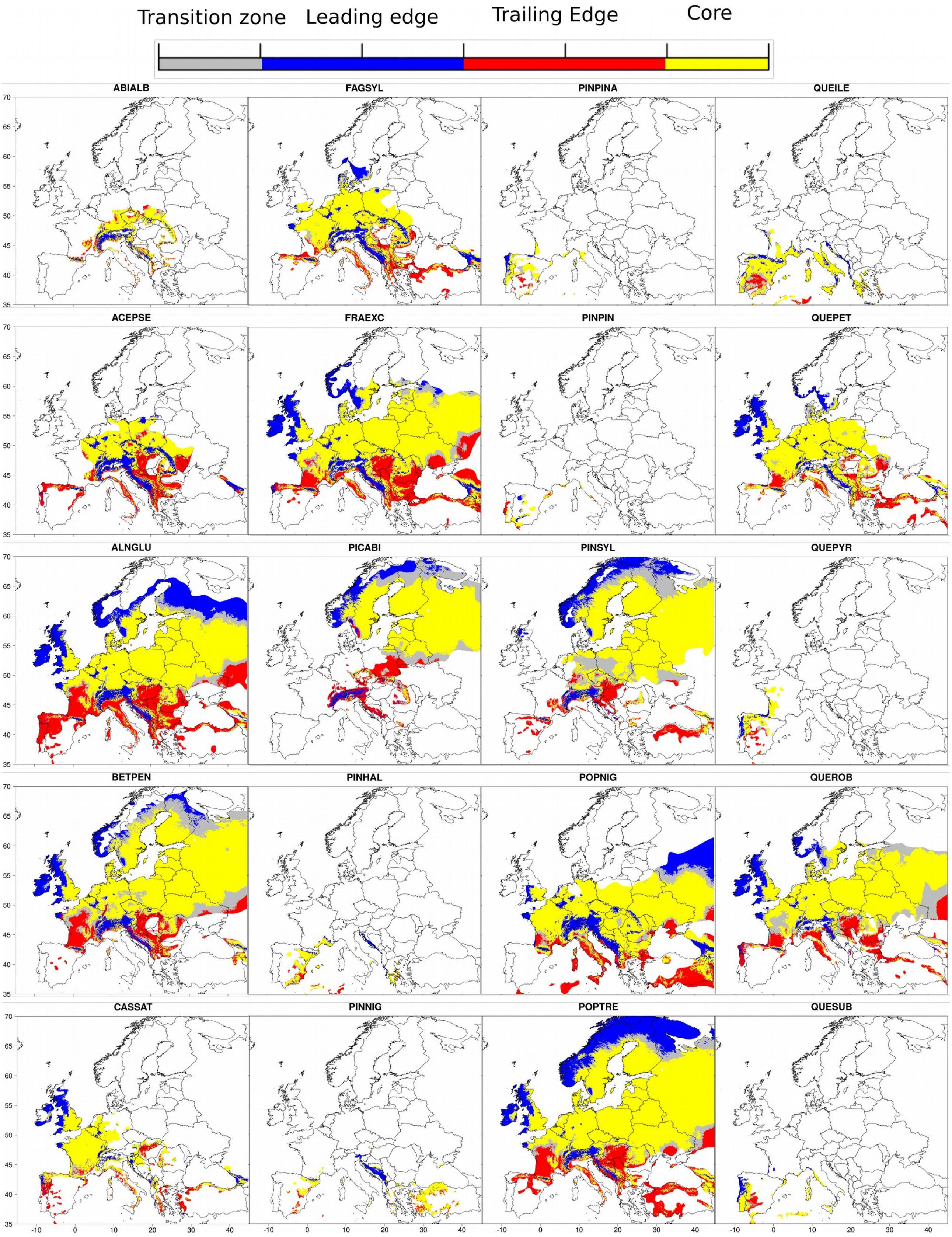


Figure S3: Climatic marginality maps of the 20 tree species studied showing four distribution ranges: core, leading edge, trailing edge and transition areas (in red, blue, red and gray, respectively).



Section 3: Observed and predicted mortality

Figure S4: Comparison between the empirical distribution of observed counts (black lines) and the predicted distribution of counts (blue lines) for each species and for plots where mortality occurs only (NB models).

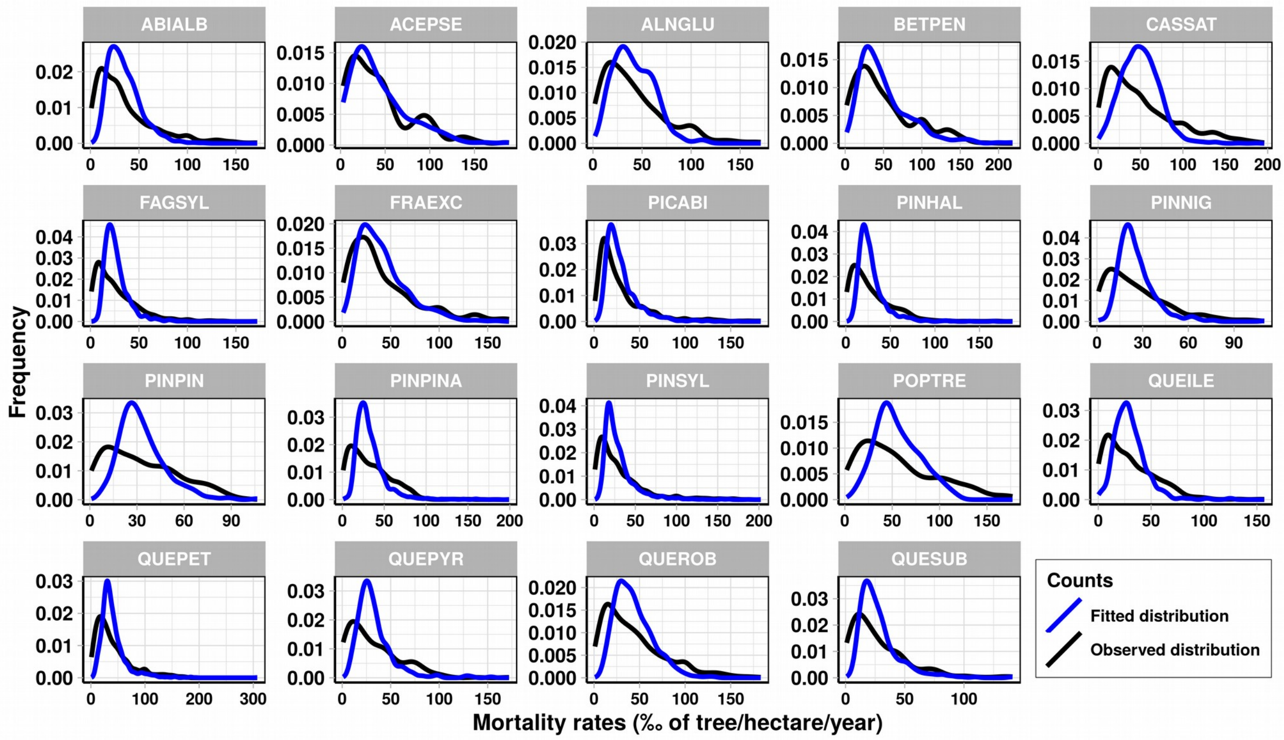


Figure S5: Observed mortality rate in all plots for each species as a percentage of dead trees by year and by hectare.

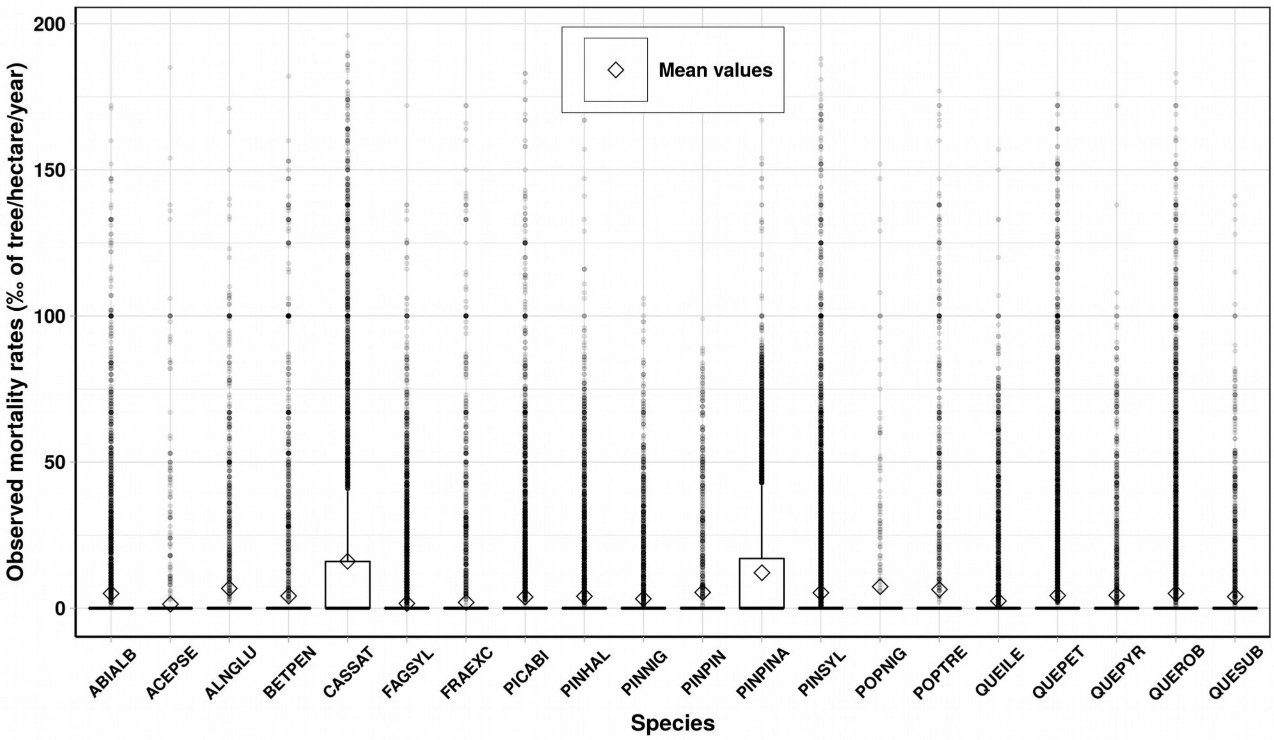


Figure S6: Predicted occurrence of mortality in all plots for each species as a probability (BIN models).

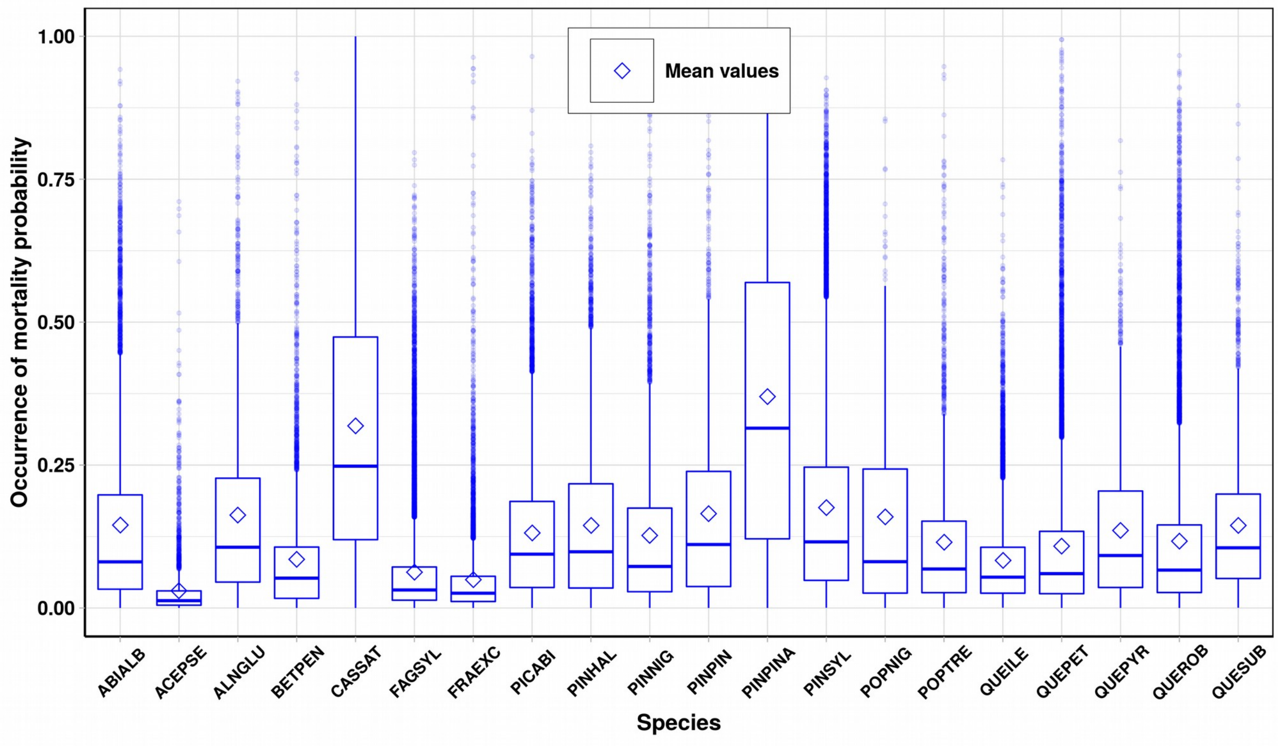
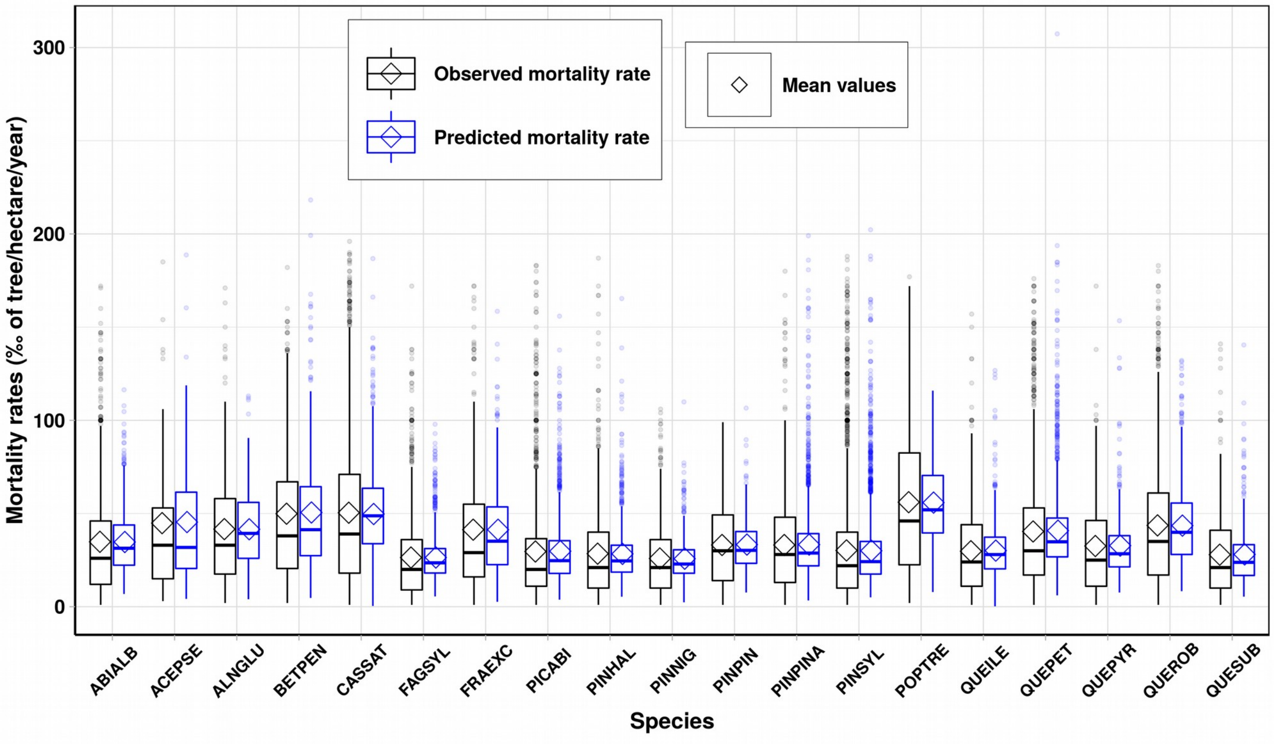
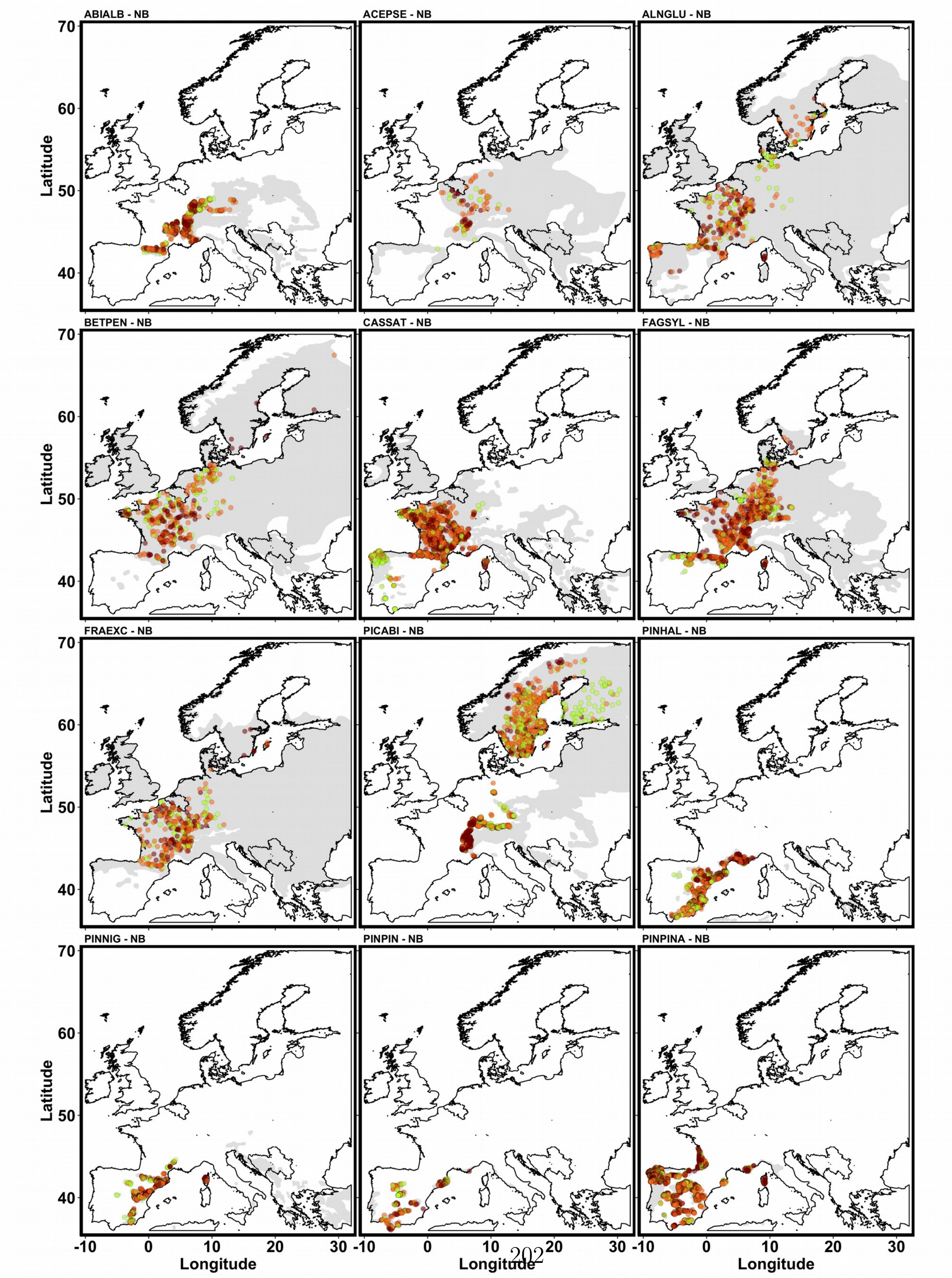


Figure S7: Observed and predicted mortality rates in plots where mortality occurs only. Black box indicate observed mortality rates and blue box indicate predicted mortality rates for each species as a percentage of dead trees by year and by hectare. (NB models).



Section 4: Mortality across climatic marginality areas

Figure S8: Predicted mortality intensity (NB) for each species. Green dots correspond to mortality predictions values lower than the first quartile (lowest values), orange dots represent values ranging from the first to the third quartile (medium values) and red dots represent values higher than the third quartile (highest values). Light grey areas display species distribution ranges.



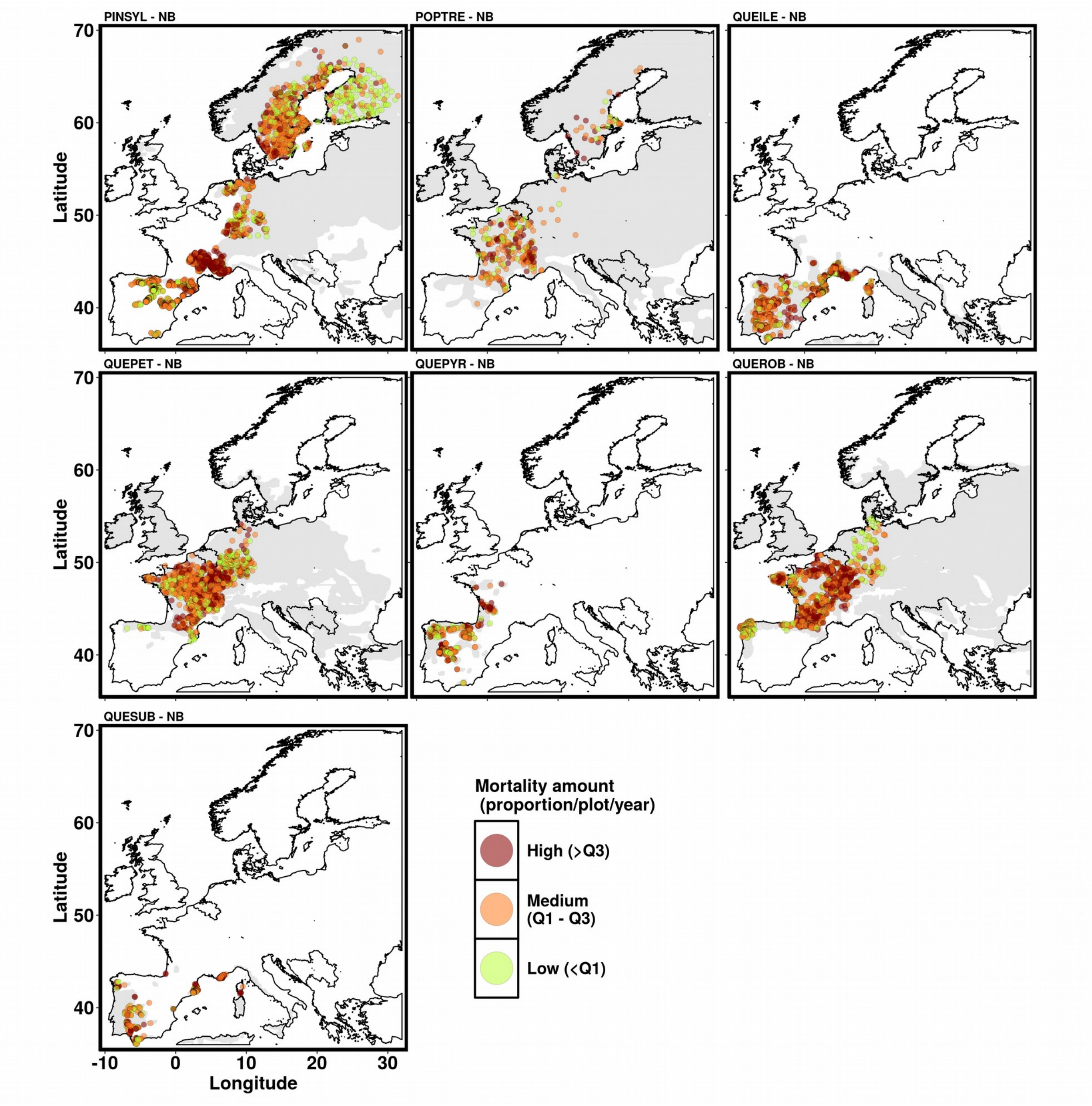
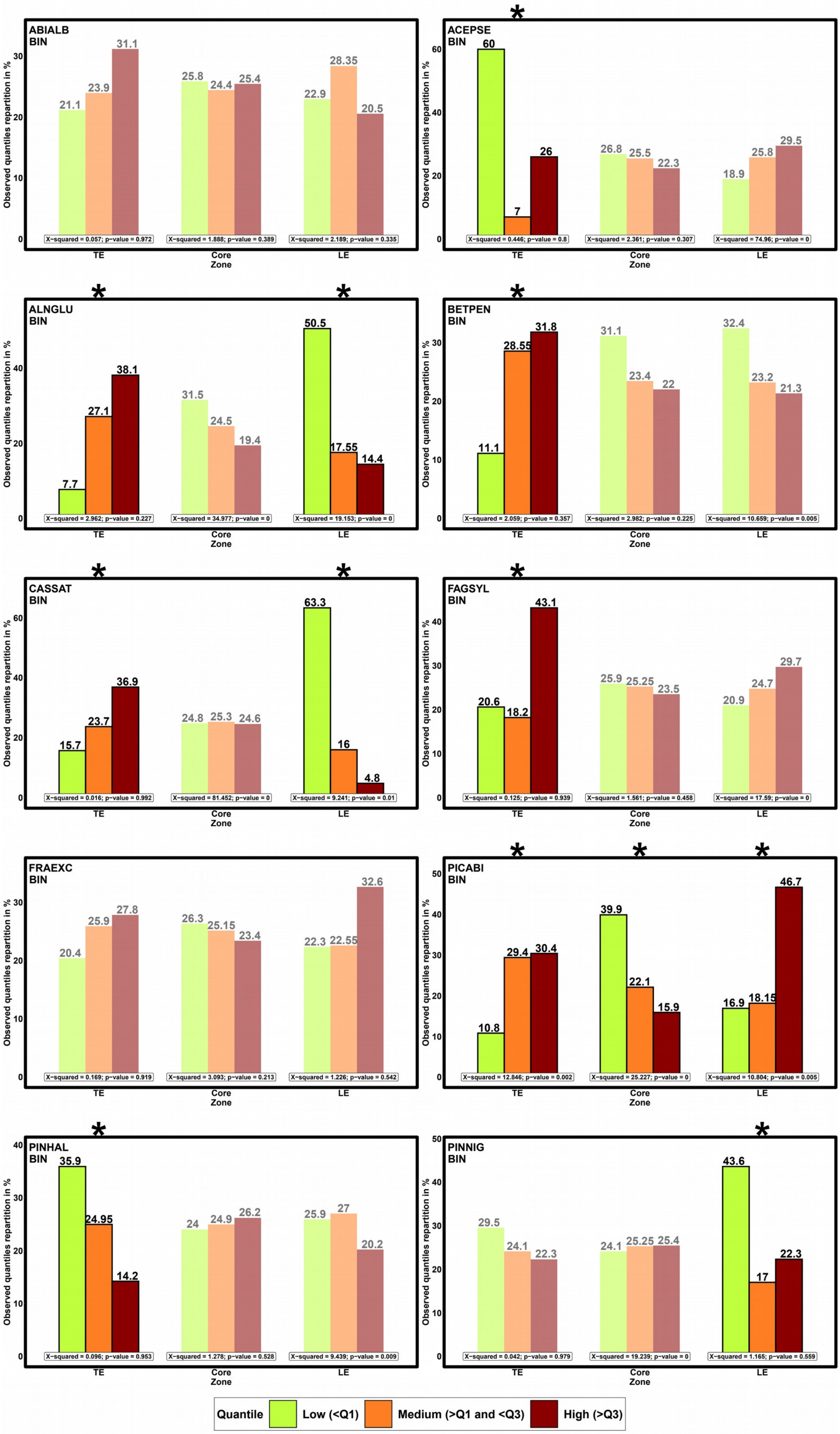


Fig S9a: Quantile repartition of the probability of mortality occurrence predictions (Fig 1) between lowest values (green bars), medium values (orange bars) and highest values (red bars) according to plots location (core, leading edge and trailing edge) and for each species. This distribution was used to test for heterogeneity of the distribution among groups with a χ-square test. Under the assumption of no spatial structure in mortality occurrence probability (null hypothesis), we expect the distribution to be evenly distributed as follow : For each area (core, leading edge, trailing edge) we expect the first quantile (lowest probability, blue bars) to represent 25% of the values, the second and third quartile (intermediate probability, green bars) to represent 50% of the values and the fourth quartile (largest probability, red bars) to represent 25% of the values. Note that for the sake of readability, we represented the green bars values divided by two. P-values < 0.05 indicate that predicted mortality are different than expected. Stars indicate significance and transparency indicate non-significance. χ-square statistics and p-values are written at the bottom of each bar groups.


ABIALB BIN
21.1 23.9 31.1 | 25.8 24.4 25.4 | 22.9 28.35 20.5
X−squared = 0.057; p−value = 0.972
X−squared = 1.888; p−value = 0.389
X−squared = 2.189; p−value = 0.335
ACEPSE BIN
60 7 26 | 26.8 25.5 22.3 | 18.9 25.8 29.5
X−squared = 0.446; p−value = 0.8
X−squared = 2.361; p−value = 0.307
X−squared = 74.96; p−value = 0
ALNGLU BIN
7.7 27.1 38.1 | 31.5 24.5 19.4 | 50.5 17.55 14.4
X−squared = 2.962; p−value = 0.227
X−squared = 34.977; p−value = 0
X−squared = 19.153; p−value = 0
BETPEN BIN
11.1 28.55 31.8 | 31.1 23.4 22 | 32.4 23.2 21.3
X−squared = 2.059; p−value = 0.357
X−squared = 2.982; p−value = 0.225
X−squared = 10.659; p−value = 0.005
CASSAT BIN
15.7 23.7 36.9 | 24.8 25.3 24.6 | 63.3 16 4.8
X−squared = 0.016; p−value = 0.992
X−squared = 81.452; p−value = 0
X−squared = 9.241; p−value = 0.01
FAGSYL BIN
20.6 18.2 43.1 | 25.9 25.25 23.5 | 20.9 24.7 29.7
X−squared = 0.125; p−value = 0.939
X−squared = 1.561; p−value = 0.458
X−squared = 17.59; p−value = 0
FRAEXC BIN
20.4 25.9 27.8 | 26.3 25.15 23.4 | 22.3 22.55 32.6
X−squared = 0.169; p−value = 0.919
X−squared = 3.093; p−value = 0.213
X−squared = 1.226; p−value = 0.542
PICABI BIN
10.8 29.4 30.4 | 39.9 22.1 15.9 | 16.9 18.15 46.7
X−squared = 12.846; p−value = 0.002
X−squared = 25.227; p−value = 0
X−squared = 10.804; p−value = 0.005
PINHAL BIN
35.9 24.95 14.2 | 24 24.9 26.2 | 25.9 27 20.2
X−squared = 0.096; p−value = 0.953
X−squared = 1.278; p−value = 0.528
X−squared = 9.439; p−value = 0.009
PINNIG BIN
29.5 24.1 22.3 | 24.1 25.25 25.4 | 43.6 17 22.3
X−squared = 0.042; p−value = 0.979
X−squared = 19.239; p−value = 0
X−squared = 1.165; p−value = 0.559
Observed quantiles repartition in %
TE
Core
LE
Zone
*
Quantile
Low (<Q1)
Medium (>Q1 and <Q3)
High (>Q3)

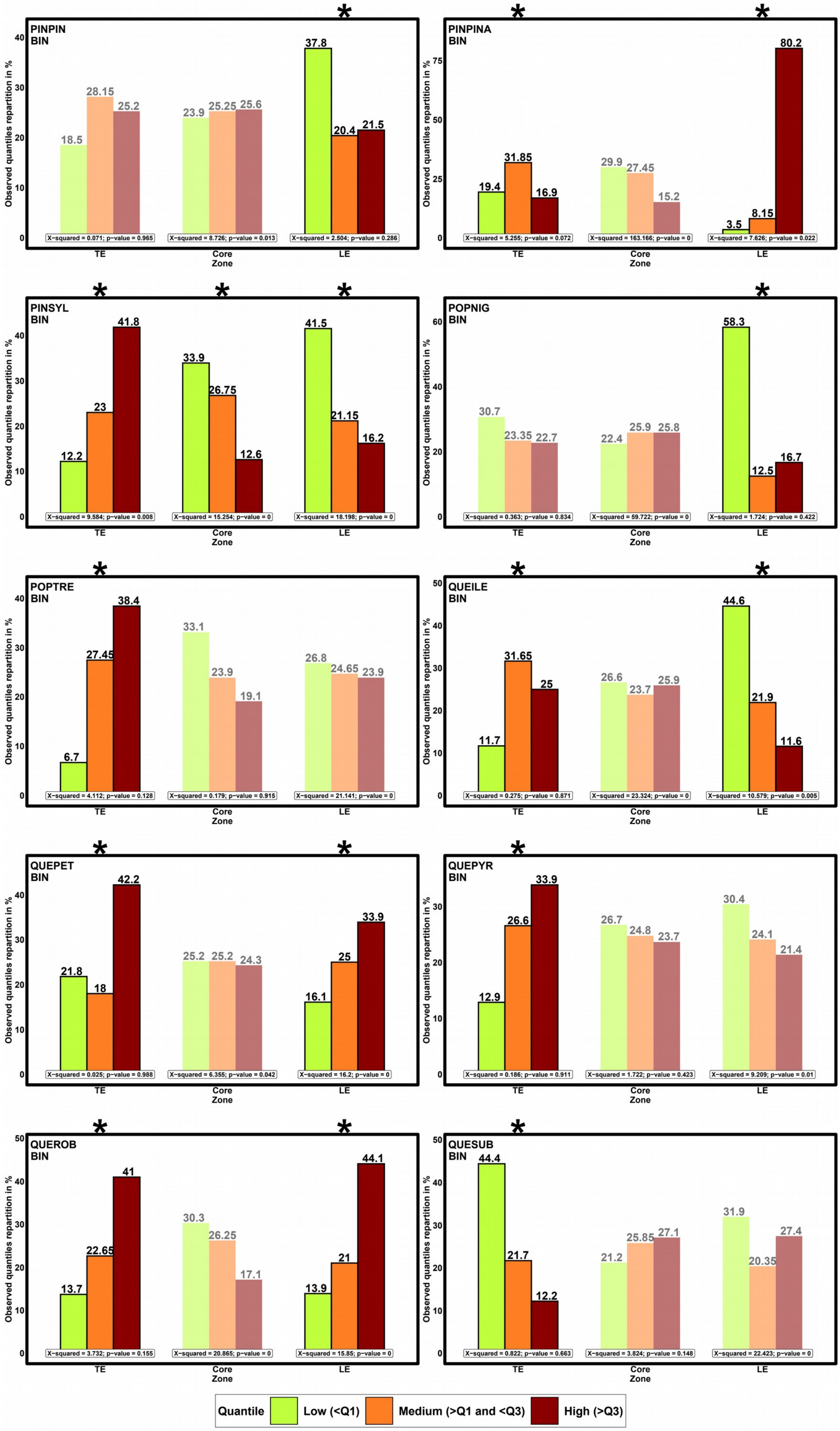
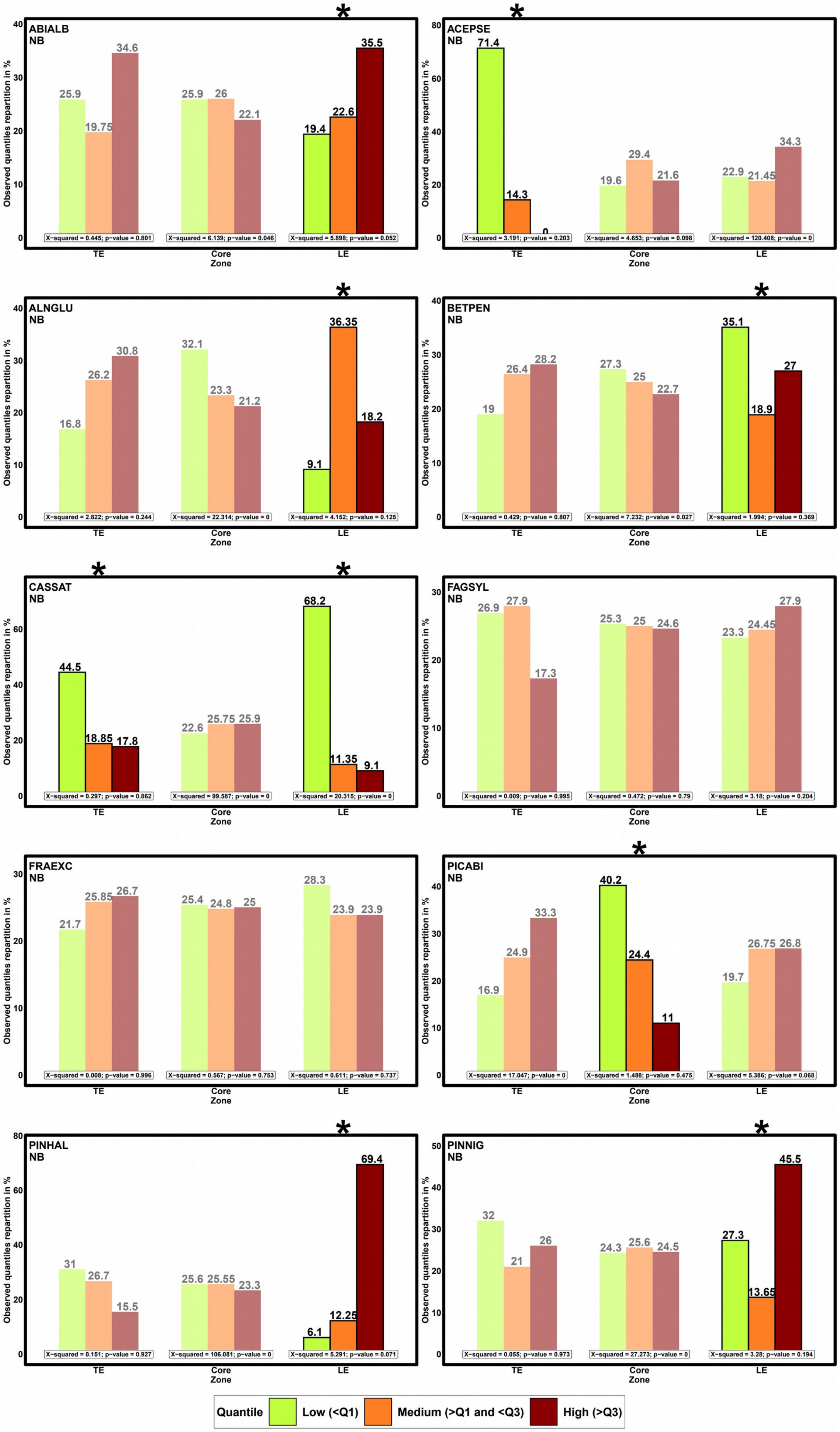
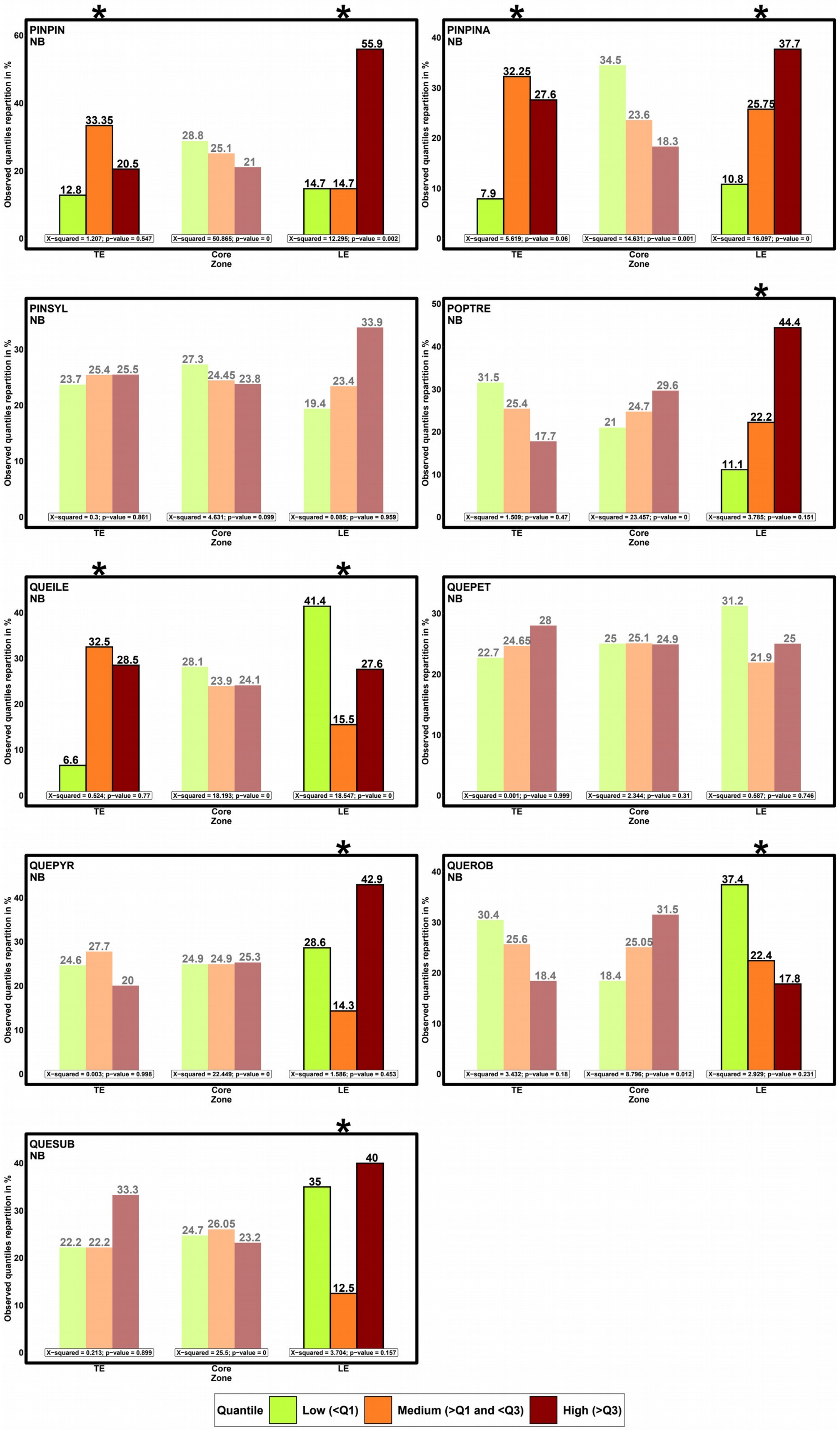

PINPIN
BIN
Observed quantiles repartition in %
18.5
28.15
25.2
23.9
25.25
25.6
37.8
20.4
21.5
X-squared = 0.071; p-value = 0.965
X-squared = 8.726; p-value = 0.013
X-squared = 2.504; p-value = 0.286
TE
Core
Zone
LE
*
PINPINA
BIN
19.4
31.85
16.9
29.9
27.45
15.2
3.5
8.15
80.2
X-squared = 5.255; p-value = 0.072
X-squared = 163.166; p-value = 0
X-squared = 7.626; p-value = 0.022
PINSYL
BIN
12.2
23
41.8
33.9
26.75
12.6
41.5
21.15
16.2
X-squared = 9.584; p-value = 0.008
X-squared = 15.254; p-value = 0
X-squared = 18.198; p-value = 0
POPNIG
BIN
30.7
23.35
22.7
22.4
25.9
25.8
58.3
12.5
16.7
X-squared = 0.363; p-value = 0.834
X-squared = 59.722; p-value = 0
X-squared = 1.724; p-value = 0.422
POPTRE
BIN
6.7
27.45
38.4
33.1
23.9
19.1
26.8
24.65
23.9
X-squared = 4.112; p-value = 0.128
X-squared = 0.179; p-value = 0.915
X-squared = 21.141; p-value = 0
QUEILE
BIN
11.7
31.65
25
26.6
23.7
25.9
44.6
21.9
11.6
X-squared = 0.275; p-value = 0.871
X-squared = 23.324; p-value = 0
X-squared = 10.579; p-value = 0.005
QUEPET
BIN
21.8
18
42.2
25.2
25.2
24.3
16.1
25
33.9
X-squared = 0.025; p-value = 0.988
X-squared = 6.355; p-value = 0.042
X-squared = 16.2; p-value = 0
QUEPYR
BIN
12.9
26.6
33.9
26.7
24.8
23.7
30.4
24.1
21.4
X-squared = 0.186; p-value = 0.911
X-squared = 1.722; p-value = 0.423
X-squared = 9.209; p-value = 0.01
QUEROB
BIN
13.7
22.65
41
30.3
26.25
17.1
13.9
21
44.1
X-squared = 3.732; p-value = 0.155
X-squared = 20.865; p-value = 0
X-squared = 15.85; p-value = 0
QUESUB
BIN
44.4
21.7
12.2
21.2
25.85
27.1
31.9
20.35
27.4
X-squared = 0.822; p-value = 0.663
X-squared = 3.824; p-value = 0.148
X-squared = 22.423; p-value = 0
Quantile
Low (<Q1)
Medium (>Q1 and <Q3)
High (>Q3)

Fig S9b: Quantile repartition of the annual intensity of mortality predictions (Fig S8) between lowest values (green bars), medium values (orange bars) and highest values (red bars) according to plots location (core, leading edge and trailing edge) and for each species. This distribution was used to test for heterogeneity of the distribution among groups with a χ-square test. Under the assumption of no spatial structure in mortality occurrence probability (null hypothesis), we expect the distribution to be evenly distributed as follow : For each area (core, leading edge, trailing edge) we expect the first quantile (lowest probability, blue bars) to represent 25% of the values, the second and third quartile (intermediate probability, green bars) to represent 50% of the values and the fourth quartile (largest probability, red bars) to represent 25% of the values. Note that for the sake of readability, we represented the green bars values divided by two. P-values < 0.05 indicate that predicted mortality are different than expected. Stars indicate significance and transparency indicate non-significant values. χ-square statistics and p-values are written at the bottom of each bar groups.


*
ABIALB
NB
Observed quantiles repartition in %
0
10
20
30
40
25.9
19.75
34.6
25.9
26
22.1
19.4
22.6
35.5
X−squared = 0.445; p−value = 0.801
X−squared = 6.139; p−value = 0.046
X−squared = 5.898; p−value = 0.052
TE
Core
Zone
LE
*
ACEPSE
NB
Observed quantiles repartition in %
0
20
40
60
80
71.4
14.3
0
19.6
29.4
21.6
22.9
21.45
34.3
X−squared = 3.191; p−value = 0.203
X−squared = 4.653; p−value = 0.098
X−squared = 120.408; p−value = 0
TE
Core
Zone
LE
*
ALNGLU
NB
Observed quantiles repartition in %
0
10
20
30
40
16.8
26.2
30.8
32.1
23.3
21.2
9.1
36.35
18.2
X−squared = 2.822; p−value = 0.244
X−squared = 22.314; p−value = 0
X−squared = 4.152; p−value = 0.125
TE
Core
Zone
LE
*
BETPEN
NB
Observed quantiles repartition in %
0
10
20
30
40
19
26.4
28.2
27.3
25
22.7
35.1
18.9
27
X−squared = 0.429; p−value = 0.807
X−squared = 7.232; p−value = 0.027
X−squared = 1.994; p−value = 0.369
TE
Core
Zone
LE
*
*
CASSAT
NB
Observed quantiles repartition in %
0
20
40
60
44.5
18.85
17.8
22.6
25.75
25.9
68.2
11.35
9.1
X−squared = 0.297; p−value = 0.862
X−squared = 99.587; p−value = 0
X−squared = 20.315; p−value = 0
TE
Core
Zone
LE
FAGSYL
NB
Observed quantiles repartition in %
0
10
20
30
26.9
27.9
17.3
25.3
25
24.6
23.3
24.45
27.9
X−squared = 0.009; p−value = 0.995
X−squared = 0.472; p−value = 0.79
X−squared = 3.18; p−value = 0.204
TE
Core
Zone
LE
FRAEXC
NB
Observed quantiles repartition in %
0
10
20
30
21.7
25.85
26.7
25.4
24.8
25
28.3
23.9
23.9
X−squared = 0.008; p−value = 0.996
X−squared = 0.567; p−value = 0.753
X−squared = 0.611; p−value = 0.737
TE
Core
Zone
LE
*
PICABI
NB
Observed quantiles repartition in %
0
10
20
30
40
16.9
24.9
33.3
40.2
24.4
11
19.7
26.75
26.8
X−squared = 17.047; p−value = 0
X−squared = 1.488; p−value = 0.475
X−squared = 5.386; p−value = 0.068
TE
Core
Zone
LE
*
PINHAL
NB
Observed quantiles repartition in %
0
20
40
60
80
31
26.7
15.5
25.6
25.55
23.3
6.1
12.25
69.4
X−squared = 0.151; p−value = 0.927
X−squared = 106.081; p−value = 0
X−squared = 5.291; p−value = 0.071
TE
Core
Zone
LE
*
PINNIG
NB
Observed quantiles repartition in %
0
10
20
30
40
50
32
21
26
24.3
25.6
24.5
27.3
13.65
45.5
X−squared = 0.055; p−value = 0.973
X−squared = 27.273; p−value = 0
X−squared = 3.28; p−value = 0.194
TE
Core
Zone
LE
Quantile
Low (<Q1)
Medium (>Q1 and <Q3)
High (>Q3)



PINPIN NB
*
*
Observed quantiles repartition in %
12.8
33.35
20.5
28.8
25.1
21
14.7
14.7
55.9
X-squared = 1.207; p-value = 0.547
X-squared = 50.865; p-value = 0
X-squared = 12.295; p-value = 0.002
TE
Core
LE
Zone
PINPINA NB
*
*
7.9
32.25
27.6
34.5
23.6
18.3
10.8
25.75
37.7
X-squared = 5.619; p-value = 0.06
X-squared = 14.631; p-value = 0.001
X-squared = 16.097; p-value = 0
PINSYL NB
23.7
25.4
25.5
27.3
24.45
23.8
19.4
23.4
33.9
X-squared = 0.3; p-value = 0.861
X-squared = 4.631; p-value = 0.099
X-squared = 0.085; p-value = 0.959
POPTRE NB
*
31.5
25.4
17.7
21
24.7
29.6
11.1
22.2
44.4
X-squared = 1.509; p-value = 0.47
X-squared = 23.457; p-value = 0
X-squared = 3.785; p-value = 0.151
QUEILE NB
*
*
6.6
32.5
28.5
28.1
23.9
24.1
41.4
15.5
27.6
X-squared = 0.524; p-value = 0.77
X-squared = 18.193; p-value = 0
X-squared = 18.547; p-value = 0
QUEPET NB
22.7
24.65
28
25
25.1
24.9
31.2
21.9
25
X-squared = 0.001; p-value = 0.999
X-squared = 2.344; p-value = 0.31
X-squared = 0.587; p-value = 0.746
QUEPYR NB
*
24.6
27.7
20
24.9
24.9
25.3
28.6
14.3
42.9
X-squared = 0.003; p-value = 0.998
X-squared = 22.449; p-value = 0
X-squared = 1.586; p-value = 0.453
QUEROB NB
*
30.4
25.6
18.4
18.4
25.05
31.5
37.4
22.4
17.8
X-squared = 3.432; p-value = 0.18
X-squared = 8.796; p-value = 0.012
X-squared = 2.929; p-value = 0.231
QUESUB NB
*
22.2
22.2
33.3
24.7
26.05
23.2
35
12.5
40
X-squared = 0.213; p-value = 0.899
X-squared = 25.5; p-value = 0
X-squared = 3.704; p-value = 0.157
Quantile
Low (<Q1)
Medium (>Q1 and <Q3)
High (>Q3)

Section 5: Simple effects

Figure S10: Effect of plot meanDBH on a) the occurrence of mortality (expressed as probability, Y-axis) and b) on the intensity of mortality by year and by plot (‰). Only species with significant effects are shown. Transparency areas indicate confidence intervals.

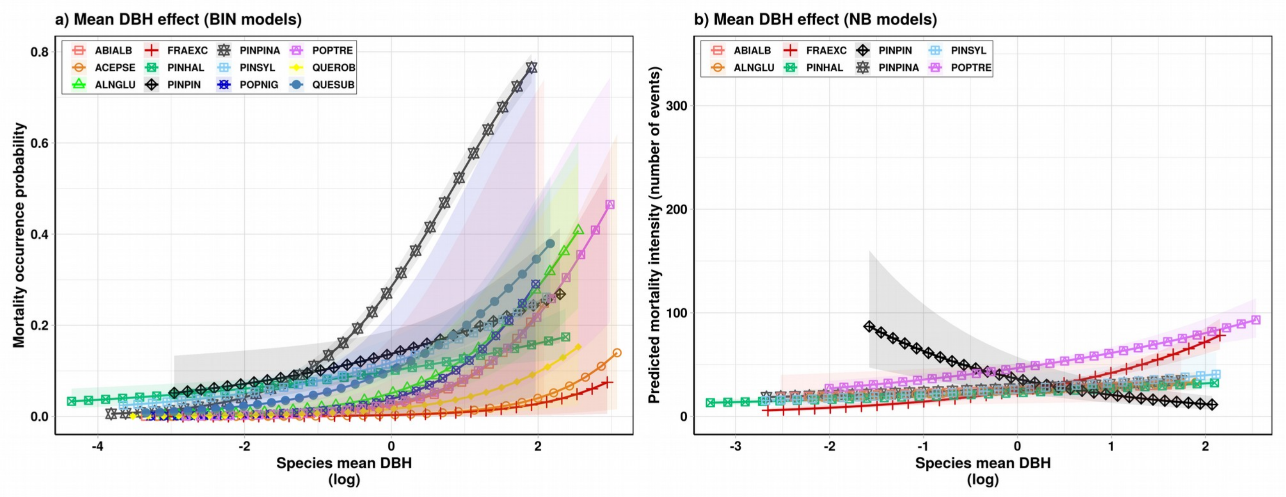


Figure S11: Effect of plot density on a) the occurrence of mortality (expressed as probability, Y-axis) and b) on the intensity of mortality by year and by plot (‰). Only species with signifciant effects are shown. Transparency areas indicate confidence intervals.

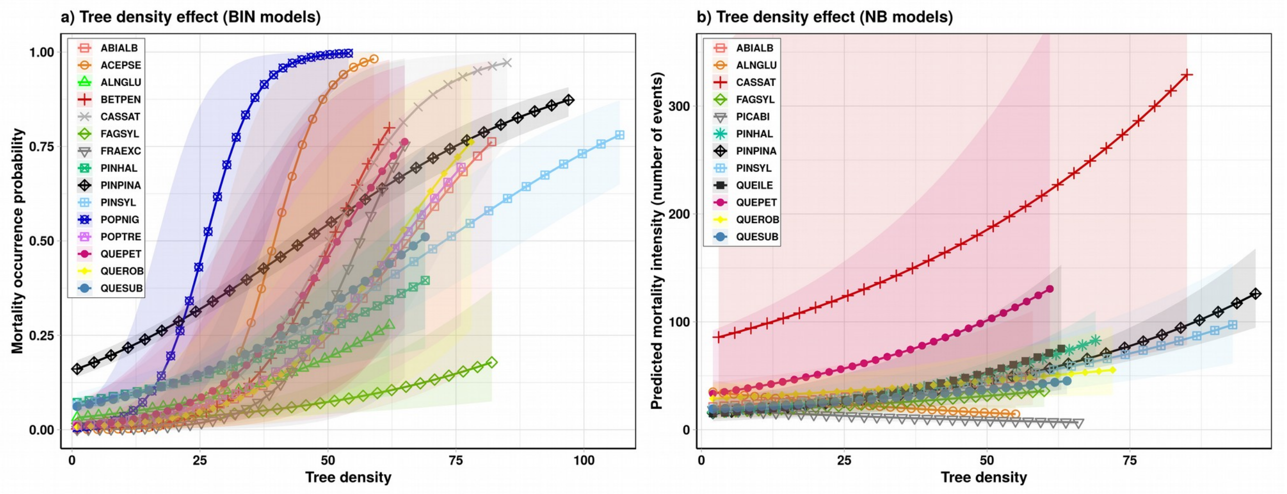


Figure S12: Effect of Census interval on a) the occurrence of mortality (expressed as probability, Y-axis) and b) on the intensity of mortality by year and by plot (‰). Only species with signifciant effects are shown. Transparency areas indicates confidence intervals.

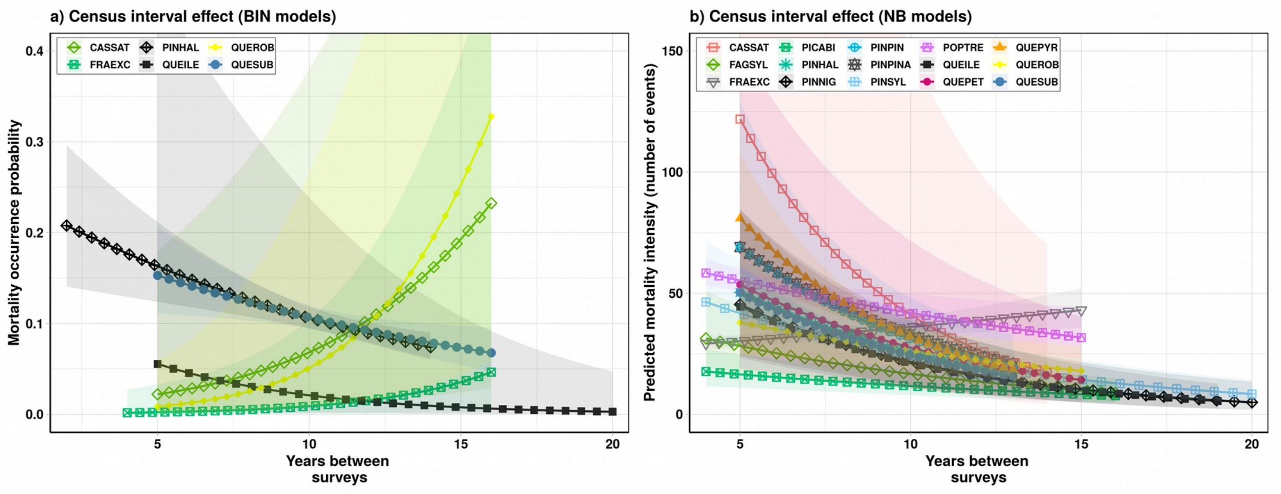
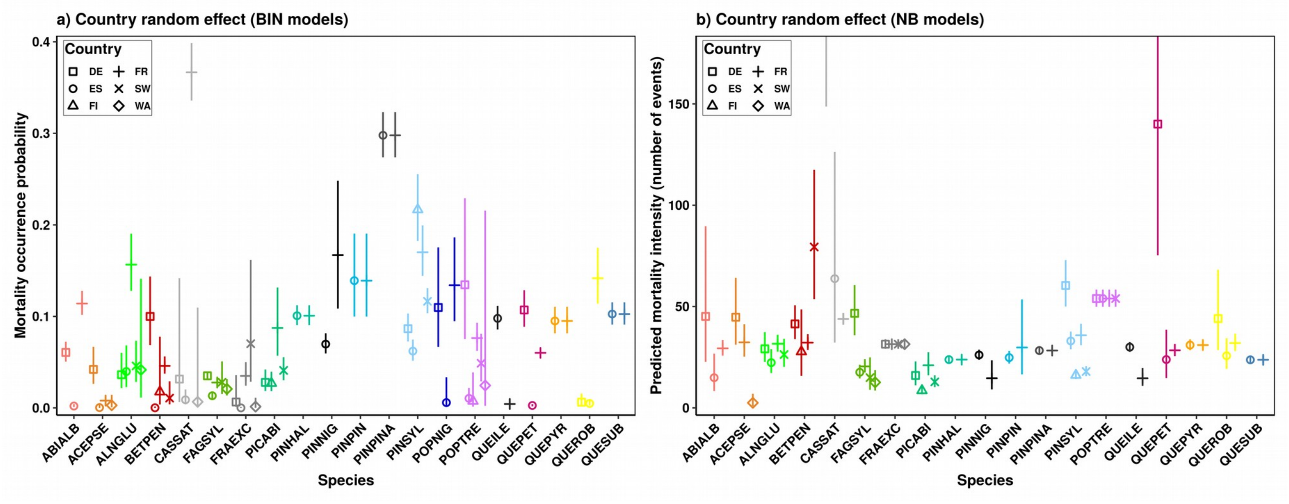


Figure S13: Effect of plot country random effect on a) the predicted occurrence of mortality (expressed as probability, Y-axis) and b) on the predicted intensity of mortality by year and by plot (‰). Every species are represented with a different color. Linerange represents standard errors.



Section 6: Interactions with climatic marginality

Figure S14: Model interactions between climatic variables and occurrence of mortality (expressed as probability, Y-axis) across the core, trailing and leading climatic margins defined for a) *Fagus sylvatica*, b) *Pinus pinaster* and c), *Quercus suber*. Black, red and blue lines represent populations at the core, trailing and leading edge of the distribution range, respectively. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colors and extrapolations outside the environmental gradients covered by the species are shown in light colors.

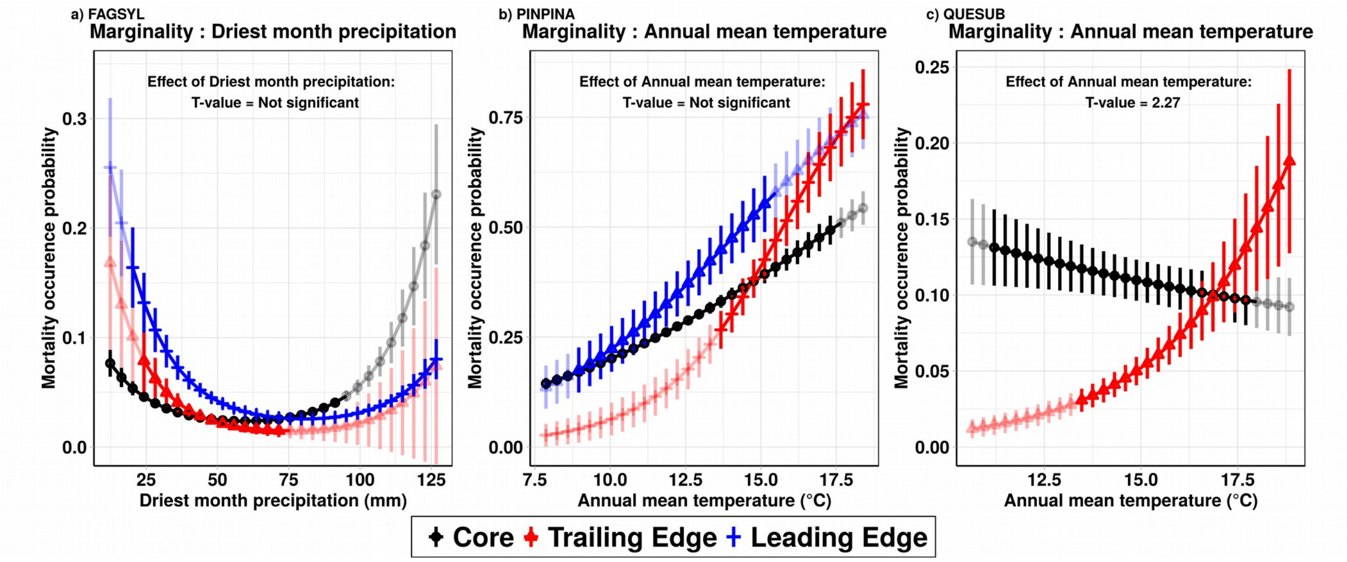


Figure S15: Statistical interactions between several climatic and competition variables and the intensity of predicted mortality by year and by plot (‰) across the core, trailing and leading edge of a) *Betula* pendula, b) *Fagus sylvatica* and c) *Picea abies*. Black, red and blue lines represent populations at the core, trailing and leading edge the distribution range, respectively. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colors and extrapolations outside the environmental gradients covered by the species are shown in light colors.

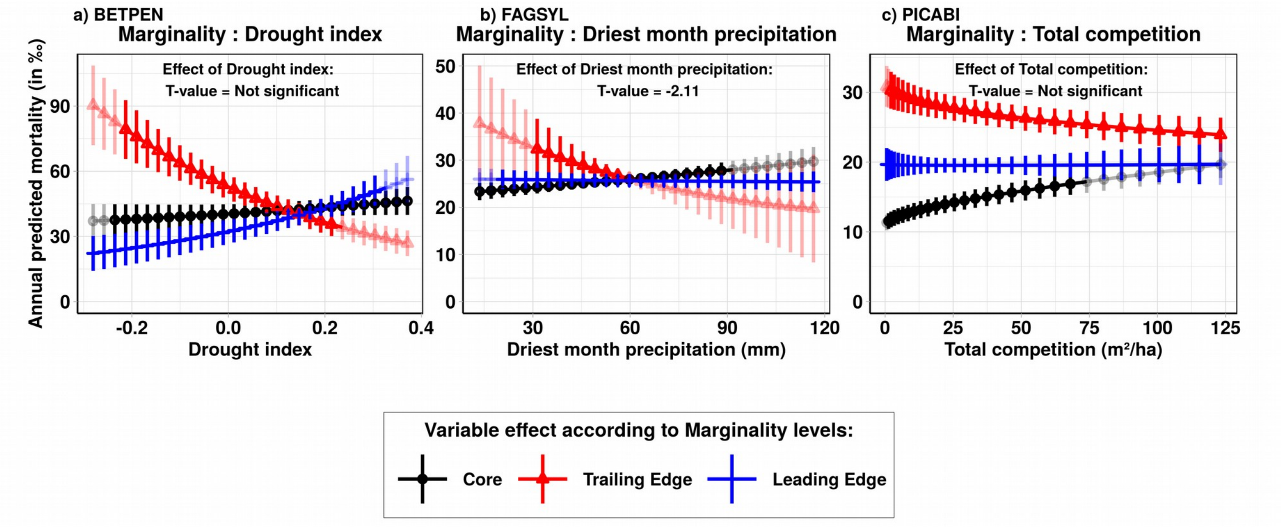


Figure S16: Other significant interactions between several climatic variables (X-axis) and mortality occurrence of mortality (expressed as probability, Y-axis) across the core, trailing and leading edge for all species. Black, red and blue lines represent populations at the core, trailing and leading edge the distribution range, respectively. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colors and extrapolations outside the environmental gradients covered by the species are shown in light colors.

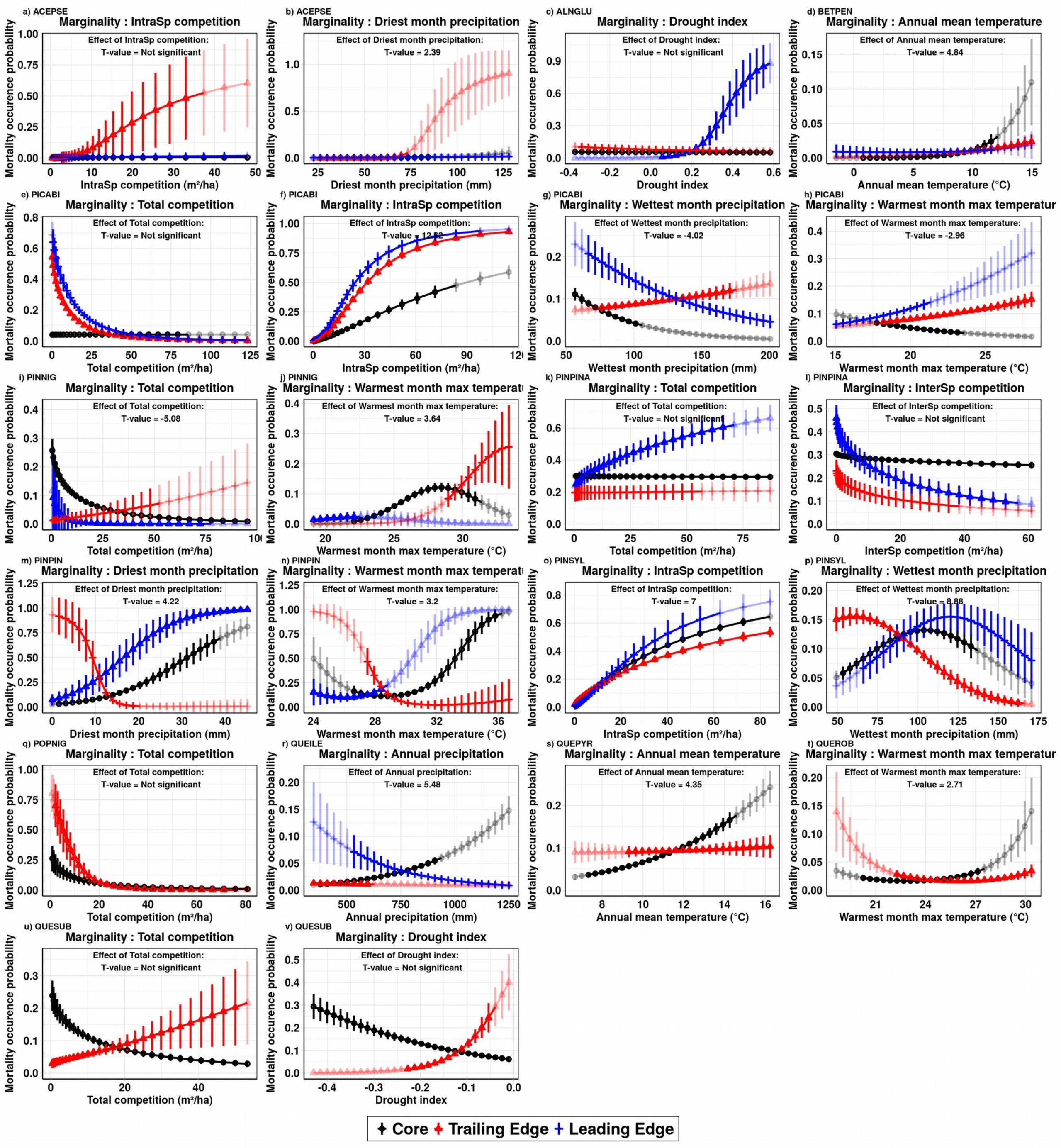
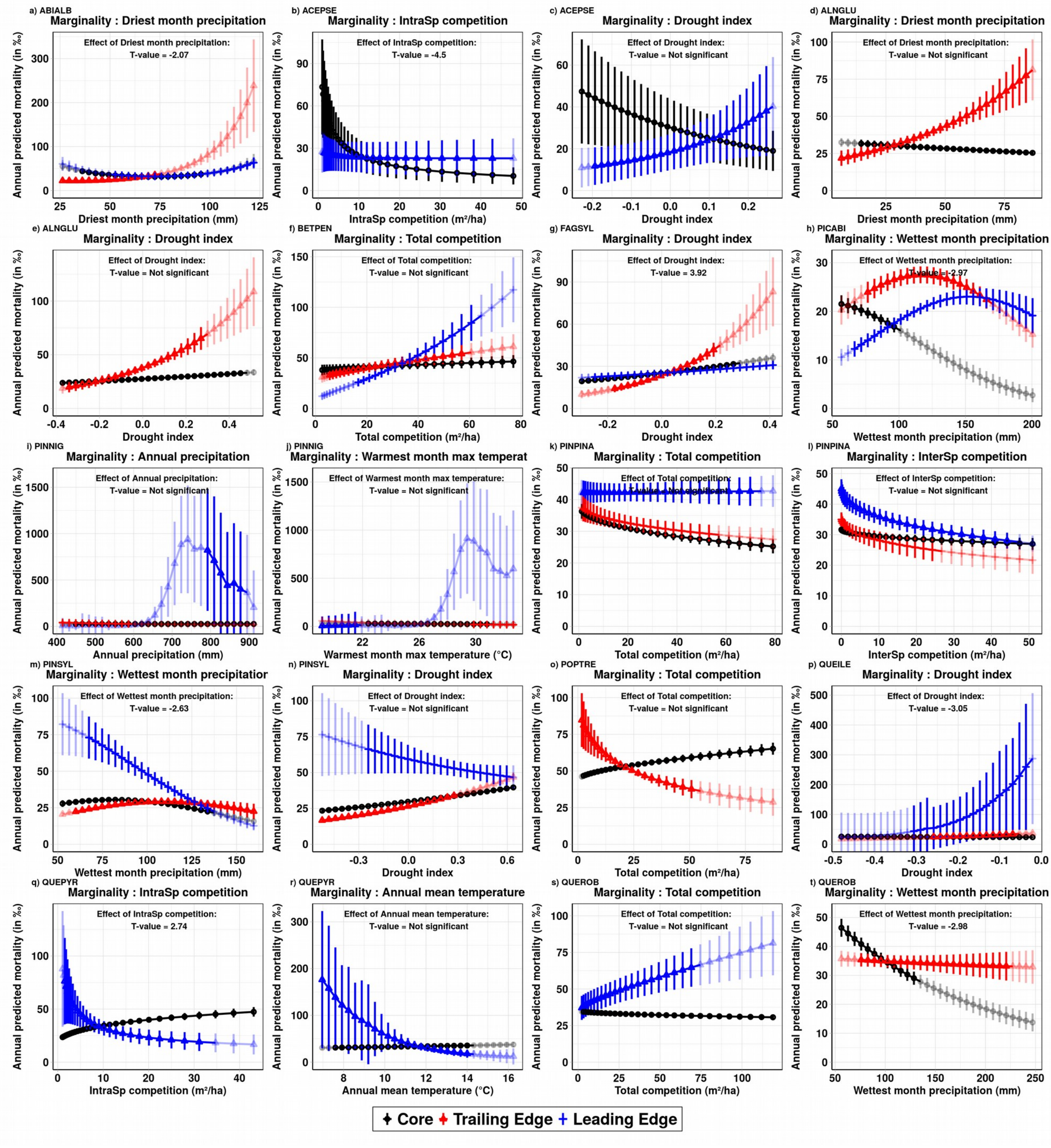


Figure S17: Other significant interactions between several climatic variables (X-axis) and the intensity of predicted mortality (expressed as proportion (‰), by year and by plot, Y-axis) across the core, trailing and leading edge for all species. Black, red and blue lines represent populations at the core, trailing and leading edge the distribution range, respectively. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colors and extrapolations outside the environmental gradients covered by the species are shown in light colors.



Annexes 4: Supplementary tables of chapter 3

Supplementary Information : Tables

Section 1: Plot and species description

National Forest Inventories harmonization

The sample plot design was different among countries. For instance, the Spanish National Inventory recorded single sample plots in a 1 km by 1 km grid whereas the Finnish National Inventory followed a cluster design, with number and grid size depending on location while the German NFI used a 4 x 4 km quadrangle grid where the samples lied on the intersection points. Most NFIs followed a nested circular subplot design whose radius differs among NFI and within which trees of different size classes were monitored. The main differences among inventories are summarized in Table S1.

Table S1: Summary of information of the NFI design for each country: Belgium (Wallonia), Finland, France, Germany, Spain and Sweden Inventories. We included the sampling dates; plot type: permanent plots (PP) the years indicate the two campaigns used in the analysis, for temporary plots (TP) the years used in the analysis are indicated. Grid size: indicates the grid dimension in km for each country. Distance between plots: indicates the distance between the plots within the grid. Plot radius: indicates the different radius (m) used within plots to sample trees. Sample tree DBH threshold: indicates the minimum DBH of the trees selected to sample a tree within a plot. N plot: number of plots per country. N trees: number of trees per country

Country	**Belgium-Wallonia**	**Finland**	**France**	**Germany**	**Spain**	**Sweden**
Sampling dates and plot type	1994-2003 2008-2011 PP	1985-1986 1995 PP	2005-2014 TP	1986- 1990, West Germany only 2001-2002 (West and East Germany)	1986-1996 1997-2007 PP	2005-2007 2008-2010 TP and PP
Grid size (km)	1x0.5	16x16 or 24x32 depending on the location.	1x1	4x4, 2.83x2.83 or 2x2 depending on region	1x1	Vary
Sampling design (Distance between plots)	Single sample plots	Cluster design (100 or 300)	Single sample plots	Cluster design (150)	Single sample plots	Cluster design (vary)
Radius (m)	2.25, 4.5, 9, 12, 18	5.64, 9.77	6, 9, 15	1, 2, 5, 10, 25	5, 10, 15, 25	3.5, 10

Sample tree DBH threshold (cm)	6.4	0	7.5	10 (1st) 7 (2nd)	7.5	1
N Plots	1238	2487	60782	29914	48133	11338
N Trees	16011	39263	637830	295029	813464	187561
NdeadTrees (and %)	216 (1.35%)	490 (1.25%)	63178 (9.91%)	5725 (1.94%)	68896 (8.47%)	3136 (1.67%)

Table S2: List of species used for modeling tree mortality, number of plots in each species ranges defined (i.e. core, transition or marginal ranges, the latest divided in leading and trailing edges) and thresholds used to define the margins. Species: species name. Code: code used for each species. E= Ecology of the species (T=temperate; M=Mediterranean/Warm Temperate). *Castanea sativa* and *Pinus nigra* were included as Mediterranean species although they can also be considered as warm temperate species (San-Miguel-Ayanz, de Rigo, Caudullo, Houston Durrant, & Mauri, 2016).

NTrees: number of trees. NdeadTrees: number of dead trees. NPlots: number of plots. MT: margin thresholds used for the WPCA. CT: core thresholds used for the WPCA. NC: number of plots containing the species within the core of the species range. NTE: Number of plots containing the species within the trailing edge of the species range. NLE: number of plots containing the species within the leading edges of the species range. NT: Number of plots containing the species within the transition zone of the species range. NA: Number of plots containing the species but located outside of its known range. Min: Minimum census interval observed on all the plots in years. Mean: Average census interval observed on all the plots in years. Max: Maximum census interval observed on all the plots in years.

Species	**E**	**Code**	**NTrees**	**NdeadTrees (and %)**	**NPlots**	**MT**	**CT**	**NC**	**NTE**	**NLE**	**NT**	**NA**	**Min**	**Mean**	**Max**
Abies alba Mill.	T	ABI ALB	50731	2517 (4.96%)	8485	0.7	0.6	5635	511	1088	530	721	7	13.4	16
Acer pseudoplatanus L.	T	ACE PSE	10500	248 (2.36%)	4442	0.55	0.5	2387	124	1284	220	427	5	13.5	16
Alnus glutinosa (L). Gaertn.	T	ALB GLU	14008	1067 (7.62%)	2879	0.6	0.5	1658	780	109	316	16	4	9.8	16
Betula pendula Roth.	T	BET PEN	24222	1851(7.64%)	8936	0.8	0.6	3843	1606	499	2517	471	4	11.6	16
Castanea sativa Mill.	M	CAS SAT	56235	12418 (22.08%)	8683	0.7	0.6	6922	600	178	926	57	7	11	16
Fagus sylvatica L.	T	FAG SYL	135856	3535 (2.60%)	26237	0.7	0.6	20167	544	3872	1607	47	4	12.4	16
Fraxinus excelsior L.	T	FRA EXC	29899	888 (2.97%)	9570	0.7	0.6	6537	1155	854	999	25	4	12.8	16

Larix decidua Mill.	T	LAR DEC	10115	388 (3.84%)	2768	0.6	0.5	315	1	159	73	2220	9	13.7	16
Picea abies (L.) H.Karst.	T	PIC ABI	259151	7117 (2.74%)	30639	0.8	0.6	6643	6264	1190	1495	15047	4	10.4	16
Pinus halepensis Mill.	M	PIN HAL	87461	4929 (5.64%)	9160	0.7	0.6	7110	606	411	867	166	2	11.3	19
Pinus nigra J.F.Arnold.	M	PIN NIG	88427	4788 (5.41%)	8360	0.7	0.6	4462	477	96	542	2783	4	11.2	20
Pinus pinea L.	M	PIN PIN	27534	2438 (8.85%)	3077	0.7	0.6	1516	246	282	667	366	6	10.9	14
Pinus pinaster Aiton.	M	PIN PINA	177972	28834 (16.20)	12610	0.8	0.6	5998	746	1357	2149	2360	7	11.3	16
Pinus sylvestris L.	T	PIN SYL	313266	16929 (5.40%)	32223	0.8	0.6	11485	8480	582	7934	3742	4	9.7	20
Populus nigra L.	T	POP NIG	4256	989 (23.24%)	878	0.7	0.6	497	90	24	58	209	7	12.1	15
Populus tremula L.	T	POP TRE	11739	1276 (10.87%)	3903	0.7	0.6	2122	872	84	816	9	4	7.7	16
Quercus ilex L.	M	QUEILE	84183	3543 (4.20 %)	15267	0.8	0.6	9055	1839	646	3701	26	6	11.2	20
Quercus petraea Liebl.	T	QUE PET	77022	4071 (5.29%)	17084	0.7	0.6	15700	486	250	617	31	9	12.8	20
Quercus pubescens Willd.	T	QUE PUB	43767	2897 (6.62%)	8406	0.7	0.5	7861	11	217	312	5	10	11.3	19
Quercus	M	QUE	33157	1734 (5.23%)	3835	0.7	0.6	2571	438	141	594	91	6	10.9	16

pyrenaica Willd.		PYR													
Quercus robur L.	T	QUE ROB	85192	5483 (6,44%)	21092	0.8	0.6	9750	3619	934	6778	11	9	12	16
Quercus suber L.	M	QUE SUB	25157	1143 (4.54%)	3416	0.7	0.6	2396	461	172	351	36	6	11.4	16

Section 2: Climatic data

Table S3: 25 climatic variables including the 21 climatic variables averaged over the last 30 years before the first inventory, 2 drought-related variables derived from SPEI indices calculated for the *i*th individual plot and the 2 climatic marginality categories obtained after the WPCA and DPCA (categories are calculated for the i^{th} individual plot).We include the variable description/name, Acronym (same as those used in Eumedclim) and units/time period. The 8 variables used for the characterization of long term climate are in bold.

Description	**Acronym**	**Unit/Time period**
Annual mean temperature	**bio1**	°C
Mean diurnal temperature range		°C
Maximal temperature of the warmest month	**bio5**	°C
Minimal temperature of the coldest month		°C
Winter mean temperature	**tmean.djf**	°C
Spring mean temperature		°C
Summer mean temperature		°C
Autumn mean temperature		°C
Annual precipitation	**bio12**	mm
Precipitation of the wettest month	**bio 13**	mm
Precipitation of the driest month	**bio14**	mm
Winter precipitation		mm
Spring precipitation		mm
Summer precipitation		mm
Autumn precipitation		mm
Annual potential evapotranspiration		mm
Minimal monthly potential evapotranspiration		mm
Maximal monthly potential evapotranspiration		mm
Annual water balance	**Ppet.mean**	mm
Minimal monthly water balance		mm
Maximal monthly water balance		mm
Monthly Standardised Precipitation-Evapotranspiration Index of the last 12 months	meanSPEI	Averaged on the time period elapsed between the two-sampling procedure
Monthly Standardised Precipitation-Evapotranspiration Index of the last 12 months	minSPEI	Minimum value on the time period elapsed between the two sampling procedure
Climatic trailing edge	TE	No unit
Climatic leading edge	LE	No unit

Table S4: Cumulative variance explained by the first two axes of the weighted principal component analysis (WPCA) for each species. Species: Code of the species. Variance explained: Variance explained by the two first axes of the WPCA. Max Variable: climatic variable with the highest contribution to the PCA. Max%: percentage of the variance of the PCA explained by the Max Variable.

Species	**Variance explained**	**Max Variable**	**Max %**
ABIALB	81.14	Annual water balance	5.54
ACEPSE	76.789	Annual water balance	5.79
ALNGLU	82.778	Annual precipitation	5.44
BETPEN	82.326	Annual precipitation	5.64
CASSAT	74.746	Annual water balance	5.9
FAGSYL	71.532	Annual water balance	6.16
FRAEXC	80.127	Annual precipitation	5.65
PICABI	82.541	Maximal temperature of the warmest month	5.46
PINHAL	78.394	Annual water balance	5.65
PINNIG	79.938	Annual water balance	5.63
PINPIN	79.315	Maximal temperature of the warmest month	5.49
PINPINA	81.222	Maximal temperature of the warmest month	5.68
PINSYL	83.609	Annual precipitation	5.33
POPNIG	77.409	Annual water balance	6.03
POPTRE	83.335	Annual water balance	5.44
QUEILE	78.287	Annual water balance	5.69
QUEPET	75.681	Annual water balance	5.75
QUEPUB	76.442	Annual water balance	5.91
QUEPYR	79.25	Maximal temperature of the warmest month	5.78
QUEROB	80.754	Annual precipitation	5.58
QUESUB	76.377	Annual water balance	5.84

Section 3: VIF

As it is not possible to calculate a Variation Inflation Factor value for models including qualitative variables, we calculated the VIF for each quantitative variable included in the best predictive model for each species. In addition, to quantify the collinearity between climatic variables and the climatic marginality, we calculated the VIF for the marginality index, which is the climatic marginality score we obtained after weighting the PCA scores. In the next following tables, all the scores for each variable is reported.

Table S5a: VIF values calculated on the variables included in the best predictive BIN model for each species. For each species, there is one column with the variable names that are included in the model and one column with the VIF scores calculated. Marginality index VIF's values are in bold.

Variable	**Marginality**	**T° variable**	**Precipitation variable**	**min_spei12**	**mean_spei12**	**BA.O**	**BA**	**Baj**	**BAIj**	**BAIj.mean**	**DBH**	**yearsbetweensurveys**	**treeNbr**
Species													
ABIALB	1.18	1.32	1.52	2.07	2.16	4.2	3.93	-	9.42	9.47	2.79	-	2.72
ACEPSE	3.34	2.19	2.74	1.59	1.56	-	3.02	4.27	-	2.23	3.73	-	2.91
ALNGLU	2.43	2.65	1.39	1.7	1.93	4.61	4.58	-	7.1	6.88	2.56	-	2.43
BETPEN	1.58	1.84	-	1.58	1.45	-	2.47	6.53	7.18	7.85	5.01	-	2.39
CASSAT	2.41	1.94	1.95	2.12	1.83	4.45	4.47	-	6.36	6.24	2.78	2.13	2.71
FAGSYL	2.11	1.47	2.02	1.67	1.43	-	1.85	2.31	6.57	6.91	-	-	2.44
FRAEXC	1.17	1.3	-	2.34	2.42	2.33	-	8.5	9.02	8.13	6.65	1.91	3.01
PICABI	4.37	1.29	4.36	2.85	2.53	-	3.76	10.9	6.83	5.5	4.55	-	-
PINHAL	1.13	5.2	7.44	1.98	1.67	-	6.84	7.09	-	1.89	3.43	3.63	5.61
PINNIG	1.42	2.16	2.47	2.28	2.25	-	2.68	2.95	-	1.62	-	-	-
PINPIN	1.46	3.96	5.47	2.85	1.93	-	3.35	6.18	-	2.24	4.46	-	-
PINPINA	1.4	1.32	2.08	1.85	2.45	2.47	4.51	-	-	2.36	2.9	-	3.87
PINSYL	2.6	2.27	1.15	2.69	2.27	-	3.68	8.7	-	1.82	4.71	-	2.09
POPNIG	1.57	1.68	1.28	1.2	-	-	3.03	7.39	-	1.96	5.3	-	2.15
POPTRE	1.94	2.13	1.55	2.15	2.16	-	1.83	-	5.72	6.83	1.96	-	2.56
QUEILE	1.25	1.25	1.67	1.79	1.81	1.84	-	2.93	2.22	-	2.8	1.65	-
QUEPYR	1.54	1.33	2.85	2.37	2.81	-	2.41	2.07	-	1.8	-	-	-
QUEPET	-	1.39	1.26	1.43	1.43	-	2.24	7.96	9.91	8.16	4.89	-	2.52
QUEROB	3.08	1.76	2.77	2.7	2.9	6.66	5.47	-	5.39	5.91	2.9	2.36	2.97
QUESUB	1.21	1.43	1.21	1.4	2.09	-	4.08	6.93	-	1.86	6.23	2.37	4.93

Table S5b VIF values calculated on the variables included in the best predictive NB model for each species. For each species, there is one column with the variable names that are included in the model and one column with the VIF scores calculated. Marginality index VIF's values are in bold.

Variables	**Marginality**	**T° related variable**	**Precipitation related variable**	**min_spei12**	**mean_spei12**	**BA.O**	**BA**	**Baj**	**BAIj**	**BAIj.mean**	**DBH**	**yearsbetweensurveys**	**treeNbr**
Species													
ABIALB	1.18	1.32	1.52	2.08	2.16	4.18	3.92	9.17	NA	9.36	2.82	-	2.69
ACEPSE	3.34	2.19	2.74	1.59	1.56	-	3.02	-	4.27	2.23	3.73	-	2.91
ALNGLU	2.43	2.65	1.39	1.7	1.93	4.61	4.58	7.1	-	6.88	2.56	-	2.43
BETPEN	1.58	1.84	-	1.58	1.45	-	2.47	7.18	6.53	7.85	5.01	-	2.39
CASSAT	2.42	1.96	1.98	2.21	1.87	4.39	4.45	5.79	-	5.71	2.85	2.1	2.71
FRAEXC	1.2	1.31	-	2.32	2.44	2.32	-	8.94	7.98	8.06	6.14	1.87	2.8
FAGSYL	2.24	1.54	2.04	1.69	1.46	-	1.81	6.44	2.35	6.42	-	-	2.41
PICABI	4.42	1.31	4.43	2.93	2.6	-	3.78	6.99	10.84	5.77	4.57	-	-
PINHAL	1.13	5.02	7.21	1.93	1.66	-	6.81	-	7.27	1.92	3.61	3.63	5.6
PINNIG	1.42	2.16	2.47	2.28	2.25	-	2.68	-	2.95	1.62	-	-	-
PINPIN	1.46	3.96	5.47	2.85	1.93	-	3.35	-	6.18	2.24	4.46	-	-
PINPINA	1.39	1.32	2.22	1.92	2.52	2.4	4.41	-	-	2.38	2.91	-	3.83
PINSYL	2.72	2.39	1.15	2.64	2.29	-	3.64	-	8.7	1.77	4.39	-	2.1
POPNIG	1.57	1.68	1.28	1.2	-	-	3.03	-	7.39	1.96	5.3	-	2.15
POPTRE	1.94	2.13	1.55	2.15	2.16	-	1.83	5.72	-	6.83	1.96	-	2.56
QUEILE	1.23	1.25	1.66	1.8	1.73	1.77	-	2.18	2.89	-	2.64	1.61	-
QUEPET	-	1.45	1.28	1.44	1.43	-	2.29	10.34	8.22	8.56	5.04	-	2.6
QUEROB	3.11	1.78	2.8	2.69	2.86	6.85	5.58	5.34	-	5.83	2.84	2.42	2.94
QUEPYR	1.54	1.33	2.85	2.37	2.81	-	2.41	-	2.07	1.8	-	-	-
QUESUB	1.21	1.43	1.21	1.4	2.09	-	4.08	-	6.93	1.86	6.23	2.37	4.93

Section 4: Response variables and biotic variables

Table S6: Biotic variables included in the model. Description: variable description. Calculation: equation used for variable calculation for the k^{th} individual of the i^{th} individual plot of the j^{th} species. Transformation: transformation of the variable before inclusion in the model. Abbreviation: abbreviated names of the variables as used in the manuscript.

Abbreviation	Description	Calculation	Transformation
Yearsbetweensurveys	Number of years between surveys	$Years = Surveydate\,1_i - Surveydate\,2_i$	None
BAI j	Species (j) basal area increment (ha^{-1} yr^{-1}) on the plot (i)	$\sum \frac{BA.ha2_{ijk} - BA.ha1_{ijk}}{Years_i}$	Square root
meanBAIj	Mean species (j) basal area increment of the plot (i) (ha^{-1} yr^{-1})	$\frac{1}{N_{ijk}} \times \sum \frac{BA.ha2_{ijk} - BA.ha1_{ijk}}{Years_i}$	Square root
DBH (log or sqrt)	Species (j) mean diameter at breast height in the plot (i) (cm)	$\frac{1}{N_{ij}} \times \sum DBH_{ijk}$	Square root or logscaled
Treenumber	Number of trees (k) in the plot (i) (No. trees ha^{-1})	$\sum k_{ij}$	logscaled
BA	Total basal area of the plot (i) (m^2 ha^{-1})	$\sum BA.ha1_{ik}$	Square root
BAj	Total basal area of the same species (j) in the plot (i) (m^2 ha^{-1})	$\sum BA.ha1_{ijk}$	Logscaled
BA.O	Total basal area of other species in the plot (i) (m^2 ha^{-1})	$\sum BA.ha1_{ik} - \sum BA.ha1_{ijk}$	Square root

Table S7: Response variables analysed. Response variables are calculated for the k^{th} individual of the i^{th} individual plot of the j^{th} species. Response: Response description and unit. Distribution: distribution used to model the corresponding response. Calculation: final form of the response variable for modeling. Link: Link function used in the corresponding model.

Response	Distribution	Calculation	Link
Species mortality occurrence (presence/absence at the plot level)	Binomial (BIN)	$Y1_{ij}$ = 0 if no event recorded $Y1_{ij}$ = 1 if at least one event recorded	logit
Species mortality intensity (Number of trees per ha per plot per year)	Zero-truncated negative binomial (NB)	$Y2_{ij} = \frac{dead\,trees_{ijk}}{numberof\,trees_{ijk}} \times \frac{1}{Years_i}$	log

Section 5: Statistical summary

Table S8a: Simple effects significance in BIN model for each species. Species: Code for the species name. Each row represents one variable. For each sppecies and each variable, the estimated coefficient is reported with the standard error in parenthesis. The last lines report the T-value associated and the significance is indicated by a star.

Species	**ABIALB**	**ACEPSE**	**ALNGLU**	**BETPEN**	**CASSAT**	**FAGSYL**	**FRAEXC**	**PICABI**	**PINHAL**	**PINNIG**	**PINPIN**	**PINPINA**	**PINSYL**	**POPNIG**	**POPTRE**	**QUEILE**	**QUEPET**	**QUEPYR**	**QUEROB**	**QUESUB**
Variable																				
BA	-0.63 (0.1) -6.45 *	-0.43 (0.19) -2.32 *	-	-0.39 (0.11) -3.64 *	-0.49 (0.05) -10.06 *	-0.74 (0.06) -12.06 *	-	-	-0.53 (0.1) -5.06 *	-1.66 (0.33) -5.08 *	-0.49 (0.17) -2.86 *	-	-	-	-0.4 (0.11) -3.5 *	-	-	-	-0.26 (0.08) -3.29 *	-
BA.O	-0.5 (0.14) -3.49 *	-	-	-	-	-	-0.51 (0.08) -6.26 *	-	-	-	-	-	-	-	-	-	0.88 (0.13) 6.73 *	-	-0.46 (0.07) -6.52 *	-
BAIj	1.36 (0.18) 7.47 *	-	1 (0.22) 4.47 *	0.85 (0.23) 3.75 *	1.03 (0.1) 10.23 *	0.32 (0.1) 3.19 *	0.45 (0.18) 2.49 *	0.39 (0.09) 4.24 *	-	-	-	-	-	-	0.92 (0.22) 4.19 *	-0.61 (0.06) -10.68 *	-1.56 (0.16) -9.6 *	-	1.33 (0.1) 13.2 *	-
meanBAIj	-2.14 (0.22) -9.73 *	-0.49 (0.17) -2.89 *	-1.83 (0.29) -6.27 *	-2.03 (0.32) -6.3 *	-1.41 (0.13) -10.53 *	-1.1 (0.13) -8.51 *	-1.5 (0.26) -5.8 *	-1 (0.1) -10.22 *	-1.13 (0.07) -15.67 *	-1.14 (0.1) -11.25 *	-1.19 (0.14) -8.75 *	-1.32 (0.09) -15.51 *	-0.73 (0.04) -20 *	-0.83 (0.25) -3.3 *	-1.7 (0.3) -5.69 *	-	1.61 (0.1) 15.98 *	-0.91 (0.11) -8.08 *	-2.35 (0.15) -15.94 *	-0.73 (0.09) -8.25 *
BAj	-	-	-	-0.79 (0.22) -3.54 *	-	1.73 (0.07) 26.37 *	-	1.75 (0.14) 12.62 *	1.48 (0.13) 11.14 *	3.12 (0.35) 8.93 *	1.91 (0.26) 7.43 *	-	0.7 (0.1) 7 *	-	-	1.7 (0.09) 19.44 *	-0.27 (0.08) -3.48 *	1.8 (0.14) 12.97 *	-	0.74 (0.19) 3.88 *
DBH	1.25 (0.09) 13.63 *	1.26 (0.18) 6.87 *	1 (0.1) 9.59 *	1.06 (0.13) 8.32 *	0.83 (0.04) 21.19 *	-	1.1 (0.09) 12.4 *	-0.29 (0.07) -4.06 *	0.27 (0.09) 3.01 *	-	0.36 (0.18) 2.07 *	1.1 (0.05) 23.16 *	0.46 (0.06) 7.65 *	1.19 (0.34) 3.47 *	1.14 (0.1) 11.13 *	-0.37 (0.07) -5.4 *	-0.82 (0.24) -3.42 *	-	0.93 (0.06) 14.73 *	0.78 (0.17) 4.59 *
I(meanSPEI^2)	-	-	-	-	-	-	-1.13 (0.45) -2.5 *	0.4 (0.14) 2.96 *	-	-	-	2.15 (0.35) 6.21 *	-	-	-	-	-	-	-	-
I(minSPEI^2)	-0.16 (0.06) -2.62 *	-	0.21 (0.1) 2.02 *	-	-	-	-	-	-1.11 (0.21) -5.16 *	1.25 (0.36) 3.43 *	1.3 (0.38) 3.39 *	-2.09 (0.33) -6.37 *	-	-	-	-0.81 (0.25) -3.3 *	-	-	-	-

I(Precipitation^2)	-0.16 (0.05) -3.24 *	-	-0.13 (0.06) -2.18 *	-	-	0.12 (0.02) 4.75 *	-	-	-	-	-	-0.32 (0.05) -5.98 *	-0.07 (0.02) -2.63 *	-	-	-	-	-	-	-
I(Temperature^2)	-	-	-	-	-0.1 (0.03) -3.8 *	-	-	-	-	-0.33 (0.1) -3.27 *	0.99 (0.3) 3.25 *	-	-	-	-	-	-	-	0.11 (0.05) 2.27 *	-
Marginality (LE)	-0.75 (0.38) -1.98	-	-3.6 (1.42) -2.53 *	-	0.93 (1.31) 0.7	0.35 (0.12) 2.96 *	1.25 (0.29) 4.23 *	1.56 (0.37) 4.22 *	-2.55 (0.84) -3.04 *	-	-	6.25 (0.97) 6.42 *	-2.29 (0.95) -2.42 *	-	-	-	-	-	-	-
Marginality (TE)	-0.05 (0.49) -0.1	-	0.94 (0.46) 2.05 *	-	2.59 (0.65) 3.97 *	-0.28 (0.32) -0.88	0.86 (0.51) 1.7	1.03 (0.28) 3.73 *	0.3 (1.13) 0.27	-	-	-2.29 (0.84) -2.71 *	0.4 (0.19) 2.07 *	-	-	-	-1.39 (0.16) -8.81 *	-	-	-
meanSPEI	-	-1.07 (0.42) -2.56 *	-	-1.62 (0.37) -4.37 *	-1.19 (0.11) -10.99 *	-1.47 (0.14) -10.57 *	-	-	2.59 (0.75) 3.48 *	1.09 (0.4) 2.76 *	-	1.51 (0.25) 6 *	-	-	-2.22 (0.3) -7.46 *	-	0.29 (0.12) 2.45 *	-3.45 (1.28) -2.7 *	-1.53 (0.18) -8.43 *	-
minSPEI	-	-	-	0.51 (0.23) 2.24 *	-	0.38 (0.1) 3.68 *	-	0.33 (0.11) 2.98 *	-3.32 (0.64) -5.17 *	3.27 (0.98) 3.34 *	3.39 (1.24) 2.73 *	-7.02 (1.06) -6.6 *	-	-	-	-2.42 (0.75) -3.25 *	0.19 (0.04) 5.24 *	-	-	-
Precipitation	-	0.79 (0.33) 2.39 *	0.44 (0.23) 1.93	-	0.82 (0.16) 5.21 *	-	-	-0.78 (0.2) -4.02 *	2.31 (0.28) 8.12 *	1.45 (0.42) 3.41 *	1.45 (0.34) 4.22 *	-	1.02 (0.12) 8.88 *	-	0.8 (0.23) 3.43 *	1.22 (0.22) 5.48 *	-	-1.93 (0.45) -4.29 *	0.57 (0.15) 3.85 *	1.39 (0.49) 2.86 *
Temperature	-	-	-	1.09 (0.23) 4.84 *	0.15 (0.04) 3.89 *	-	-	-0.31 (0.11) -2.96 *	0.48 (0.1) 4.59 *	1.63 (0.45) 3.64 *	1.07 (0.34) 3.2 *	-	0.44 (0.06) 8.02 *	-	-	0.48 (0.06) 7.85 *	0.09 (0.01) 7.94 *	0.4 (0.09) 4.35 *	0.2 (0.07) 2.71 *	0.94 (0.41) 2.27 *
treeNbr	0.07 (0.01) 5.1 *	0.21 (0.03) 7.16 *	0.04 (0.02) 2.58 *	0.12 (0.02) 7.35 *	0.1 (0.01) 13.69 *	0.03 (0.01) 3.87 *	0.13 (0.02) 8.09 *	-	0.03 (0.01) 3.42 *	-	-	0.04 (0) 13.38 *	0.04 (0) 11.48 *	0.21 (0.04) 5.07 *	0.07 (0.01) 4.83 *	-	-	-	0.08 (0.01) 8.43 *	0.04 (0.01) 3.45 *
yearsbetweensurveys	-	-	-	-	0.24 (0.1) 2.4 *	-	0.28 (0.14) 2 *	-	-0.1 (0.03) -3.08 *	-	-	-	-	-	-	-0.2 (0.05) -3.91 *		-	0.37 (0.08) 4.77 *	-0.08 (0.04) -2.18 *

Table S8b: Simple effects significance in NB model for each species. Species: Code for the species name. Each row represents one variable. For each species and each variable, the estimated coefficient is reported with the standard error in parenthesis. The last lines report the T-value associated and the significant ones are indicated by a star.

Species Variable	**ABIALB**	**ACEPSE**	**ALNGLU**	**BETPEN**	**CASSAT**	**FAGSYL**	**FRAEXC**	**PICABI**	**PINHAL**	**PINNIG**	**PINPIN**	**PINPINA**	**PINSYL**	**POPTRE**	**QUEILE**	**QUEPET**	**QUEPYR**	**QUEROB**	**QUESUB**
BA	-0.16 (0.08) -2.07 *	0.35 (0.12) 2.96 *	-0.21 (0.07) -3.21 *	-	-0.34 (0.03) -11.52 *	-	-	-	-	-	-0.35 (0.09) -3.77 *	-	0.12 (0.03) 3.53 *	-	-	-	-	-	-
BA.O	0.19 (0.05) 3.92 *	-	0.31 (0.1) 3.26 *	-	0.36 (0.06) 6.54 *	-	0.42 (0.1) 4.36 *	-	-	-	-	-	-	0.26 (0.06) 4.45 *	-0.1 (0.04) -2.33 *	-	-	0.06 (0.03) 2.22 *	-
BAIj	-0.34 (0.03) -11.51 *	-0.8 (0.18) -4.53 *	-	-	-	-0.16 (0.03) -5.7 *	-	-0.33 (0.02) -16.04 *	-0.52 (0.03) -17.03 *	-0.39 (0.07) -5.78 *	-0.57 (0.06) -9.19 *	-0.51 (0.05) -10.57 *	-0.28 (0.02) -14.86 *	-0.38 (0.05) -8.3 *	-0.4 (0.03) -12.38 *	0.19 (0.06) 3 *	-0.47 (0.05) -8.71 *	-0.45 (0.05) -9.3 *	-0.28 (0.04) -6.33 *
meanBAIj	-	0.81 (0.24) 3.4 *	-0.44 (0.06) -7.36 *	-0.43 (0.06) -7.38 *	-0.45 (0.02) -18.71 *	-	-0.23 (0.06) -3.96 *	-	-	-0.16 (0.07) -2.22 *	-	-0.18 (0.08) -2.34 *	-	-	-	-0.39 (0.08) -5.15 *	-	0.16 (0.07) 2.26 *	-
BAj	-	-0.66 (0.15) -4.5 *	-	-0.68 (0.06) -10.47 *	-	-0.48 (0.06) -7.51 *	-0.71 (0.05) -13.56 *	-	-	-	0.99 (0.17) 5.65 *	-	-0.7 (0.06) -10.94 *	-	-0.12 (0.05) -2.24 *	-0.88 (0.05) -17.94 *	0.64 (0.23) 2.74 *	-	-0.25 (0.06) -3.84 *
DBH	0.12 (0.05) 2.13 *	-	0.15 (0.06) 2.3 *	0.42 (0.05) 7.94 *	0.24 (0.03) 9.2 *	0.16 (0.04) 4.02 *	0.54 (0.06) 8.44 *	-0.15 (0.03) -5.83 *	0.17 (0.04) 4.73 *	-	-0.55 (0.12) -4.65 *	0.14 (0.04) 4.01 *	0.2 (0.04) 5.46 *	0.27 (0.06) 4.88 *	-	0.57 (0.04) 14.77 *	-	-	-
I(meanSPEI^2)	-0.64 (0.23) -2.81 *	-	-	-	-0.61 (0.19) -3.23 *	-	-	-0.16 (0.07) -2.29 *	-	-	-	-0.66 (0.2) -3.29 *	-	-	-	-	-2.75 (0.94) -2.94 *	-	-1.18 (0.32) -3.67 *
I(minSPEI^2)	-	0.62 (0.22) 2.79 *	-	0.48 (0.11) 4.33 *	-	0.07 (0.03) 2.56 *	0.42 (0.11) 3.75 *	0.08 (0.04) 2.32 *	-	0.71 (0.28) 2.56 *	-	-	-	-	-	0.34 (0.07) 4.78 *	-	0.23 (0.07) 3.23 *	-
I(Precipitation^2)	0.08 (0.03)	-	-	-	-	-	-	-0.06 (0.02)	0.2 (0.08)	-	0.2 (0.09)	0.1 (0.03)	-0.04 (0.01)	-	-	-	-	-	0.09 (0.02)

	2.54 *							-2.42 *	2.53 *		2.36 *	3.56 *	-2.94 *						3.54 *
I(Temperature ^2)	-	-	-	-	-	-	-	-	0.22 (0.06) 3.91 *	-	-	-0.03 (0.01) -2.09 *	-0.06 (0.02) -3.82 *	-	-	-	-	0.09 (0.03) 3.26 *	0.11 (0.03) 3.86 *
Marginality (LE)	-	-1.94 (0.39) -4.93 *	0.88 (0.78) 1.13	-0.69 (0.26) -2.66 *	-0.15 (0.31) -0.49	-	-	0.2 (0.11) 1.81	1.3 (0.5) 2.58 *	-	4.05 (1.27) 3.2 *	-0.9 (0.42) -2.13 *	0.64 (0.22) 2.99 *	-	-	-	0.47 (0.27) 1.77	-	-
Marginality (TE)	-	-0.62 (1.35) -0.46	-0.52 (0.23) -2.21 *	0.2 (0.2) 1.03	-0.84 (0.29) -2.94 *	-	-	0.6 (0.12) 5 *	0.01 (0.41) 0.03	-	0.4 (1.24) 0.32	0.16 (0.37) 0.44	-0.09 (0.06) -1.54	-	-	-	-0.02 (0.16) -0.11	-	-
meanSPEI	0.61 (0.21) 2.86 *	-	-	-	0.67 (0.17) 3.89 *	0.37 (0.09) 3.92 *	-	0.34 (0.07) 4.86 *	-	-3.81 (0.96) -3.95 *	-	1.03 (0.46) 2.24 *	-	-	-1.5 (0.49) -3.05 *	-	3.81 (1.36) 2.81 *	-	-
minSPEI	-	1.69 (0.54) 3.12 *	0.28 (0.11) 2.43 *	1.14 (0.29) 3.96 *	0.34 (0.08) 4.33 *	-	1.03 (0.24) 4.36 *	-	-	1.65 (0.7) 2.34 *	-	0.29 (0.11) 2.73 *	-	-	-	0.89 (0.14) 6.29 *	-	0.67 (0.15) 4.42 *	-
Precipitation	-0.13 (0.07) -2.07 *	-	-	-	-	-0.11 (0.05) -2.11 *	-0.47 (0.09) -4.96 *	-0.28 (0.09) -2.97 *	-	-	-	-	-0.16 (0.06) -2.63 *	-	-	-0.2 (0.04) -5.39 *	-	-0.16 (0.06) -2.98 *	-
Temperature	-0.09 (0.04) -2.19 *	-	-	-	0.26 (0.07) 3.97 *	-0.14 (0.06) -2.21 *	-	-	0.14 (0.06) 2.3 *	-	-	-0.42 (0.11) -3.87 *	-	-	-	-	-	-	0.12 (0.05) 2.54 *
treeNbr	0.02 (0.01) 2.47 *	-	-0.02 (0.01) -2.74 *	-	0.02 (0) 6.06 *	0.01 (0) 3.03 *	-	-0.02 (0) -6.72 *	0.02 (0) 7.47 *	-	-	0.02 (0) 8.75 *	0.02 (0) 9.66 *	-	0.03 (0) 6.54 *	0.02 (0) 4.95 *	-	0.01 (0) 2.08 *	0.01 (0) 3.41 *
yearsbetweensurveys	-0.1 (0.05) -1.96	-	-	-	-0.22 (0.08) -2.87 *	-0.11 (0.03) -3.81 *	0.04 (0.01) 2.84 *	-0.07 (0.03) -2.64 *	-0.14 (0.02) -8.12 *	-0.15 (0.04) -3.35 *	-0.16 (0.06) -2.79 *	-0.15 (0.01) -10.2 *	-0.11 (0.02) -5.74 *	-0.06 (0.02) -2.66 *	-0.15 (0.03) -4.87 *	-0.13 (0.05) -2.63 *	-0.19 (0.03) -5.8 *	-0.07 (0.04) -2.06 *	-0.15 (0.02) -7.13 *

Table S8c: Interaction effects significance in BIN model for each species. Species: Code for the species name. Each row represents one variable. For each species and each variable, the estimated coefficient is reported with the standard error in parenthesis. The last lines report the T-value associated and the significance is indicated by a star.

Species Variable	ABIALB	ACEPSE	ALNGLU	BETPEN	CASSAT	FAGSYL	FRAEXC	PICABI	PINHAL	PINNIG	PINPIN	PINPINA	PINSYL	POPNIG	POPTRE	QUEILE	QUEPET	QUEPYR	QUEROB	QUESUB
BA X BA.O	0.15 (0.05) 3.2 *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BA X BAj	-	-	-	-	-	0.11 (0.04) 2.63 *	-	-	-0.21 (0.04) -4.96 *	-	-0.22 (0.09) -2.51 *	-	-	-	-	-	-0.36 (0.1) -3.56 *	-0.26 (0.08) -3.34 *	-	-
BA X minSPEI	-	-	-	-	-	-	-	-	-	-0.79 (0.22) -3.6 *	-	-	0.44 (0.05) 8.89 *	0.68 (0.23) 2.91 *	-	-	-	0.28 (0.09) 3.14 *	-	0.27 (0.08) 3.29 *
BA.O X minSPEI	-0.38 (0.14) -2.62 *	-	0.32 (0.07) 4.4 *	-	-	-	-	-	-	-	-	-	-	-	-	0.11 (0.04) 2.47 *	-	-	-	-
BAj X minSPEI	-	-	-	-0.93 (0.15) -6.26 *	-	-	-	-	-	0.86 (0.23) 3.73 *	-	-	-0.46 (0.09) -5.13 *	-0.86 (0.32) -2.71 *	-	-	-	-	-	-
Marginality (LE) X BA	-	-	-	-	-	-	-	-1.11 (0.23) -4.82 *	-	-0.79 (0.37) -2.12 *	-	0.32 (0.13) 2.53 *	-	1.59 (0.84) 1.89	-	-	-	-	-	-0.56 (0.41) -1.37
Marginality (LE) X BA.O	-	-	-	-	-	-	-	-	-	-	-	-0.4 (0.11) -3.73 *	-	-	-	-	-	-	-	-
Marginality (LE) X BAj	-	0.5 (0.31) 1.61	-	-	-	-	-	0.68 (0.3) 2.26 *	-	-	-	-	0.28 (0.22) 1.26	-	-	-	-	-	-	-
Marginality (LE) X meanSPEI	1.22 (0.52) 2.33 *	-	5.5 (1.73) 3.18 *	1.51 (0.58) 2.61 *	-1.17 (2.05) -0.57	-	-	-0.96 (0.33) -2.94 *	1.71 (0.7) 2.44 *	-5.33 (1.67) -3.2 *	4.62 (3.2) 1.44	-	2.32 (0.77) 3.02 *	-	2.26 (0.96) 2.35 *	-	-	-	0.18 (0.59) 0.3	0.55 (1.22) 0.45
Marginality (LE) X minSPEI	-0.82 (0.38) -2.16 *	-	-2.22 (1.15) -1.93	-	0.93 (0.95) 0.98	-	1.39 (0.42) 3.3 *	-	-2.23 (0.7) -3.17 *	3.01 (1.6) 1.88	-1.27 (0.75) -1.7	-1.09 (0.41) -2.65 *	-2.17 (0.74) -2.93 *	-	-	-0.68 (0.37) -1.86	-	-	-	-
Marginality (LE) X Precipitation	-	-0.34 (0.43) -0.79	-	-	-	-0.33 (0.08) -4.01 *	-	0.27 (0.23) 1.2	-	-	0.7 (0.42) 1.68	-	0.14 (0.15) 0.9	-	-	-0.92 (0.24) -3.79 *	-	-	-	-

Marginality (LE) X Temperature	-	-	-	-0.96 (0.29) -3.32 *	-	-	-	0.5 (0.17) 2.89 *	-	1.46 (0.71) 2.06 *	1.92 (1.21) 1.59	0.18 (0.15) 1.21	-	-	-	-	-	-0.14 (0.26) -0.55	-0.27 (0.15) -1.77	0.07 (0.24) 0.31
Marginality (TE) X BA	-	-	-	-	-	-	-	-1.09 (0.12) -8.79 *	-	0.93 (0.26) 3.56 *	-	0 (0.14) 0.03	-	-1.09 (0.42) -2.62 *	-	-	-	-	-	0.82 (0.32) 2.59 *
Marginality (TE) X BA.O	-	-	-	-	-	-	-	-	-	-	-	-0.29 (0.14) -2.04 *	-	-	-	-	-	-	-	-
Marginality (TE) X BAj	-	2.22 (0.68) 3.27 *	-	-	-	-	-	0.72 (0.21) 3.46 *	-	-	-	-	-0.24 (0.07) -3.39 *	-	-	-	-	-	-	-
Marginality (TE) X meanSPEI	-0.52 (0.56) -0.92	-	-0.18 (0.55) -0.33	0.98 (0.44) 2.23 *	-1.32 (0.48) -2.72 *	-	-	-1.04 (0.2) -5.12 *	-0.14 (0.94) -0.14	-4.73 (2.32) -2.04 *	-4.32 (2.09) -2.07 *	-	-1.13 (0.19) -6.07 *	-	2.06 (0.52) 3.93 *	-	-	-	1.03 (0.27) 3.8 *	4.97 (1.57) 3.16 *
Marginality (TE) X minSPEI	0.19 (0.57) 0.34	-	0.62 (0.46) 1.36	-	1.7 (0.5) 3.4 *	-	0.62 (0.39) 1.58	-	0.21 (0.66) 0.32	2 (0.87) 2.29 *	1.36 (0.5) 2.73 *	3.76 (0.76) 4.97 *	0.24 (0.14) 1.74	-	-	0.47 (0.14) 3.34 *	-	-	-	-
Marginality (TE) X Precipitation	-	2.67 (1.07) 2.5 *	-	-	-	-0.34 (0.31) -1.11	-	0.71 (0.21) 3.39 *	-	-	-8.95 (3.08) -2.91 *	-	-0.42 (0.11) -3.97 *	-	-	-0.56 (0.2) -2.84 *	-	-	-	-
Marginality (TE) X Temperature	-	-	-	-0.67 (0.23) -2.9 *	-	-	-	0.39 (0.13) 2.92 *	-	-1.9 (0.69) -2.76 *	-4.15 (1.36) -3.04 *	0.51 (0.23) 2.23 *	-	-	-	-	0.57 (0.14) 4.2 *	-0.37 (0.15) -2.4 *	-0.42 (0.13) -3.3 *	0.5 (0.18) 2.72 *
meanSPEI X BA	-0.31 (0.12) -2.5 *	-	-	-	-	0.25 (0.09) 2.8 *	-	-	-	-	-	-	-0.45 (0.1) -4.76 *	-	-	-	-	1.05 (0.4) 2.65 *	-	-
meanSPEI X BA.O	0.74 (0.16) 4.6 *	-	0.38 (0.22) 1.74	-	-	-	-	-	-	-	-	0.39 (0.13) 3.04 *	-	-	-	-	-	-	-	-
meanSPEI X BAj	-	-	-	1.04 (0.21) 4.92 *	-	-	-	-	-	-	-	-	0.4 (0.11) 3.57 *	-	-	0.6 (0.15) 3.91 *	-	-	-	-
meanSPEI X minSPEI	-	-	-	-	-	-	1.09 (0.25) 4.42 *	-	1.47 (0.45) 3.29 *	-	-0.91 (0.44) -2.07 *	-	-	-	-	0.67 (0.16) 4.28 *	0.12 (0.04) 3.38 *	-1.68 (0.82) -2.05 *	-	0.67 (0.18) 3.77 *
Precipitation X BA	-	-	-	-	0.12 (0.03) 3.52 *	-	-	0.41 (0.08) 5.11 *	-	-	-	-	-0.09 (0.03) -3.07 *	-	-	-	-	0.34 (0.1) 3.32 *	-0.17 (0.04) -4.57 *	0.28 (0.11) 2.44 *
Precipitatio	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.16	-0.23	-	0.2	-

n X BA.O															(0.05) 3.21 *	(0.04) -6.24 *		(0.04) 5.31 *	
Precipitation X BAj	-	-0.57 (0.17) -3.36 *	-	-	-	-	-	-0.34 (0.1) -3.33 *	-	-	-	-	-	-	-	-	-	-	-	-
Precipitation X meanSPEI	-	-	-0.62 (0.29) -2.11 *	-	-0.85 (0.19) -4.51 *	-0.32 (0.09) -3.54 *	-	0.82 (0.14) 6.01 *	-	-	-	-0.4 (0.14) -2.88 *	-1.16 (0.11) -10.71 *	-	-1.07 (0.32) -3.32 *	-0.63 (0.22) -2.89 *	-	-	-	-
Precipitation X minSPEI	-	-	0.56 (0.21) 2.69 *	-	0.65 (0.14) 4.67 *	-	-	-	1.31 (0.19) 6.74 *	0.68 (0.29) 2.31 *	-	-	0.8 (0.09) 8.88 *	-	1 (0.26) 3.87 *	0.56 (0.16) 3.53 *	-	-1 (0.29) -3.42 *	0.3 (0.11) 2.63 *	0.83 (0.32) 2.63 *
Temperature X BA	-0.1 (0.05) -2.1 *	-	-0.32 (0.1) -3.33 *	-0.25 (0.1) -2.53 *	-	-0.16 (0.04) -4.56 *	-	0.19 (0.07) 2.92 *	-	-0.28 (0.08) -3.48 *	-	0.12 (0.04) 2.88 *	-	-	-	-	-	-	-	-
Temperature X BA.O	-	-	0.41 (0.11) 3.88 *	-	0.07 (0.03) 2.03 *	-	-0.13 (0.06) -2.28 *	-	-	-	-	-	-	-	-	-	-	-	-	-
Temperature X BAj	-	-	-	-0.22 (0.1) -2.17 *	-	0.16 (0.04) 4.13 *	-0.13 (0.06) -2.29 *	-0.27 (0.08) -3.48 *	-	-	-0.24 (0.1) -2.45 *	-	-	-	-	-	-	-	-	-
Temperature X meanSPEI	-	0.93 (0.32) 2.87 *	-	-	-	-	-	0.38 (0.1) 3.98 *	1.41 (0.23) 6.24 *	-	-	0.65 (0.18) 3.54 *	0.32 (0.11) 3.03 *	-	-	-	-0.07 (0.03) -2.03 *	-	-	-
Temperature X minSPEI	-0.11 (0.06) -2.02 *	-0.62 (0.17) -3.59 *	-	-	-	-	-	-	-	0.84 (0.29) 2.86 *	-	-0.24 (0.04) -6.54 *	-	-	-0.54 (0.12) -4.33 *	-	-	-	-	0.63 (0.26) 2.44 *
Temperature X Precipitation	-0.16 (0.06) -2.51 *	-0.25 (0.13) -2.01 *	-	-	-	-	-	-0.32 (0.06) -5.75 *	0.15 (0.06) 2.41 *	-	1.82 (0.55) 3.3 *	0.22 (0.08) 2.68 *	0.22 (0.06) 3.88 *	0.49 (0.18) 2.67 *	-	-		-	-	-

Table S8d: Interaction effects significance in NB model for each species. Species: Code for the species name. Each row represents one variable. For each species and each variable, the estimated coefficient is reported with the standard error in parenthesis. The last lines report the T-value associated and the significance is indicated by a star.

Species	**ABIALB**	**ACEPSE**	**ALNGLU**	**BETPEN**	**CASSAT**	**FAGSYL**	**FRAEXC**	**PICABI**	**PINHAL**	**PINNIG**	**PINPIN**	**PINPINA**	**PINSYL**	**POPTRE**	**QUEILE**	**QUEPET**	**QUEPYR**	**QUEROB**	**QUESUB**
Variable																			
BA x BA.O	-0.06 (0.03) -2.18 *	-	0.06 (0.03) 1.95	-	-	-	-	-	-	-	-	-	-	-0.07 (0.03) -2.36 *	-	-	-	-	-
BA x BAj	-	0.18 (0.08) 2.22 *	-	-	-	-	-	0.14 (0.03) 5.18 *	-	-	-	-	-	-	-	-	-	-	-
BA x minSPEI	0.12 (0.06) 1.98	-	-	-	-	-	-	-	-	-	-	0.1 (0.02) 4.12 *	-	-	-	-	-	-	-
BA.O x minSPEI	-	-	0.15 (0.06) 2.51 *	-	0.09 (0.04) 2.13 *	-	0.33 (0.1) 3.27 *	-	-	-	-	-	-	-	-	-	-	-	-
BAj x minSPEI	-	-	-	-	-	-	-	-	-	-0.31 (0.06) -5.12 *	-	-	-0.12 (0.04) -2.7 *	-	-	-	0.36 (0.17) 2.14 *	-	-
Marginality (LE) x BA	-	-	-	0.4 (0.13) 3.12 *	-	-0.06 (0.05) -1.18	-	-0.1 (0.06) -1.7	-	-	-	0.12 (0.04) 3.36 *	-	0.29 (0.2) 1.45	-	-	-	0.16 (0.08) 1.97	-
Marginality (LE) x BA.O	-	-	-	-	-	-	-	-	-	-	-	-0.14 (0.03) -4.3 *	-	-	-	-	-	-	-
Marginality (LE) x BAj	-	0.58 (0.19) 3.01 *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.68 (0.27) -2.51 *	-	-
Marginality (LE) x meanSPEI	-	1.41 (0.37) 3.79 *	-0.84 (0.83) -1.02	0.48 (0.32) 1.5	-	-0.08 (0.15) -0.52	-	-	-	-	-	-	-0.32 (0.24) -1.34	-	2.36 (0.75) 3.14 *	-	-	-	-
Marginality (LE) x minSPEI	-	-1.37 (0.43) -3.18 *	0.53 (0.55) 0.96	-0.46 (0.23) -2.05 *	0.17 (0.33) 0.5	-	-	-	-	-	1.18 (0.44) 2.65 *	-0.82 (0.34) -2.45 *	-	-	-0.94 (0.28) -3.4 *	-	-	-0.31 (0.15) -2.09 *	0.56 (0.2) 2.85 *
Marginality (LE) x	-0.03 (0.09)	-	-0.34 (0.22)	-	-	-0.07 (0.05)	-	0.5 (0.13)	-	5.53 (2.11)	-	-	-0.17 (0.09)	-	-	-	-	0.12 (0.08)	-

Precipitation	-0.39		-1.59			-1.48		3.7 *		2.62 *			-1.87					1.53	
Marginality (LE) x Temperature	0.18 (0.08) 2.18 *	-	-	-	-	-	0.26 (0.12) 2.22 *	-	0.69 (0.3) 2.28 *	3.71 (1.45) 2.56 *	2.3 (0.74) 3.1 *	-	-	-	0.75 (0.2) 3.66 *	0.23 (0.09) 2.64 *	-0.47 (0.17) -2.78 *	0.23 (0.09) 2.7 *	-
Marginality (TE) x BA	-	-	-	0.16 (0.07) 2.11 *	-	0.31 (0.16) 1.93	-	-0.14 (0.04) -3.35 *	-	-	-	0.07 (0.06) 1.06	-	-0.28 (0.12) -2.21 *	-	-	-	-0.06 (0.04) -1.41	-
Marginality (TE) x BA.O	-	-	-	-	-	-	-	-	-	-	-	-0.16 (0.07) -2.09 *	-	-	-	-	-	-	-
Marginality (TE) x BAj	-	-0.98 (0.41) -2.39 *	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.06 (0.16) -0.39	-	-
Marginality (TE) x meanSPEI	-	1.64 (0.92) 1.79	0.61 (0.26) 2.34 *	-0.56 (0.22) -2.54 *	-	0.73 (0.28) 2.6 *	-	-	-	-	-	-	0.25 (0.06) 4.51 *	-	0.7 (0.43) 1.64	-	-	-	-
Marginality (TE) x minSPEI	-	-1.31 (1.21) -1.08	-0.9 (0.28) -3.26 *	0.15 (0.21) 0.75	-0.52 (0.21) -2.52 *	-	-	-	-	-	-0.04 (0.68) -0.06	0.08 (0.2) 0.42	-	-	-0.21 (0.1) -2.03 *	-	-	-0.06 (0.07) -0.93	0.11 (0.08) 1.33
Marginality (TE) x Precipitation	0.4 (0.13) 3.14 *	-	0.25 (0.12) 2.11 *	-	-	-0.25 (0.12) -2.01 *	-	0.34 (0.12) 2.8 *	-	-0.15 (0.27) -0.53	-	-	0.11 (0.04) 2.76 *	-	-	-	-	0.16 (0.07) 2.45 *	-
Marginality (TE) x Temperature	0.36 (0.08) 4.24 *	-	-	-	-	-	0.04 (0.06) 0.7	-	-0.07 (0.24) -0.3	-0.16 (0.19) -0.85	-0.03 (0.14) -0.25	-	-	-	-0.13 (0.12) -1.11	-0.14 (0.05) -2.94 *	-0.02 (0.09) -0.27	-0.21 (0.08) -2.62 *	-
meanSPEI x BA	-	-	0.35 (0.11) 3.08 *	-	-	-	-	-	-0.27 (0.12) -2.28 *	-	-	-	-	-	-	-	-	-	-
meanSPEI x BA.O	-	-	-0.2 (0.1) -2	-	-	-	-0.41 (0.13) -3.22 *	-	-	-	-	-	-	-	-	-	-	-	-
meanSPEI x BAj	-	-0.61 (0.25) -2.49 *	-	-	-	-	-	-	0.33 (0.12) 2.67 *	0.87 (0.2) 4.35 *	-	-	0.26 (0.05) 5.27 *	-	0.48 (0.11) 4.45 *	-0.16 (0.06) -2.57 *	-	-	-
meanSPEI x minSPEI	0.51 (0.25) 2.09 *	-	-	-	0.94 (0.19) 5.09 *	-	-	-	-	-2.44 (0.69) -3.54 *	-	0.69 (0.31) 2.22 *	-	-	-0.69 (0.29) -2.33 *	-	2.63 (0.98) 2.68 *	-	0.58 (0.19) 3.07 *
Precipitation x BA	-	-	-	-	0.04 (0.02) 2.34 *	-	-	-	-0.07 (0.03) -2.5 *	-	-	-0.11 (0.02) -4.59 *	-	-	-	-	-	-0.06 (0.02) -2.64 *	-
Precipitation x BAj	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05 (0.02)	-0.19 (0.06)	-	-

																2.6 *	-3.33 *		
Precipitation x meanSPEI	-	-	-	-	-	-	0.65 (0.14) 4.7 *	-	1.03 (0.22) 4.72 *	-	-	-	0.13 (0.06) 2.28 *	-0.22 (0.1) -2.16 *	-	-	-	-	-
Precipitation x minSPEI	-0.13 (0.06) -2.12 *	-0.27 (0.1) -2.69 *	-	-	-	-0.17 (0.04) -4.25 *	-0.58 (0.11) -5.09 *	-	-0.15 (0.05) -2.73 *	-	-	-	-0.13 (0.05) -2.54 *	-	-	-0.19 (0.04) -4.62 *	-	-	-
Temperature x BA	-	0.13 (0.06) 2.19 *	0.14 (0.05) 2.9 *	-	-	-	-	-	-	-	-	-	-0.1 (0.03) -3.45 *	0.24 (0.08) 3.14 *	-	-	-	-	-
Temperature x BA.O	-0.09 (0.03) -3.25 *	-	-	-	-	-	-0.08 (0.03) -2.28 *	-	-	-	-	-	-	-	-	-	-	-	-
Temperature x BAj	-	0.3 (0.1) 2.93 *	-	-	-	-	-	-	-	-	0.16 (0.05) 3.42 *	-	0.21 (0.03) 6.97 *	-	-	0.08 (0.02) 3.5 *	-	-	-
Temperature x meanSPEI	-	-	-	-	-	-	-	-	0.74 (0.21) 3.55 *	-	-	-	-	-	-	-0.27 (0.07) -3.98 *	-	-	-
Temperature x minSPEI	-	-	0.13 (0.07) 1.85	-	0.17 (0.05) 3.31 *	-0.14 (0.05) -2.71 *	-	-	-	-	-	-0.28 (0.07) -3.93 *	-	-	-	-	-	-0.12 (0.04) -3.2 *	-
Temperature x Precipitation	-	-	-0.15 (0.07) -2.29 *	-	-	-	-	-	0.37 (0.11) 3.35 *	-	-	-	-	-	-	-	-	-	-

Annexes 5: Supplementary figures of chapter 4

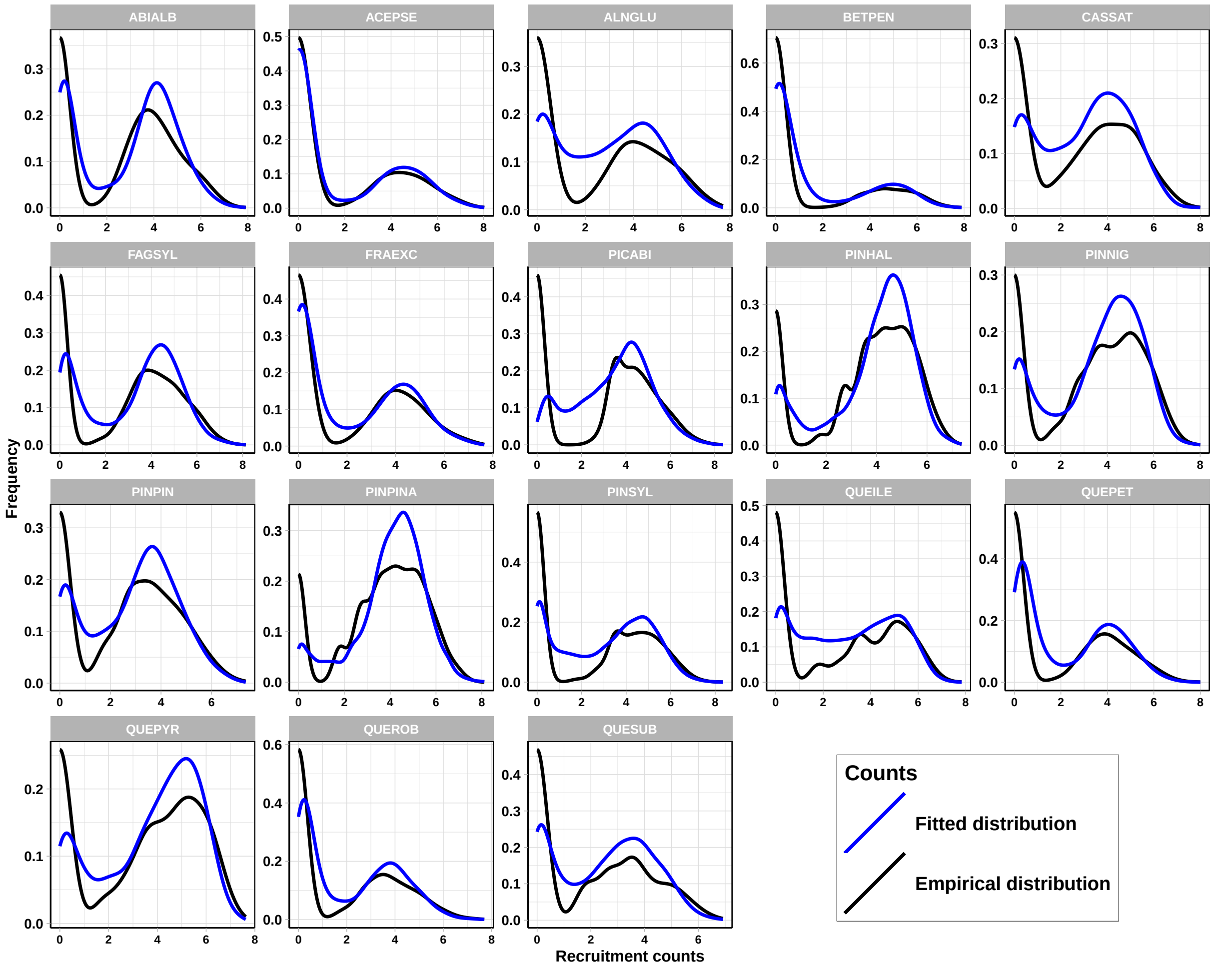


Figure S1: Comparison between the empirical distribution of observed counts (black lines) and the predicted distribution of counts (blue lines) for each of the 18 species.

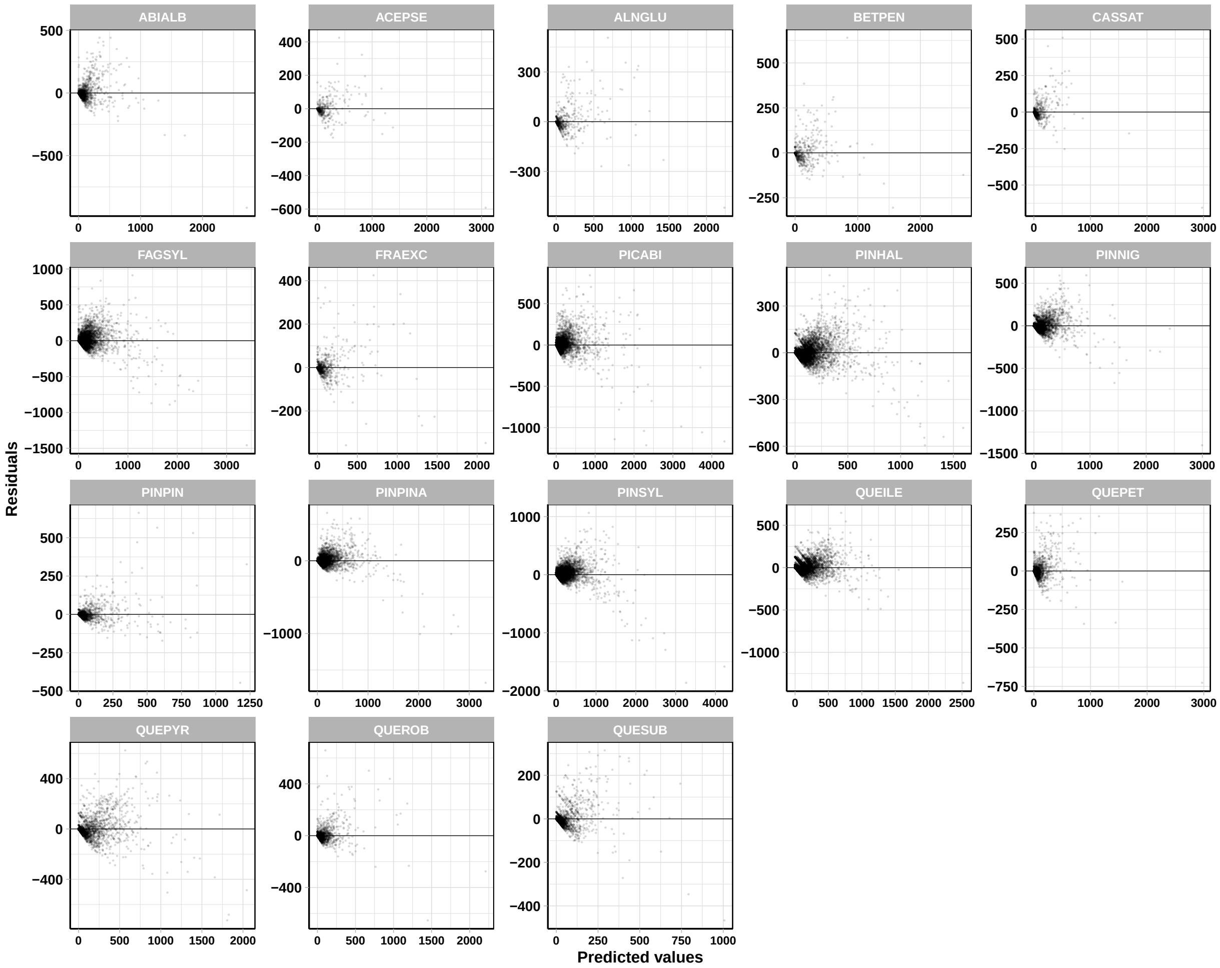


Figure S2: Residuals vs. fitted new tree abundance for the 18 species. The x and y axis have different scales for each species. Points are expected to be distributed around the black line ($y = 0$).

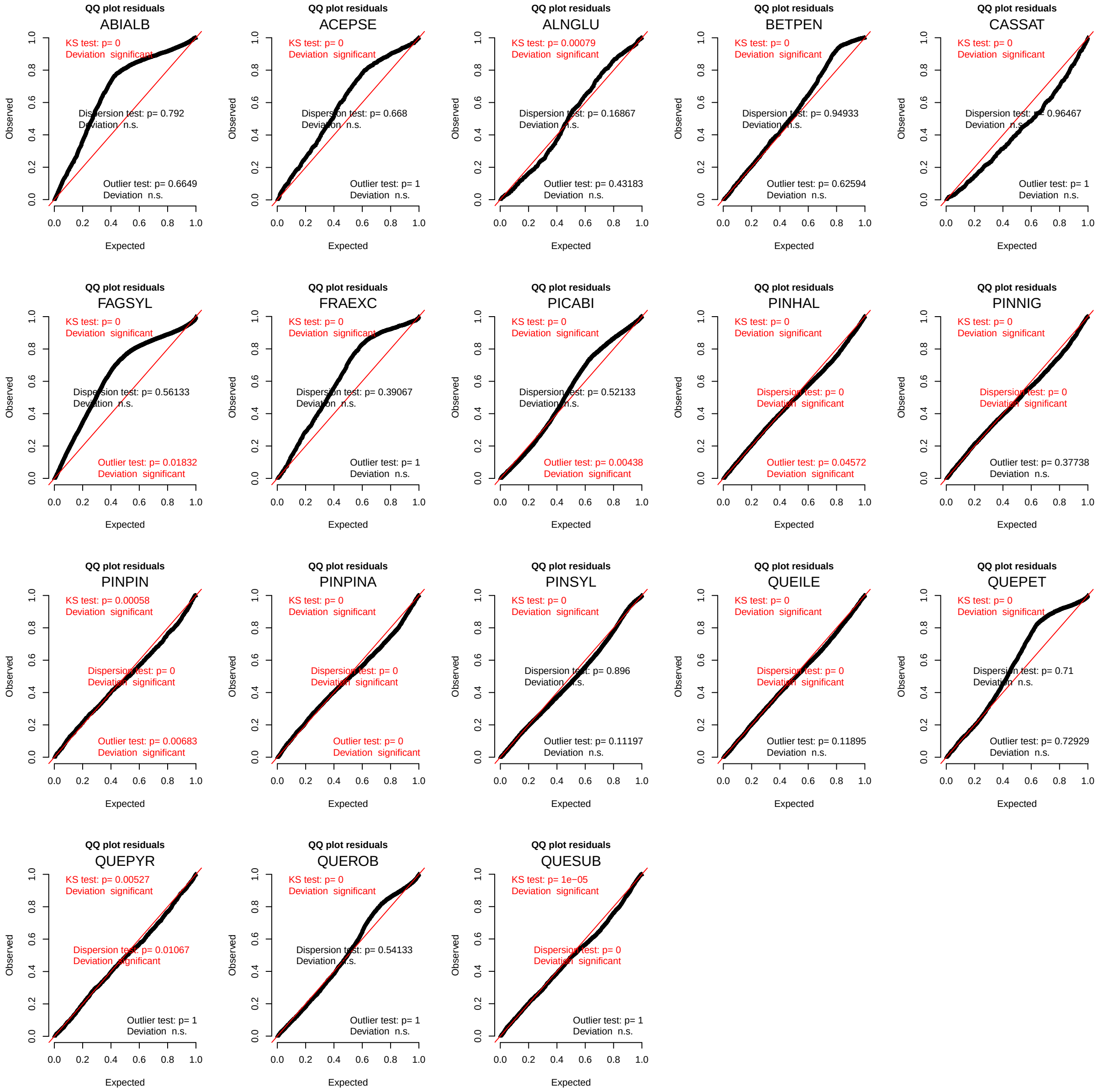


Figure S3: Quantile-quantile plots of the expected residuals (based on 3000 simulations) vs observed residuals. For each species, p-value and significance of the dispersion test, uniformity Kolmogorov-Smirnov test and outliers test are written on the plot (see Table S10 for more details)

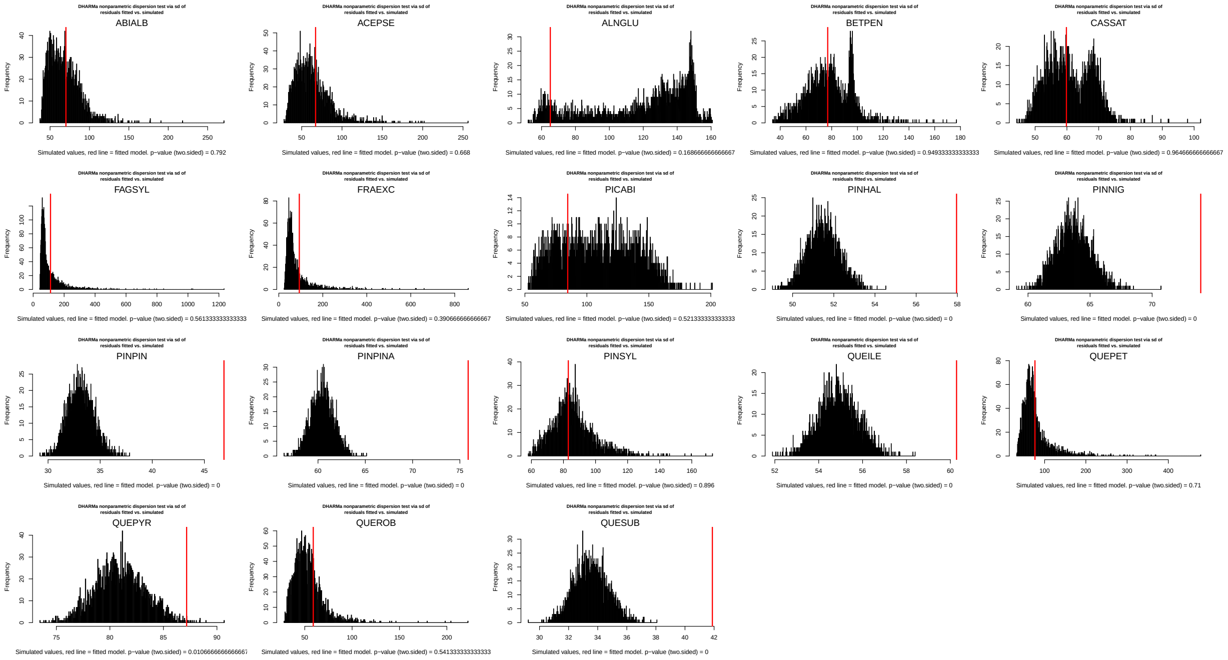


Figure S4: Histogram of the dispersion of the simulated residuals (black lines) and dispersion in the observed residuals (red line) for each species based on 3000 simulations. Red lines are expected to lay within the ranges of the black lines under the assumption of no under or overdispersion. See Table S10 for statistical tests.

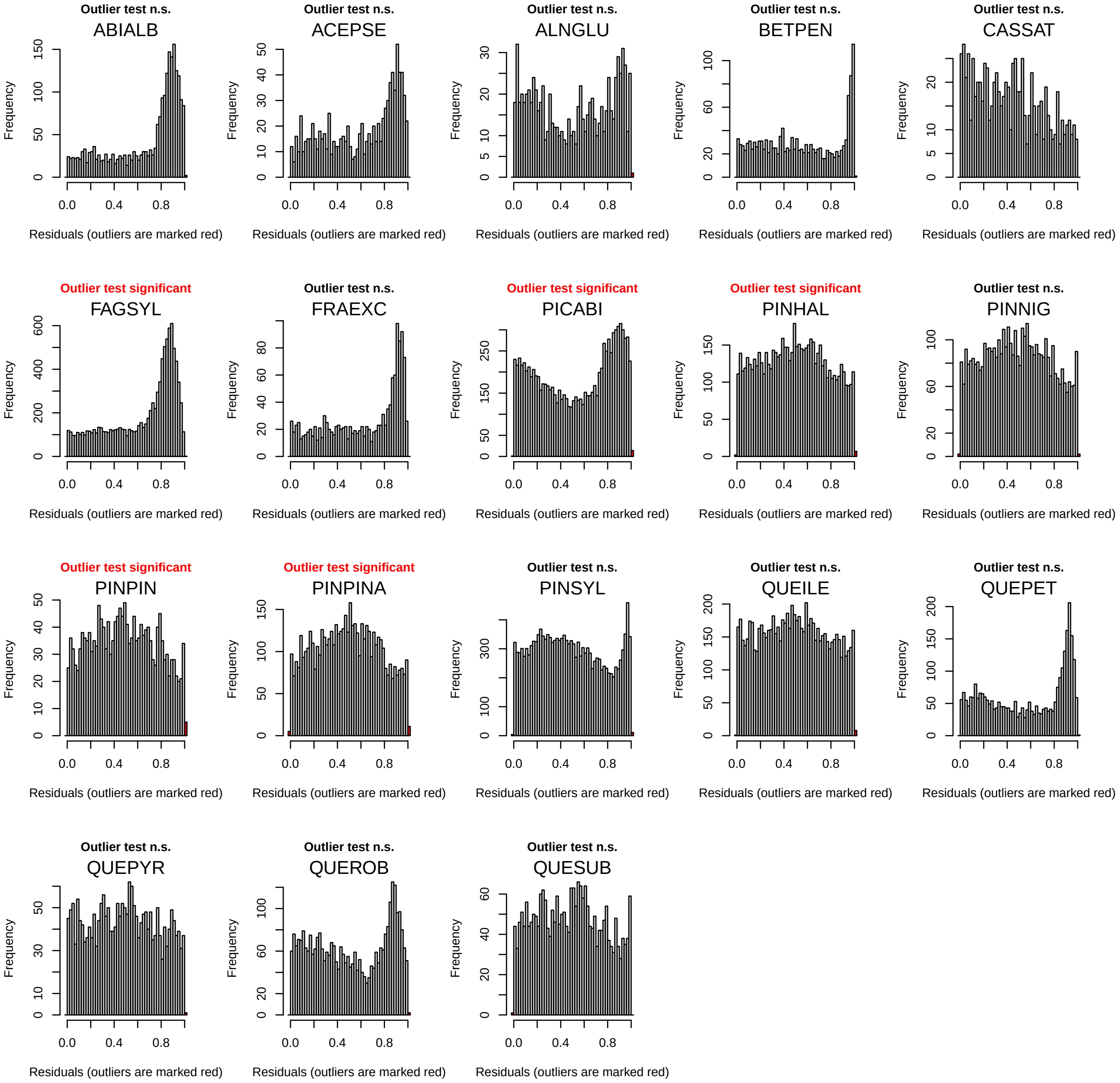
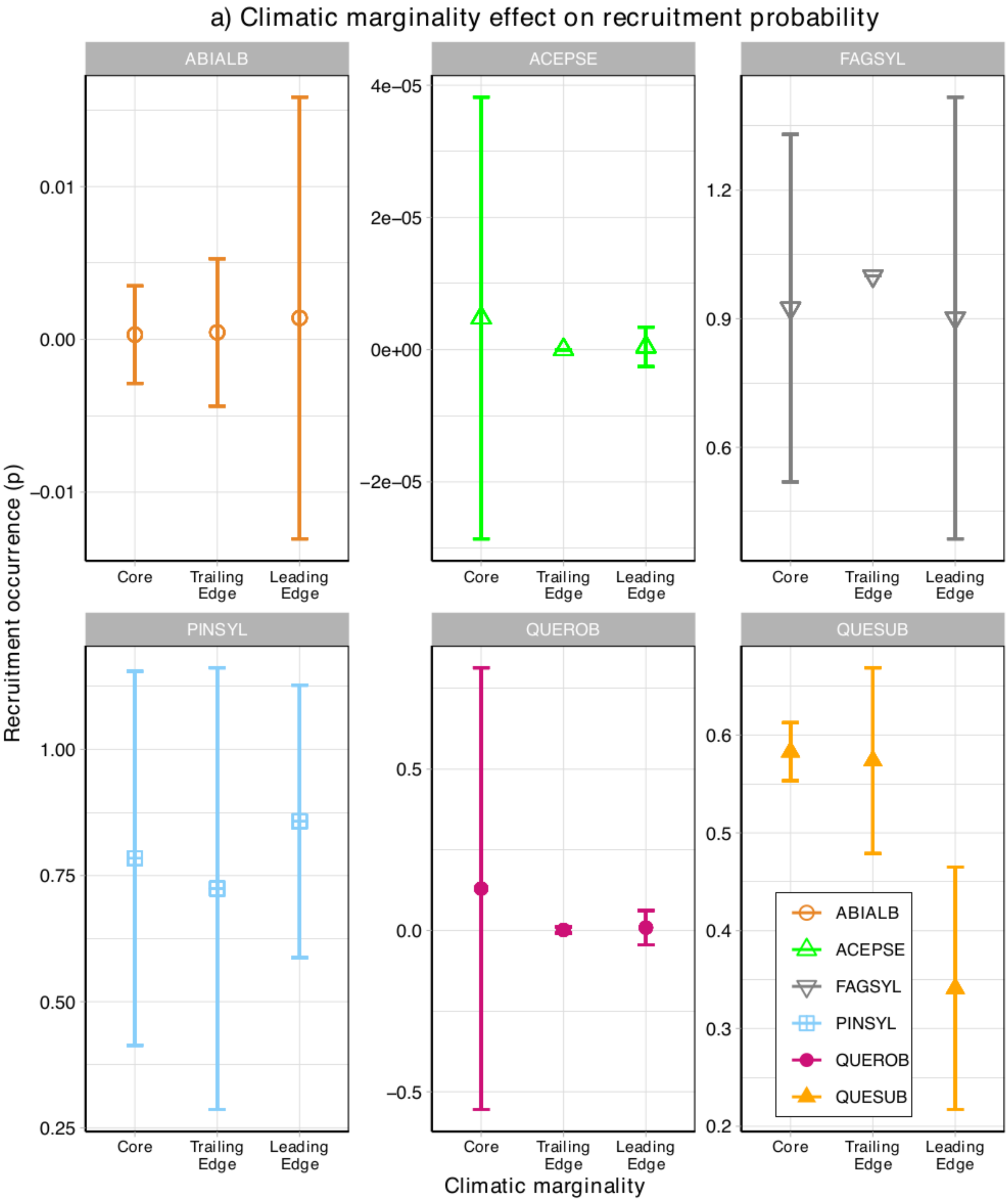


Figure S5: Histogram of the outliers frequency based on 3000 simulations. Red bars indicate if there are more or less simulation outliers than expected under the null hypothesis (fitted model).


a) Climatic marginality effect on recruitment probability
ABIALB
ACEPSE
FAGSYL
PINSYL
QUEROB
QUESUB
0.01
0.00
−0.01
4e−05
2e−05
0e+00
−2e−05
1.2
0.9
0.6
1.00
0.75
0.50
0.25
0.5
0.0
−0.5
0.6
0.5
0.4
0.3
0.2
Core
Trailing Edge
Leading Edge
Recruitment occurrence (p)
Climatic marginality
ABIALB
ACEPSE
FAGSYL
PINSYL
QUEROB
QUESUB

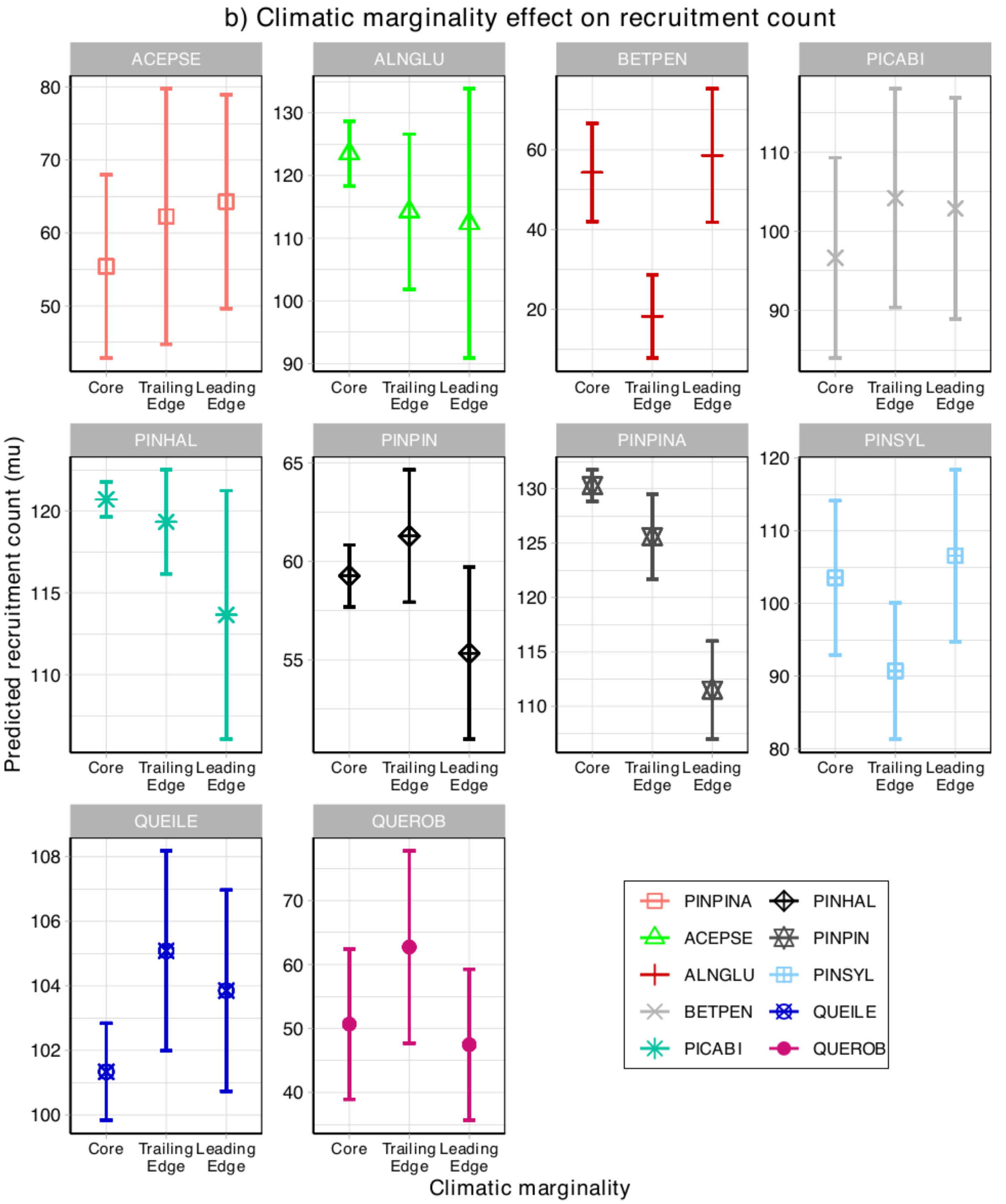
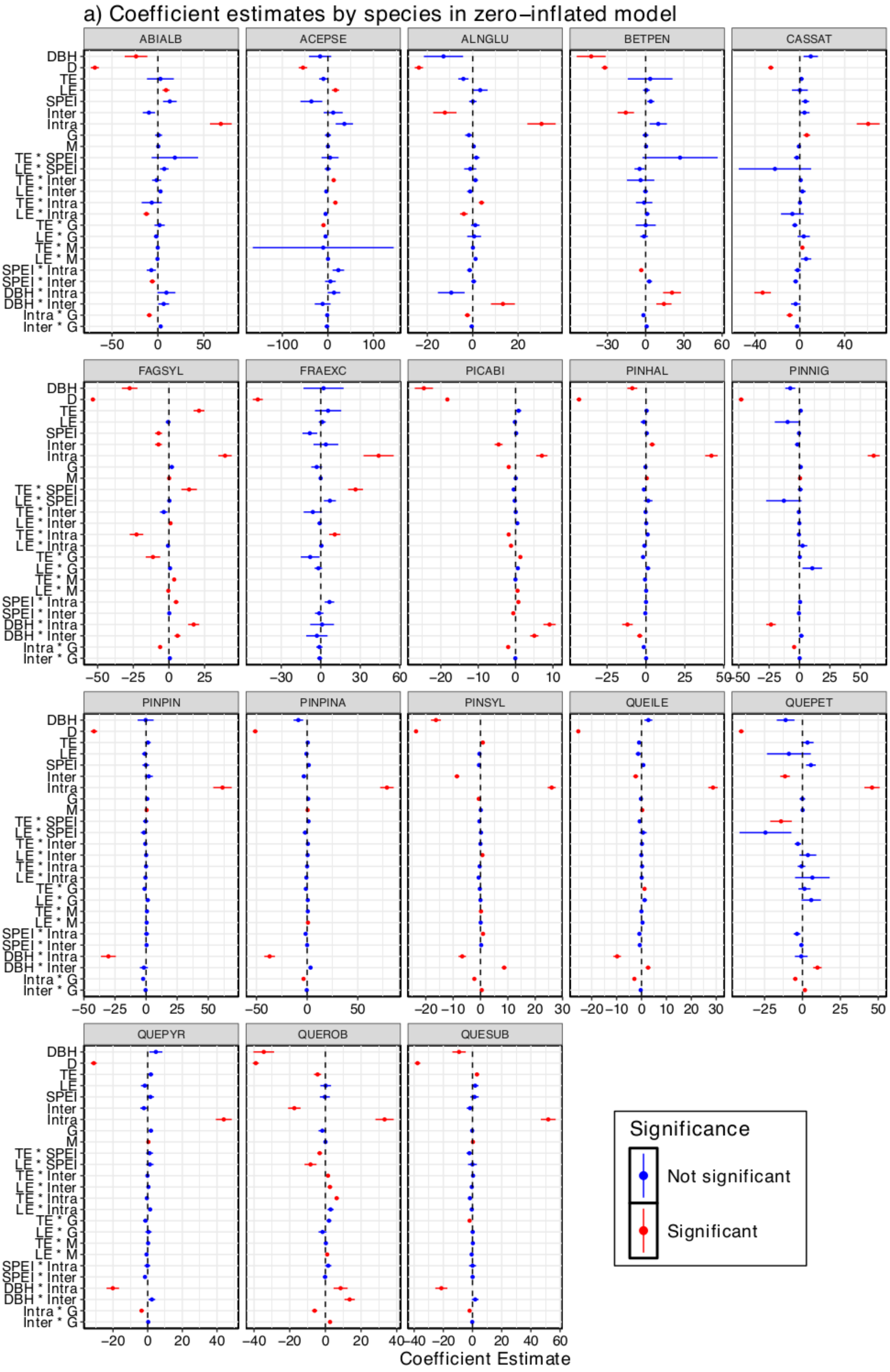


Figure S6: Significant effect of Climatic marginality (x-axis) on both a) predicted occurrence of recruitment (expressed as a probability, y-axis, left panel) and b) predicted recruitment rate per plot (expressed as a count, y-axis, right panel) across species.


a) Coefficient estimates by species in zero−inflated model
ABIALB
ACEPSE
ALNGLU
BETPEN
CASSAT
FAGSYL
FRAEXC
PICABI
PINHAL
PINNIG
PINPIN
PINPINA
PINSYL
QUEILE
QUEPET
QUEPYR
QUEROB
QUESUB
DBH
D
TE
LE
SPEI
Inter
Intra
G
M
TE * SPEI
LE * SPEI
TE * Inter
LE * Inter
TE * Intra
LE * Intra
TE * G
LE * G
TE * M
LE * M
SPEI * Intra
SPEI * Inter
DBH * Intra
DBH * Inter
Intra * G
Inter * G
−50 0 50
−100 0 100
−20 0 20
−30 0 30 60
−40 0 40
−50 −25 0 25
−30 0 30 60
−20 −10 0 10
−25 0 25 50
−50 −25 0 25 50
−50 −25 0 25 50
−50 0 50
−20 −10 0 10 20 30
−20 −10 0 10 20 30
−25 0 25 50
−20 0 20 40
−40 −20 0 20 40
−40 −20 0 20 40 60
Coefficient Estimate
Significance
Not significant
Significant

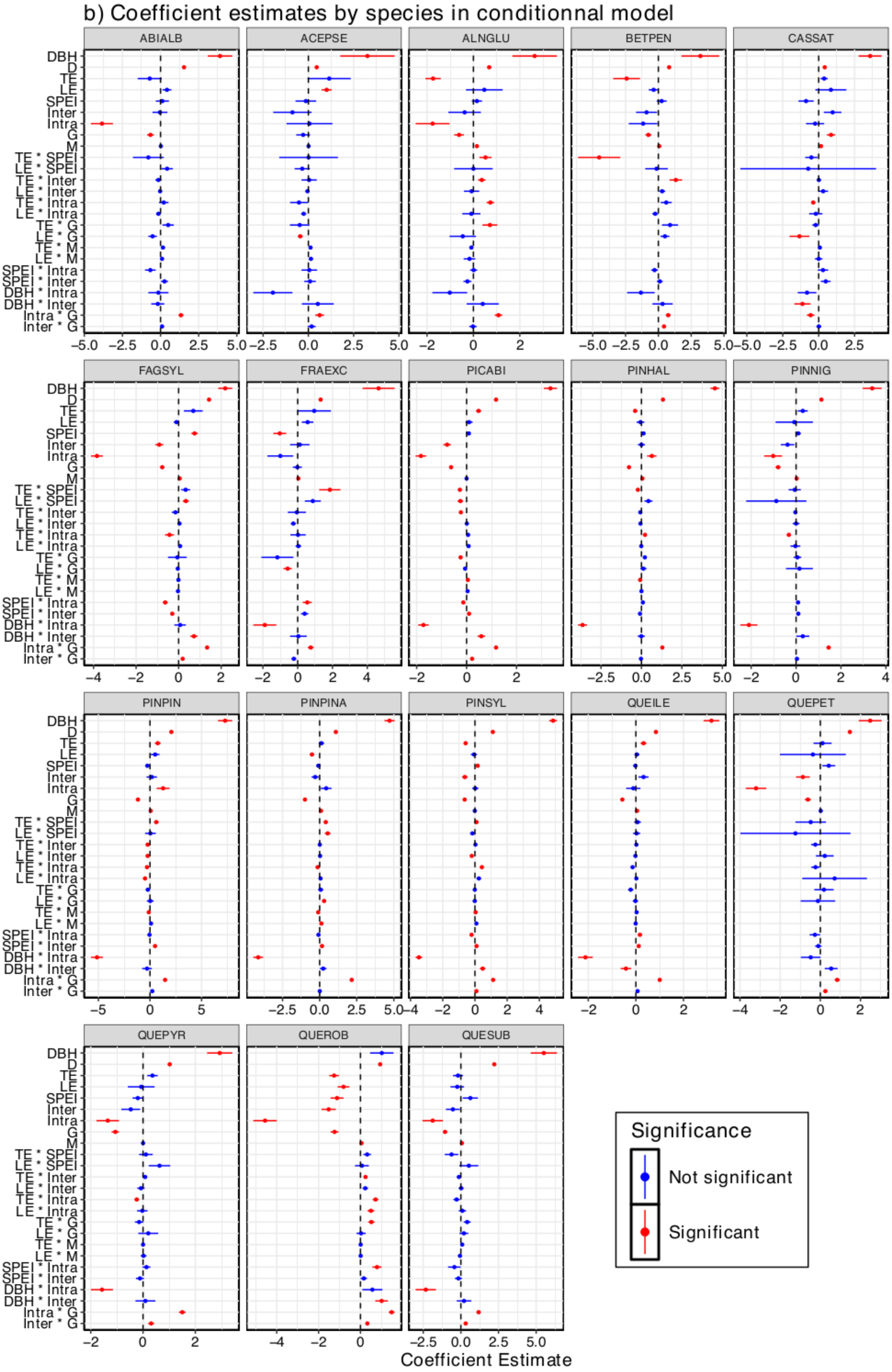


Figure S7: Dwplot showing coefficient estimates for main effect and interactions and significance in both zero-inflated (a) and conditional model (b). Red points indicate significance and blue dots are not significant. Lines indicate the confidence interval (95%)

Annexes 6: Supplementary tables of chapter 4

Supplementary Information

National Forest Inventories harmonization

The sample plot design was different among countries. For instance, the Spanish National Inventory recorded single sample plots in a 1 km by 1 km grid whereas the Finnish National Inventory followed a cluster design, with number and grid size depending on location while the German NFI used a 4 x 4 km quadrangle grid where the samples lied on the intersection points. Most NFIs followed a nested circular subplot design whose radius differs among NFI and within which trees of different size classes were monitored. The main differences among inventories are summarized in Table S1.

Table S1: Summary of information of the NFI design for each country: Belgium (Wallonia), Finland, France, Germany, Spain and Sweden Inventories. We included the sampling dates; plot type: permanent plots (PP) the years indicate the two campaigns used in the analysis, for temporary plots (TP) the years used in the analysis are indicated. Grid size: indicates the grid dimension in km for each country. Distance between plots: indicates the distance between the plots within the grid. Plot radius: indicates the different radius (m) used within plots to sample trees. Sample tree DBH threshold: indicates the minimum DBH of the trees selected to sample a tree within a plot. N plot: number of plots per country. N trees: number of trees per country

Country	**Belgium-Wallonia**	**Finland**	**Germany**	**Spain**	**Sweden**
Sampling dates and plot type	1994-2003 2008-2011 PP	1985-1986 1995 PP	1986- 1990, West Germany only 2001-2002 (West and East Germany)	1986-1996 1997-2007 PP	2005-2007 2008-2010 TP and PP
Grid size (km)	1x0.5	16x16 or 24x32 depending on the location.	4x4, 2.83x2.83 or 2x2 depending on region	1x1	Vary
Sampling design (Distance between plots)	Single sample plots	Cluster design (100 or 300)	Cluster design (150)	Single sample plots	Cluster design (vary)
Radius (m)	2.25, 4.5, 9, 12, 18	5.64, 9.77	1, 2, 5, 10, 25	5, 10, 15, 25	3.5, 10
Sample tree DBH threshold (cm)	6.4	0	10 (1st) 7 (2nd)	7.5	1
N Plots	1238	2487	29914	48133	11338
N Trees	16011	39263	295029	813464	187561

Table S2: List of species used for modeling tree recruitment, number of plots in each species ranges defined (i.e. core, transition or marginal ranges, the latest divided in leading and trailing edges) and thresholds used to define the margins. Species: species name. Code: code used for each species. NTrees: number of trees. NRecrut: number of recruited trees (and percentage). NPlots: Total number of plots. DE, ES, FI, FR, SW, WA : number of plots by country with DE = Germany, ES = Spain, FI = Finland, SW = Sweden and WA = Wallonia. MT: margin thresholds used for the WPCA. CT: core thresholds used for the WPCA. NC: number of plots containing the species within the core of the species range. TE: Number of plots containing the species within the trailing edge of the species range. LE: number of plots containing the species within the leading edges of the species range. CI (Census interval): Average census interval observed on all the plots in years ; Minimum and maximum census interval are indicated in parenthesis.

Species	**Code**	**NTrees**	**Nrecrut (and %)**	**Nplots**	**DE**	**ES**	**FI**	**SW**	**WA**	**MT**	**CT**	**NC**	**NTE**	**NLE**	**CI**
Abies alba Mill.	ABIALB	16529	4671 (28.26%)	2246	2080	166	0	0	0	0.7	0.6	1893	68	285	13.75 (10-16)
Acer pseudoplatanus L.	ACEPSE	3937	1714 (43.54%)	945	822	36	0	0	87	0.55	0.5	630	24	291	13.46 (6-16)
Alnus glutinosa (L). Gaertn.	ALNGLU	6674	2060 (30.87%)	848	350	209	0	273	16	0.6	0.5	607	197	44	10.33 (4-16)
Betula pendula Roth.	BETPEN	8858	3107 (35.08%)	1475	850	86	207	332	0	0.8	0.6	1364	25	86	11.61 (4-16)
Castanea sativa Mill.	CASSAT	10611	3002 (28.29%)	810	60	733	0	0	17	0.7	0.6	497	280	33	11.07 (7-16)
Fagus sylvatica L.	FAGSYL	78095	19576 (25.07%)	9841	8047	1366	0	74	354	0.7	0.6	8264	174	1403	13.21 (4-16)
Fraxinus excelsior L.	FRAEXC	6769	2529 (37.36%)	1374	1102	133	0	64	75	0.7	0.6	1217	52	105	13.05 (4-16)
Picea abies (L.) H.Karst.	PICABI	221418	57001 (25.74%)	9717	3456	0	968	5293	0	0.8	0.6	5665	3338	714	8.48 (4-16)
Pinus halepensis Mill.	PINHAL	82298	26051 (31.65%)	6482	0	6482	0	0	0	0.7	0.6	5695	557	230	11.37 (2-19)
Pinus nigra J.F.Arnold.	PINNIG	75409	22774 (30.2%)	4280	0	4280	0	0	0	0.7	0.6	3822	417	41	11.2 (4-20)
Pinus pinea L.	PINPIN	27070	6932 (25.61%)	1747	0	1747	0	0	0	0.7	0.6	1292	222	233	10.99 (6-14)
Pinus pinaster Aiton.	PINPINA	151692	40495 (26.7%)	5334	0	5334	0	0	0	0.8	0.6	3713	639	982	11.45 (7-16)
Pinus sylvestris L.	PINSYL	270967	63878 (23.57%)	14976	2461	5392	1414	5709	0	0.8	0.6	9111	5381	484	9.06 (4-20)
Quercus ilex L.	QUEILE	73585	21127 (28.71%)	7897	0	7897	0	0	0	0.8	0.6	5767	1707	423	11.13 (6-20)
Quercus petraea Liebl.	QUEPET	17835	4277 (23.98%)	3040	2480	560	0	0	0	0.7	0.6	2913	95	32	13.27 (9-20)

Quercus pyrenaica Willd.	QUEPYR	31430	9407 (29.93%)	2176	0	2176	0	0	0	0.7	0.6	1696	372	108	10.89 (6-16)
Quercus robur L.	QUEROB	21910	6015 (27.45%)	3177	2148	1029	0	0	0	0.8	0.6	2167	849	161	12.82 (9-16)
Quercus suber L.	QUESUB	23329	3808 (16.32%)	2380	0	2380	0	0	0	0.7	0.6	1887	392	101	11.36 (6-16)

Table S3: Mean, minimum and maximum values of individual-level variables by country. Country: Code of the country with DE = Germany, ES = Spain, FI = Finland, SW = Sweden and WA = Wallonia. DBHall: all individual mean dbh, DBHrecrut: recruited individual mean dbh; CI : Average census interval observed on all individuals in years.

Country	**DBHall**	**DBHrecrut**	**CI**
DE	354.96 (100-1700)	309.76 (100-1625)	13.88 (11-16)
ES	234.47 (0-6248)	204.31 (99.5-1344)	11.28 (2-20)
FI	174.42 (100-617)	124.53 (100-382)	9.41 (5-10)
SW	183.83 (100-987)	115.01 (100-686)	4.48 (4-5)
WA	367.97 (92.29-1292.17)	315.35 (101.84-550.6)	11.33 (6-15)

Table S4: 21 climatic variables averaged over the last 30 years before the first inventory drought-related variables derived from SPEI indices calculated for the *i*th individual plot and climatic marginality categories obtained after the WPCA and DPCA (categories are calculated for the i^{th} individual plot).We include the variable description/name and units/time period. Stars indicate that the variable was used for the calculation of climatic marginality.

Description	**Unit/Time period**
Annual mean temperature*	°C
Mean diurnal temperature range*	°C
Maximal temperature of the warmest month*	°C
Minimal temperature of the coldest month*	°C
Winter mean temperature*	°C
Spring mean temperature*	°C
Summer mean temperature*	°C
Autumn mean temperature*	°C
Annual precipitation*	mm
Precipitation of the wettest month*	mm
Precipitation of the driest month*	mm
Winter precipitation*	mm
Spring precipitation*	mm
Summer precipitation*	mm
Autumn precipitation*	mm
Annual potential evapotranspiration*	mm
Minimal monthly potential evapotranspiration*	mm
Maximal monthly potential evapotranspiration*	mm
Annual water balance*	mm
Minimal monthly water balance*	mm
Maximal monthly water balance	mm
Monthly Standardised Precipitation-Evapotranspiration Index of the last 12 months	Averaged on the time period elapsed between the two-sampling procedure
Climatic trailing edge (TE)	Adimensional
Climatic leading edge (LE)	Adimensional

Table S5: Response and biotic predictors included in the model. These are calculated for the k^{th} individual of the i^{th} plot and the j^{th} species. Name: Abbreviation included the acronym for the variable. Description: Variable description and units. Calculation: equation used for the variable calculation. Transformation: transformation of the variable before inclusion in the model. *CI*: Census interval (in years). *Ba.ha1total:* Total basal area of the plot.

Abbreviation	Description	Calculation	Transformation
R	Response: Species recruitment count at the plot scale (trees ha^{-1})	$= \sum newtrees_{ijk}$	None
M	Predictor: Species mortality rate at the plot scale (trees. ha^{-1} yr^{-1})	$= \frac{\sum deadtrees_{ijk}}{numberoftrees_{ijk}} \times \frac{1}{CI_i}$	Logscaled
G	Predictor: Mean basal area increment of the species in the plot (cm^2 ha^{-1} yr^{-1})	$\frac{1}{N_{ijk}} \times \sum \frac{Ba.ha2_{ijk} - Ba.ha1_{ijk}}{CI_i}$	Square root
DBH	Predictor: Mean diameter at breast height of the species in the plot (cm)	$\frac{1}{N_{ij}} \times \sum dbh_{ijk}$	Logscaled
D	Predictor: Number of trees in the plot (No. trees ha^{-1})	$\sum k_{ij}$	Logscaled
Intra	Predictor: Total basal area of the species in the plot (cm^2 ha^{-1})	$\sum Ba.ha1_{ijk}$	Logscaled
Inter	Predictor: Total basal area of all other species in the plot (cm^2 ha^{-1})	$\sum Ba.ha1_{total} - \sum Ba.ha1_{ijk}$	Square root

Table S6: Mean, standard error, minimum and maximum values of plot-level variables by species. Species: Acronym of the species. R: Recruitment count per hectare; DBH: plot mean dbh, D: plot density. SPEI12: minimum ; Inter: heterospecific basal area of the plot; Intra: conspecific basal area of the plot; G: plot growth rate; M: Annual mortality rate per hectare. Rr: Annual tree recruitment rate per hectare.

Species	**R**	**DBH (cm)**	**D (treesha)**	**SPEI12**	**Inter (cm^{2}ha-1)**	**Intra (cm^{2}ha.1)**	**G (cm^2/ha/y)**	**M (No. trees/ha/yr)**	**Rr (rate/ha/yr)**
ABIALB	74.16 (149.24) 0-1799	384.43 (141.16) 101-1277	5.96 (6.19) 1-75	0.16 (0.13) -0.16-0.55	21.17 (15.37) 0-86.91	15.66 (12.02) 0.41-76	0.09 (0.05) 0-0.34	1.41 (6.72) 0-70	18.93 (20.96) 0-89
ACEPSE	66.27 (182.39) 0-2483	281.59 (119.28) 99.5-751.33	2.57 (2.16) 1-15	0.21 (0.14) -0.38-0.67	21.9 (14.78) 0-88	7.45 (6.09) 0.41-48	0.09 (0.06) 0-0.38	0.95 (5.87) 0-59	12.76 (20.63) 0-129
ALNGLU	89.15 (199.05) 0-1720	224.12 (88.34) 100-710	6.31 (6.6) 1-52	0.26 (0.33) -0.54-1.32	14.3 (12.49) 0-79.04	9.28 (10.4) 0.26-64	0.05 (0.04) 0-0.29	4.4 (14) 0-123	20.81 (31.9) 0-208
BETPEN	55.15 (161.58) 0-2562	234.19 (90.96) 102-646.67	2.53 (2.43) 1-26	0.28 (0.27) -0.52-1.28	17.09 (12.97) 0-70.29	6.16 (6.04) 0.26-40	0.07 (0.05) 0-0.33	2.17 (10.31) 0-125	9.5 (19.26) 0-125
CASSAT	78.67 (169.11) 0-2320	388.51 (251.86) 100-1371	8.85 (8.97) 1-55	0.02 (0.19) -0.54-0.43	11.16 (11.24) 0-71.25	10.48 (13.21) 0.4-102.61	0.04 (0.04) 0-0.7	5.49 (14.93) 0-97	25.46 (28.45) 0-120
FAGSYL	93.67 (180.23) 0-2015	334.55 (149.7) 100-1498	6.71 (7.14) 1-65	0.17 (0.18) -0.54-1.17	14.85 (14.54) 0-112.21	15.49 (11.25) 0.27-90.73	0.08 (0.05) 0-0.58	1.35 (6.79) 0-86	19.29 (21.96) 0-208
FRAEXC	61.69 (156.62) 0-1759	302.23 (129.99) 101-894	3.41 (2.8) 1-33	0.19 (0.18) -0.52-1.22	18.67 (13.96) 0-94.77	9.12 (8.22) 0.26-103.91	0.09 (0.05) 0-0.54	1.37 (8.08) 0-133	15.21 (21.1) 0-130
PICABI	101.81 (211.77) 0-3436	224.9 (112.45) 100-868	10.64 (8.36) 1-69	0.32 (0.32) -0.52-1.33	8.25 (9.43) 0-80.9	15.9 (16.31) 0.25-114.35	0.05 (0.05) 0-0.39	2.54 (10.25) 0-174	27.56 (37.23) 0-234
PINHAL	113.41 (150.47) 0-1369	214.31 (68.56) 99.5-955	10.98 (8.75) 1-69	-0.17 (0.22) -0.71-0.26	1.37 (3.6) 0-39.51	6.16 (5.56) 0.39-39.52	0.03 (0.01) 0-0.11	3.76 (11.93) 0-96	30.79 (24.98) 0-232
PINNIG	117.06 (190.34) 0-2387	237.24 (91.63) 99.5-891.5	12.61 (11.69) 1-87	-0.17 (0.22) -0.46-0.21	3.91 (6.18) 0-47.82	7.91 (8.08) 0.39-56.42	0.02 (0.01) 0-0.11	3.2 (11) 0-98	25.14 (24.83) 0-99
PINPIN	57.69 (120.68) 0-1553	271.71 (107.21)	10.16 (9.32) 1-68	-0.07 (0.17) -0.65-0.28	4.53 (6.54) 0-47.07	6.96 (6.65)	0.03 (0.01) 0-0.14	5.49 (15.44) 0-99	21.15 (23.72) 0-96

		100.5-1101				0.39-52.37			
PINPINA	126.04 (196.91) 0-1945	262.72 (88.48) 99.5-738	20.84 (15.67) 1-97	-0.03 (0.19) -0.65-0.45	3.17 (6.32) 0-60.96	13.73 (11.51) 0.39-68.39	0.03 (0.02) 0-0.13	14.51 (22.25) 0-121	28.29 (24.37) 0-109
PINSYL	95.42 (187.61) 0-2642	234.07 (94.65) 99.5-800	13.1 (13.21) 1-93	0.19 (0.34) -0.54-1.33	6.51 (9.79) 0-100.1	11.9 (11.07) 0.25-76.28	0.03 (0.03) 0-0.46	3.52 (11.55) 0-188	22.39 (32.58) 0-241
QUEILE	95.33 (167.28) 0-1528	264.46 (160.65) 99.5-1522	6.45 (6.19) 1-63	-0.08 (0.19) -0.65-0.45	3.11 (5.77) 0-66.74	4.29 (4.05) 0.39-47.02	0.01 (0.01) 0-0.24	2.54 (10.44) 0-107	24.09 (27.2) 0-132
QUEPET	54.31 (131.6) 0-2244	352.61 (169.16) 100-1686	4.83 (5.4) 1-54	0.14 (0.18) -0.54-0.84	16.15 (12.7) 0-85.9	11.82 (9.35) 0.39-68	0.06 (0.04) 0-0.36	2.16 (8.66) 0-76	13.31 (18.85) 0-93
QUEPYR	147.43 (226.64) 0-1829	256.71 (154.38) 99.5-1321	11.64 (10.44) 1-58	0.03 (0.17) -0.54-0.67	4.88 (8.93) 0-61.73	7.51 (7.67) 0.39-67.27	0.02 (0.01) 0-0.11	4.72 (14.4) 0-97	27.97 (27.31) 0-98
QUEROB	43 (113.46) 0-1934	383.35 (182.62) 99.5-1532	4.94 (5.55) 1-43	0.17 (0.19) -0.54-0.84	17.34 (14.19) 0-104.37	9.78 (8.55) 0.4-58.67	0.06 (0.05) 0-0.39	3.78 (12.54) 0-88	15.09 (21.89) 0-105
QUESUB	41.35 (88.94) 0-905	335.97 (159.15) 99.5-1465	8.74 (7.76) 1-58	-0.06 (0.13) -0.47-0.31	4.45 (6.46) 0-48.38	7.23 (6.31) 0.39-39.43	0.02 (0.01) 0-0.16	3.18 (10.66) 0-88	14.74 (19.99) 0-139

As it is not possible to calculate a Variation Inflation Factor value for models including qualitative variables, we calculated the VIF for the quantitative variables included in the best predictive model for each species. In addition, to quantify the collinearity between climatic variables and the climatic marginality, we calculated the VIF for the marginality index, which is the climatic marginality score we obtained after weighting the PCA scores. In the next following tables, all the scores for each variable is reported.

Table S7 VIF values calculated on the variables included in the best predictive model for each species. For each species, there is one column for each variable that is included in the model. The values reported are the VIF scores calculated.

Species	DBH	D	Marginality	SPEI12	Inter	Intra	G	M
ABIALB	1.4	4.38	1.09	1.17	1.48	3.72	1.45	1.04
ACEPSE	1.52	2.89	1.17	1.08	1.33	2.53	1.6	1.08
ALNGLU	1.52	3.3	1.71	1.16	1.3	3.8	1.64	1.14
BETPEN	1.49	2.78	1.14	1.08	1.33	2.98	1.45	1.16
CASSAT	2.67	5.1	1.29	1.11	1.57	6.16	1.22	1.13
FAGSYL	1.43	4.14	1.07	1.16	1.59	3.01	1.82	1.04
FRAEXC	1.46	3.19	1.18	1.08	1.26	3.48	1.64	1.06
PICABI	3.23	4.42	2.05	1.04	1.21	7.71	1.65	1.06
PINHAL	1.4	6.16	1.06	1.05	1.14	6.32	1.22	1.12
PINNIG	1.73	8.99	1.23	1.4	1.14	9.08	1.37	1.1
PINPIN	1.75	8.51	1.04	1.01	1.32	8.39	1.22	1.11
PINPINA	1.62	7.63	1.09	1.15	1.23	8.08	1.37	1.33
PINSYL	2.52	5.03	1.6	1.44	1.43	4.48	1.18	1.09
QUEILE	2.21	4.9	1.08	1.04	1.16	5.16	1.05	1.06
QUEPET	1.69	4.54	1.22	1.43	1.46	3.85	1.89	1.08
QUEPYR	1.97	7.5	1.09	1.06	1.18	6.98	1.09	1.07
QUEROB	1.62	4.93	3.44	1.22	1.32	4.4	1.99	1.21
QUESUB	2.39	12.07	1.27	1.19	1.18	11.45	1.08	1.06

Table S8: Model adequation tests and simulation tests: Species: Code for the species name. Chi-square (p-value): Statistic and associated p-value of the chi-square test between fitted and observed distribution of regeneration values; Dispersion (p-value): Ratio of standard deviation of observed residuals vs. simulated residuals and associated p-value; Uniformity KS (p-value): one-sample D value of the Kolmogorov-Smirnov testing for uniformity between observed and simulated residuals and associated p-value ; Zero-inflation (p-value): ratio of expected zeros with simulation under H0 = fitted model and the observed zeros and associated p-value; Location of quantiles p-value: associated p-value of the quantiles regression comparing the location of observed VS expected quantiles via qgam; Outliers p-value : tests if the number of observations outside the simulations envelope are larger different than expected

Species	Chi-square (p-value)	Dispersion (p-value)	Uniformity KS (p-value)	Zero-inflation (p-value)	Location of quantiles p-value	Outlier p-value
ABIALB	804068 (0.39)	1.03 (0.79)	**0.34** **(0)**	0.55 (0.29)	**0**	0.66
ACEPSE	196560 (0.37)	1.07 (0.67)	**0.19** **(0)**	0.83 (0.26)	**0**	1
ALNGLU	175536 (0.36)	0.55 (0.17)	**0.07** **(0)**	0.95 (0.84)	**0**	0.43
BETPEN	321550 (0.39)	0.98 (0.95)	**0.13** **(0)**	0.9 (0.27)	**0**	0.63
CASSAT	110160 (0.39)	0.98 (0.96)	**0.12** **(0)**	1.45 (0.33)	**0**	1
FAGSYL	7262658 (0.42)	1.04 (0.56)	**0.27** **(0)**	0.68 (0.54)	**0**	**0.02**
FRAEXC	347622 (0.38)	1.22 (0.39)	**0.23** **(0)**	0.77 (0.29)	**0**	1
PICABI	7141995 (0.42)	0.78 (0.52)	**0.11** **(0)**	0.93 (0.88)	**0**	**0**
PINHAL	1912190 (0.44)	**1.13** **(0)**	**0.04** **(0)**	1 (0.96)	**0**	**0.05**
PINNIG	1164160 (0.43)	**1.16** **(0)**	**0.05** **(0)**	1 (0.97)	**0**	0.38
PINPIN	293496 (0.41)	**1.41** **(0)**	**0.05** **(0)**	0.99 (0.73)	**0**	**0.01**
PINPINA	2629662 (0.41)	**1.26** **(0)**	**0.05** **(0)**	0.99 (0.45)	**0**	**0**
PINSYL	9764352 (0.44)	0.97 (0.9)	**0.04** **(0)**	1.06 (0.78)	**0**	0.11
QUEILE	1310902 (0.46)	**1.1** **(0)**	**0.03** **(0)**	1 (0.82)	**0**	0.12
QUEPET	1009280 (0.41)	0.98 (0.71)	**0.19** **(0)**	0.77 (0.35)	**0**	0.73
QUEPYR	435200 (0.41)	**1.08** **(0.01)**	**0.04** **(0.01)**	1 (0.93)	**0**	1
QUEROB	892737 (0.42)	1.11 (0.54)	**0.08** **(0)**	0.87 (0.46)	**0**	1
QUESUB	299880 (0.44)	**1.25** **(0)**	**0.05** **(0)**	1 (1)	**0**	1

Table S9a: Direct effect and interactions estimates, standard errors (in parenthesis) and significance (stars) for zero inflated part (binomial) of the models for each species (one column by species). Variable: Variable name. Signif: total number of species in which the variable has a significant effect. NA indicates that the variable has not been included in the model.

Species **Variable**	**ABI ALB**	**ACE PSE**	**ALN GLU**	**BET PEN**	**CAS SAT**	**FAG SYL**	**FRA EXC**	**PIC ABI**	**PIN HAL**	**PIN NIG**	**PIN PIN**	**PIN PINA**	**PIN SYL**	**QUE ILE**	**QUE PET**	**QUE PYR**	**QUE ROB**	**QUE SUB**	**Signif**
Intercept	18.98 (16.85)	21.39 (27.2)	12.78 (8.6)	47.69 (12.78) *	-14.34 (7.39) *	17.08 (8.54) *	0.8 (19.11)	21.47 (2.97) *	12.25 (3.35) *	9.93 (4.29) *	2.24 (6.89)	10.04 (5.03) *	13.91 (2.77) *	-0.79 (1.69)	8.15 (9.65)	-5.17 (3.98)	35.74 (9.31) *	11.74 (4.79) *	10
D	-68.72 (4.42) *	-54.66 (9.31) *	-23.73 (1.82) *	-32.07 (2.41) *	-25.84 (2.4) *	-53.34 (1.46) *	-47.8 (3.82) *	-18.25 (0.4) *	-43.02 (1.47) *	-48.01 (2) *	-41.92 (2.56) *	-51.23 (2.39) *	-23.56 (0.47) *	-25.38 (0.62) *	-40.41 (1.66) *	-31.14 (1.72) *	-39.03 (1.68) *	-37.66 (1.9) *	18
DBH	-23.8 (12.33) *	-17.06 (24.34)	-12.88 (8.64)	-42.77 (11.34) *	9.77 (6.41)	-27.56 (5.47) *	2.13 (15.24)	-24.54 (2.44) *	-8.79 (3.19) *	-7.61 (4.11)	-0.36 (6.43)	-8.68 (4.73)	-16.28 (1.81) *	2.76 (1.59)	-11.12 (5.85)	4.73 (3.73)	-34.55 (5.79) *	-9.21 (4.58) *	8
G	0.79 (3.79)	0.2 (6.58)	-1.68 (1.64)	-0.12 (2.32)	6.19 (2.98) *	1.98 (1.45)	-3.08 (4.14)	-1.84 (0.36) *	-0.32 (0.78)	1.01 (0.93)	0.91 (1.66)	1.07 (1.26)	-0.62 (0.3) *	-0.21 (0.59)	-0.06 (1.82)	1.87 (1.27)	-1.72 (2.11)	-0.22 (1.09)	3
M	0.38 (0.26)	0.1 (0.37)	0.45 (0.25)	0.33 (0.24)	-0.8 (0.79)	0.15 (0.07) *	-0.08 (0.22)	0.04 (0.06)	0.52 (0.08) *	0.45 (0.09) *	0.46 (0.17) *	0.5 (0.14) *	0.1 (0.06)	0.29 (0.07) *	0.09 (0.12)	0.4 (0.14) *	0.04 (0.19)	0.3 (0.12) *	8
Intra	68.61 (11.85) *	36.1 (18.96)	30.32 (6.24) *	9.89 (6.77)	60.97 (10.21) *	39.31 (4.68) *	43.94 (11.44) *	7.04 (1.5) *	42.08 (4.01) *	61.03 (4.91) *	61.45 (7.42) *	78.71 (6.67) *	26.02 (1.46) *	28.7 (1.87) *	45.9 (5.02) *	43.93 (4.58) *	33.2 (5.11) *	51.89 (5.08) *	16
Inter	-9.78 (6.69)	11.64 (20.8)	-12.28 (5.14) *	-15.6 (6.43) *	4.17 (4.51)	-7.34 (2.38) *	3.87 (9.4)	-4.54 (1.06) *	4 (1.74) *	-1.69 (1.99)	2.12 (3.31)	-3.23 (2.04)	-8.61 (0.87) *	-2.34 (1) *	-11.51 (3.15) *	-2.2 (2.08)	-17.42 (3.48) *	-1.66 (2.28)	9
SPEI	13.02 (7.42)	-36.25 (23.98)	0.06 (1.63)	4.01 (2.75)	5.01 (3.33)	-7.28 (2.42) *	-8.31 (5.6)	0.16 (0.31)	0.53 (0.86)	-0.4 (1.23)	-0.23 (2.62)	1.61 (1.5)	-0.53 (0.34)	0.71 (0.7)	5.57 (3.19)	1.58 (2.04)	-0.3 (2.78)	1.37 (2.86)	1

Leading edge (LE)	8.89 (3.78) *	16.75 (8) *	3.29 (3.26)	0.6 (2.64)	0.07 (7.07)	-0.56 (1.72)	1.12 (2.64)	-0.16 (0.52)	-1.29 (2.11)	-9.78 (10.55)	-1 (2.24)	-0.65 (1.81)	-0.38 (0.7)	-1.32 (1)	-8.96 (14.46)	-1.68 (2.2)	0.16 (3)	1.81 (2.24)	2
Trailing edge (TE)	2.74 (14.62)	-9.86 (9.32)	-4.12 (2.25)	3.54 (17.55)	1.44 (1.99)	21.08 (3.8) *	5.56 (9.97)	0.8 (0.71)	0.41 (1.2)	0.99 (1.31)	1.47 (2.24)	0.61 (1.69)	0.85 (0.43) *	-0.98 (0.56)	3.3 (4.02)	1.8 (1.4)	-4.38 (1.98) *	3.04 (1.4) *	4
LE x M	-0.47 (0.63)	0.24 (0.53)	1.24 (0.77)	NA	5.58 (4.66)	-0.44 (0.17) *	NA	0.53 (0.14) *	0.13 (0.36)	NA	0.48 (0.42)	0.84 (0.37) *	0.07 (0.22)	0.4 (0.34)	NA	-0.68 (0.54)	1.02 (0.43) *	-0.59 (0.48)	4
TE x M	-0.16 (1.49)	-10.23 (154.54)	0.09 (0.41)	NA	2.31 (0.93) *	3.67 (1.21) *	NA	-0.03 (0.09)	-0.59 (0.34)	NA	0.71 (0.38)	0.68 (0.44)	0.18 (0.09) *	-0.03 (0.11)	NA	0.25 (0.28)	0.28 (0.26)	0.25 (0.4)	3
LE x G	-1.86 (2.53)	-5.12 (3.37)	0.63 (3.05)	-1.27 (2.96)	3.51 (5.45)	0.77 (0.88)	-1.8 (2.82)	0.6 (0.48)	1.26 (1.5)	10.51 (8.03)	1.3 (1.7)	0.64 (1.26)	0 (0.56)	1.25 (0.92)	5.78 (6.39)	0.46 (1.8)	-1.59 (2.23)	0.15 (1.38)	0
TE x G	1.87 (5.58)	-9.63 (4.43) *	1.14 (1.87)	0.06 (7.89)	-4.39 (2.38)	-11.22 (5.05) *	-8.04 (7.13)	1.28 (0.35) *	-1.83 (1.1)	0.22 (1.04)	-1.18 (1.63)	-1.25 (1.66)	-0.24 (0.25)	1.22 (0.51) *	1.34 (4)	-1.29 (1.36)	2.03 (1.31)	-1.99 (0.95) *	5
LE x SPEI	6.95 (4.73)	-0.21 (6.8)	-1.09 (2.67)	-4.76 (3.98)	-22.16 (32.3)	0.3 (1.35)	6.93 (4.56)	-0.22 (0.47)	1.45 (2.74)	-12.84 (14.59)	-1.63 (2.55)	-1.91 (2.36)	0.17 (0.6)	0.62 (1.46)	-24.44 (17.11)	1.25 (2.14)	-8.33 (3.36) *	-0.04 (3.02)	1
TE x SPEI	18.5 (25.33)	4.73 (18.68)	1.59 (1.44)	27.02 (29.52)	-2.58 (2.69)	14.13 (5.44) *	26.39 (5.66) *	-0.49 (0.42)	-1.3 (0.92)	0.63 (1.98)	-0.35 (2.11)	1.35 (1.6)	-0.4 (0.32)	-0.74 (0.62)	-14.16 (7.11) *	1.09 (1.98)	-3.19 (1.38) *	-2.11 (1.98)	4
LE x Intra	-12.49 (3.18) *	-5.04 (3.78)	-3.91 (1.67) *	1.16 (1.81)	-6.63 (10.12)	-0.67 (0.85)	0.48 (1.65)	-1.22 (0.37) *	-0.95 (1.35)	2.52 (3.86)	-0.52 (1)	-0.75 (0.99)	-0.66 (0.55)	0.09 (0.61)	6.53 (11.41)	1.41 (0.97)	2.92 (1.68)	-0.48 (1.23)	3
TE x Intra	-6.69 (10.98)	16.45 (4.67) *	3.89 (1.18) *	-1.18 (6.44)	0.16 (1.21)	-22.73 (4.74) *	10.64 (4.25) *	-1.84 (0.33) *	1.09 (0.68)	-0.47 (0.64)	-0.04 (1)	-0.02 (0.98)	-0.3 (0.22)	0.23 (0.35)	-0.62 (2.5)	-0.48 (0.83)	6.32 (1.16) *	-1.76 (1.11)	6

LE x Inter	2.87 (1.54)	-3.51 (3.03)	-1.12 (1.34)	-0.16 (1.84)	2.34 (2.92)	1.09 (0.38) *	-0.79 (1.73)	0.47 (0.28)	0.2 (0.48)	-0.13 (1.08)	0.06 (0.55)	0.48 (0.31)	0.7 (0.3) *	-0.07 (0.29)	3.59 (5.54)	0.42 (0.67)	2.56 (1.24) *	-0.49 (0.6)	3
TE x Inter	-1.42 (4.94)	12.71 (4.53) *	1.19 (1.11)	-3.97 (10.76)	0.8 (0.91)	-3.64 (2.64)	-6 (6.96)	0.04 (0.21)	-0.22 (0.52)	-0.52 (0.34)	-0.64 (0.68)	0.75 (0.41)	-0.01 (0.14)	0.18 (0.25)	-3.07 (2.09)	-0.12 (0.51)	1.47 (0.7) *	0.39 (0.54)	2
DBH x Intra	9.28 (9.79)	13.35 (13.83)	-9.46 (5.89)	20.72 (7) *	-33.16 (7.42) *	17.32 (3.88) *	1.01 (9.04)	9.09 (1.64) *	-11.88 (3.41) *	-23.44 (3.91) *	-30.3 (5.99) *	-37 (5.25) *	-6.68 (1.36) *	-9.77 (1.52) *	-0.8 (4.21)	-20.15 (3.6) *	8.54 (3.94) *	-21.36 (4.13) *	13
DBH x Inter	6.3 (5.93)	-11.51 (17.31)	13.31 (5.27) *	14.35 (5.94) *	-3.7 (4.1)	5.97 (2.04) *	-2.94 (8.09)	5.02 (1.1) *	-3.99 (1.67) *	1.49 (1.92)	-1.77 (3.2)	3.39 (1.92)	8.65 (0.86) *	2.64 (0.96) *	9.88 (2.8) *	2.4 (1.93)	13.61 (2.91) *	1.84 (2.28)	9
Intra x G	-9.36 (2.78) *	-1.44 (4.21)	-2.35 (1.16) *	-1.74 (1.4)	-8.96 (2.74) *	-6.19 (1.06) *	-1.03 (2.36)	-1.98 (0.33) *	-1.4 (0.86)	-4.4 (0.92) *	-2.35 (1.37)	-3.53 (1.29) *	-2.25 (0.28) *	-2.86 (0.63) *	-4.74 (1.34) *	-3.55 (1.26) *	-6.04 (1.44) *	-1.98 (0.94) *	13
Inter x G	3.03 (1.61)	-2.07 (5.19)	-0.44 (0.93)	0.79 (1.32)	-2.37 (1.64)	0.65 (0.58)	-0.82 (1.91)	-0.07 (0.22)	0.11 (0.42)	0.14 (0.46)	-0.4 (0.76)	-0.4 (0.5)	0.46 (0.14) *	-0.32 (0.32)	1.63 (0.79) *	0.31 (0.72)	2.63 (0.83) *	-0.18 (0.54)	3
SPEI x Intra	-7.18 (4.98)	22.94 (12.69)	-1.35 (1.13)	-3.44 (1.64) *	-1.93 (2.84)	5 (1.67) *	6.62 (3.59)	0.75 (0.26) *	0.04 (0.86)	0.51 (1.09)	0.39 (1.97)	-1.48 (1.42)	0.93 (0.3) *	-0.84 (0.67)	-3.63 (2.23)	-0.22 (1.67)	1.59 (1.75)	0.04 (2.38)	4
SPEI x Inter	-6.05 (2.98) *	5.5 (11.71)	0.44 (1.11)	2.85 (2.18)	-3.7 (2.11)	0.23 (0.92)	-1.15 (3.2)	-0.61 (0.21) *	-0.41 (0.41)	-0.46 (0.59)	0.38 (1.25)	0 (0.66)	0.26 (0.22)	-0.7 (0.37)	-0.73 (1.38)	-1.57 (0.98)	-0.17 (1.22)	0.07 (1.23)	2

Table S9b Direct effect and interactions estimates, standard errors (in parenthesis) and significance (stars) for conditional (negative binomial) part of the models for each species (one column by species). Variable: Variable name. Signif: total number of species in which the variable has a significant effect. NA indicates that the variable has not been included in the model.

Species Variable	ABI ALB	ACE PSE	ALN GLU	BET PEN	CAS SAT	FAG SYL	FRA EXC	PIC ABI	PINH AL	PIN NIG	PIN PIN	PIN PINA	PIN SYL	QUE ILE	QUE PET	QUE PYR	QUE ROB	QUE SUB	Signif
Intercept	-5.67 (0.93) *	-5.56 (1.83) *	-4.16 (0.95) *	-4.94 (1.44) *	-6.42 (0.9) *	-4.45 (0.52) *	-7.84 (1.08) *	-5.1 (0.28) *	-6.7 (0.28) *	-5.32 (0.45) *	-9.37 (0.74) *	-6.54 (0.38) *	-6.38 (0.25) *	-5.4 (0.32) *	-4.32 (0.68) *	-4.59 (0.49) *	-1.63 (0.69) *	-7.4 (0.87) *	18
D	1.54 (0.09) *	0.46 (0.07) *	0.68 (0.08) *	0.82 (0.09) *	0.42 (0.11) *	1.43 (0.04) *	1.32 (0.08) *	1.18 (0.03) *	1.33 (0.04) *	1.13 (0.05) *	2.07 (0.1) *	1.09 (0.04) *	1.11 (0.03) *	0.84 (0.03) *	1.47 (0.08) *	1.02 (0.07) *	0.94 (0.07) *	2.22 (0.13) *	18
DBH	3.9 (0.8) *	3.26 (1.5) *	2.64 (0.96) *	3.2 (1.44) *	3.58 (0.8) *	2.19 (0.33) *	4.65 (0.92) *	3.36 (0.26) *	4.54 (0.27) *	3.39 (0.42) *	7.28 (0.69) *	4.71 (0.34) *	4.85 (0.24) *	3.17 (0.33) *	2.48 (0.57) *	2.93 (0.48) *	1.02 (0.56)	5.51 (0.87) *	17
G	-0.66 (0.22) *	-0.29 (0.38)	-0.62 (0.21) *	-0.76 (0.23) *	0.86 (0.29) *	-0.77 (0.08) *	-0.02 (0.26)	-0.62 (0.05) *	-0.77 (0.07) *	-0.8 (0.11) *	-1.17 (0.18) *	-0.99 (0.11) *	-0.64 (0.04) *	-0.57 (0.07) *	-0.62 (0.15) *	-1.06 (0.14) *	-1.24 (0.19) *	-1.05 (0.14) *	16
M	0.02 (0.03)	0.01 (0.02)	0.15 (0.03) *	0.07 (0.03) *	0.16 (0.05) *	0.05 (0.01) *	0.04 (0.02) *	0 (0.01)	0.06 (0.01) *	0.03 (0.01) *	0.07 (0.02) *	0.09 (0.01) *	-0.01 (0.01)	0.05 (0.01) *	0.02 (0.02)	0 (0.02)	0.05 (0.02) *	0.07 (0.02) *	12
Intra	-3.84 (0.72) *	0.06 (1.27)	-1.76 (0.73) *	-1.16 (1.09)	-0.25 (0.63)	-3.84 (0.28) *	-1 (0.74)	-1.83 (0.21) *	0.64 (0.29) *	-1.02 (0.4) *	1.27 (0.62) *	0.44 (0.36)	0.02 (0.19)	-0.11 (0.3)	-3.2 (0.51) *	-1.35 (0.43) *	-4.56 (0.56) *	-1.87 (0.68) *	11
Inter	-0.04 (0.49)	-0.88 (1.06)	-0.38 (0.7)	-0.9 (0.8)	0.97 (0.61)	-0.91 (0.19) *	0.12 (0.56)	-0.78 (0.15) *	0 (0.22)	-0.38 (0.3)	0.17 (0.5)	-0.3 (0.24)	-0.63 (0.18) *	0.32 (0.21)	-0.87 (0.34) *	-0.47 (0.36)	-1.52 (0.34) *	-0.53 (0.46)	5
SPEI	0.12 (0.43)	-0.14 (0.57)	0.15 (0.22)	0.25 (0.38)	-0.88 (0.53)	0.75 (0.15) *	-1.03 (0.37) *	0.09 (0.06)	0.13 (0.07)	0.1 (0.11)	-0.26 (0.21)	-0.09 (0.12)	0.17 (0.05) *	-0.02 (0.09)	0.42 (0.32)	-0.2 (0.2)	-1.12 (0.31) *	0.63 (0.5)	4

Leading edge (LE)	0.42 (0.29)	1.01 (0.28) *	0.47 (0.79)	-0.36 (0.37)	0.85 (1.08)	-0.1 (0.13)	0.57 (0.33)	0.1 (0.14)	-0.06 (0.24)	-0.08 (0.83)	0.5 (0.42)	-0.52 (0.13) *	-0.06 (0.19)	0.04 (0.1)	-0.37 (1.64)	-0.07 (0.51)	-0.81 (0.28) *	-0.24 (0.45)	3
Trailing edge (TE)	-0.71 (0.79)	1.15 (1.19)	-1.74 (0.33) *	-2.42 (1.02) *	0.38 (0.25)	0.69 (0.44)	0.95 (0.96)	0.48 (0.1) *	-0.39 (0.12) *	0.3 (0.22)	0.75 (0.28) *	0.12 (0.18)	-0.58 (0.05) *	0.32 (0.12) *	0.11 (0.45)	0.36 (0.2)	-1.26 (0.23) *	-0.19 (0.33)	8
LE x M	0.1 (0.08)	0.14 (0.11)	-0.17 (0.25)	NA	0 (0.26)	-0.02 (0.03)	NA	0.04 (0.03)	0 (0.04)	NA	0.1 (0.07)	0.12 (0.03) *	0.09 (0.07)	-0.01 (0.03)	NA	0.02 (0.11)	0.01 (0.07)	-0.06 (0.11)	1
TE x M	0.16 (0.11)	0.12 (0.08)	-0.09 (0.07)	NA	0.08 (0.09)	-0.01 (0.05)	NA	0.05 (0.02) *	-0.08 (0.03) *	NA	-0.12 (0.06) *	-0.1 (0.03) *	0.04 (0.01) *	0.02 (0.03)	NA	0 (0.04)	0.01 (0.03)	0.09 (0.1)	5
LE x G	-0.52 (0.28)	-0.45 (0.14) *	-0.46 (0.57)	0.5 (0.34)	-1.34 (0.69) *	-0.04 (0.07)	-0.58 (0.24) *	-0.06 (0.06)	0.12 (0.19)	0.15 (0.6)	0.02 (0.33)	0.3 (0.11) *	-0.01 (0.12)	-0.02 (0.11)	-0.12 (0.86)	0.2 (0.38)	0.03 (0.22)	0.2 (0.29)	4
TE x G	0.5 (0.37)	-0.48 (0.54)	0.71 (0.32) *	0.89 (0.61)	-0.21 (0.23)	-0.06 (0.44)	-1.17 (0.92)	-0.24 (0.04) *	0.21 (0.11)	0.06 (0.17)	-0.21 (0.2)	0.07 (0.17)	-0.02 (0.03)	-0.22 (0.11)	0.18 (0.48)	-0.15 (0.16)	0.52 (0.15) *	0.42 (0.24)	3
LE x SPEI	0.43 (0.38)	-0.34 (0.42)	0 (0.83)	-0.14 (0.86)	-0.73 (4.72)	0.34 (0.14) *	0.87 (0.46)	-0.25 (0.11) *	0.43 (0.25)	-0.88 (1.34)	0.04 (0.52)	0.55 (0.19) *	-0.16 (0.14)	0.03 (0.15)	-1.24 (2.74)	0.63 (0.41)	0.07 (0.33)	0.53 (0.63)	3
TE x SPEI	-0.8 (1.01)	0.01 (1.62)	0.52 (0.26) *	-4.51 (1.61) *	-0.51 (0.43)	0.33 (0.21)	1.85 (0.61) *	-0.27 (0.06) *	-0.22 (0.09) *	-0.06 (0.27)	0.61 (0.22) *	0.41 (0.13) *	0.1 (0.04) *	0.07 (0.14)	-0.48 (0.76)	0.11 (0.26)	0.32 (0.18)	-0.62 (0.45)	8
LE x Intra	-0.14 (0.15)	-0.26 (0.14)	-0.09 (0.39)	-0.24 (0.22)	-0.2 (0.46)	0.07 (0.07)	0.04 (0.16)	0.08 (0.07)	-0.02 (0.09)	-0.03 (0.22)	-0.48 (0.18) *	0.06 (0.06)	0.24 (0.14)	0.02 (0.04)	0.71 (1.61)	-0.03 (0.2)	0.5 (0.16) *	0.1 (0.24)	2
TE x Intra	0.21 (0.31)	-0.52 (0.49)	0.73 (0.16) *	0.6 (0.42)	-0.38 (0.15) *	-0.43 (0.21) *	0.02 (0.44)	0.06 (0.04)	0.22 (0.06) *	-0.32 (0.09) *	-0.29 (0.1) *	-0.14 (0.07) *	0.43 (0.03) *	-0.14 (0.08)	-0.24 (0.21)	-0.24 (0.09) *	0.72 (0.13) *	-0.28 (0.21)	10

LE x Inter	-0.03 (0.13)	-0.05 (0.12)	-0.08 (0.33)	0.29 (0.24)	0.31 (0.34)	0.04 (0.04)	-0.25 (0.15)	0.01 (0.06)	-0.06 (0.05)	0 (0.15)	-0.23 (0.1) *	0.03 (0.04)	-0.2 (0.08) *	-0.02 (0.04)	0.22 (0.44)	-0.08 (0.14)	0.23 (0.13)	0.02 (0.16)	2
TE x Inter	-0.14 (0.2)	0.04 (0.42)	0.36 (0.16) *	1.33 (0.48) *	0.02 (0.14)	-0.15 (0.17)	-0.05 (0.52)	-0.23 (0.03) *	-0.07 (0.06)	-0.03 (0.06)	-0.23 (0.09) *	0.01 (0.05)	0.03 (0.03)	0.02 (0.06)	-0.25 (0.21)	0.08 (0.08)	0.24 (0.08) *	-0.13 (0.12)	5
DBH x Intra	-0.14 (0.66)	-1.96 (1.08)	-1.02 (0.75)	-1.33 (1.05)	-0.81 (0.65)	0.07 (0.27)	-1.89 (0.66) *	-1.73 (0.21) *	-3.64 (0.28) *	-2.1 (0.38) *	-5.13 (0.58) *	-4.14 (0.33) *	-3.48 (0.2) *	-2.12 (0.31) *	-0.48 (0.49)	-1.57 (0.42) *	0.57 (0.48)	-2.33 (0.67) *	10
DBH x Inter	-0.18 (0.43)	0.52 (0.88)	0.4 (0.69)	0.32 (0.77)	-1.13 (0.56) *	0.72 (0.17) *	0.04 (0.48)	0.59 (0.15) *	-0.01 (0.22)	0.3 (0.29)	-0.29 (0.47)	0.24 (0.22)	0.48 (0.17) *	-0.42 (0.22) *	0.55 (0.32)	0.09 (0.38)	1.01 (0.3) *	0.21 (0.48)	6
Intra x G	1.34 (0.16) *	0.62 (0.24) *	1.08 (0.16) *	0.75 (0.18) *	-0.56 (0.26) *	1.34 (0.06) *	0.75 (0.17) *	1.18 (0.04) *	1.29 (0.07) *	1.45 (0.09) *	1.46 (0.14) *	2.16 (0.11) *	1.13 (0.04) *	1 (0.07) *	0.84 (0.13) *	1.5 (0.13) *	1.49 (0.14) *	1.18 (0.14) *	18
Inter x G	0.1 (0.11)	0.18 (0.22)	-0.02 (0.16)	0.43 (0.13) *	0.01 (0.17)	0.19 (0.04) *	-0.22 (0.14)	0.22 (0.03) *	-0.03 (0.05)	0.04 (0.07)	0.22 (0.12)	0.01 (0.07)	0.09 (0.03) *	0.07 (0.05)	0.25 (0.08) *	0.31 (0.11) *	0.33 (0.08) *	0.32 (0.09) *	8
SPEI x Intra	-0.67 (0.35)	0.05 (0.43)	0.01 (0.15)	-0.29 (0.25)	0.3 (0.36)	-0.63 (0.12) *	0.55 (0.26) *	-0.13 (0.06) *	0.09 (0.07)	0.09 (0.09)	-0.05 (0.17)	-0.08 (0.11)	-0.21 (0.05) *	0.17 (0.08) *	-0.27 (0.26)	0.13 (0.15)	0.79 (0.22) *	-0.43 (0.42)	6
SPEI x Inter	0.26 (0.23)	0.09 (0.32)	-0.26 (0.17)	0.11 (0.22)	0.49 (0.34)	-0.3 (0.08) *	0.4 (0.21)	0.1 (0.05) *	-0.09 (0.05)	0.1 (0.08)	0.49 (0.17) *	0.16 (0.08) *	0.1 (0.05) *	0.12 (0.06) *	-0.1 (0.16)	-0.12 (0.15)	0.16 (0.15)	-0.16 (0.24)	6

Annexes 7: Supplementary figures of chapter 5

Figure S1: Model verification for the absolute stand basal area model, *Quercus Rubra* with test of linearity,, homogeneity of variance, collinearity, outliers and normality of residuals

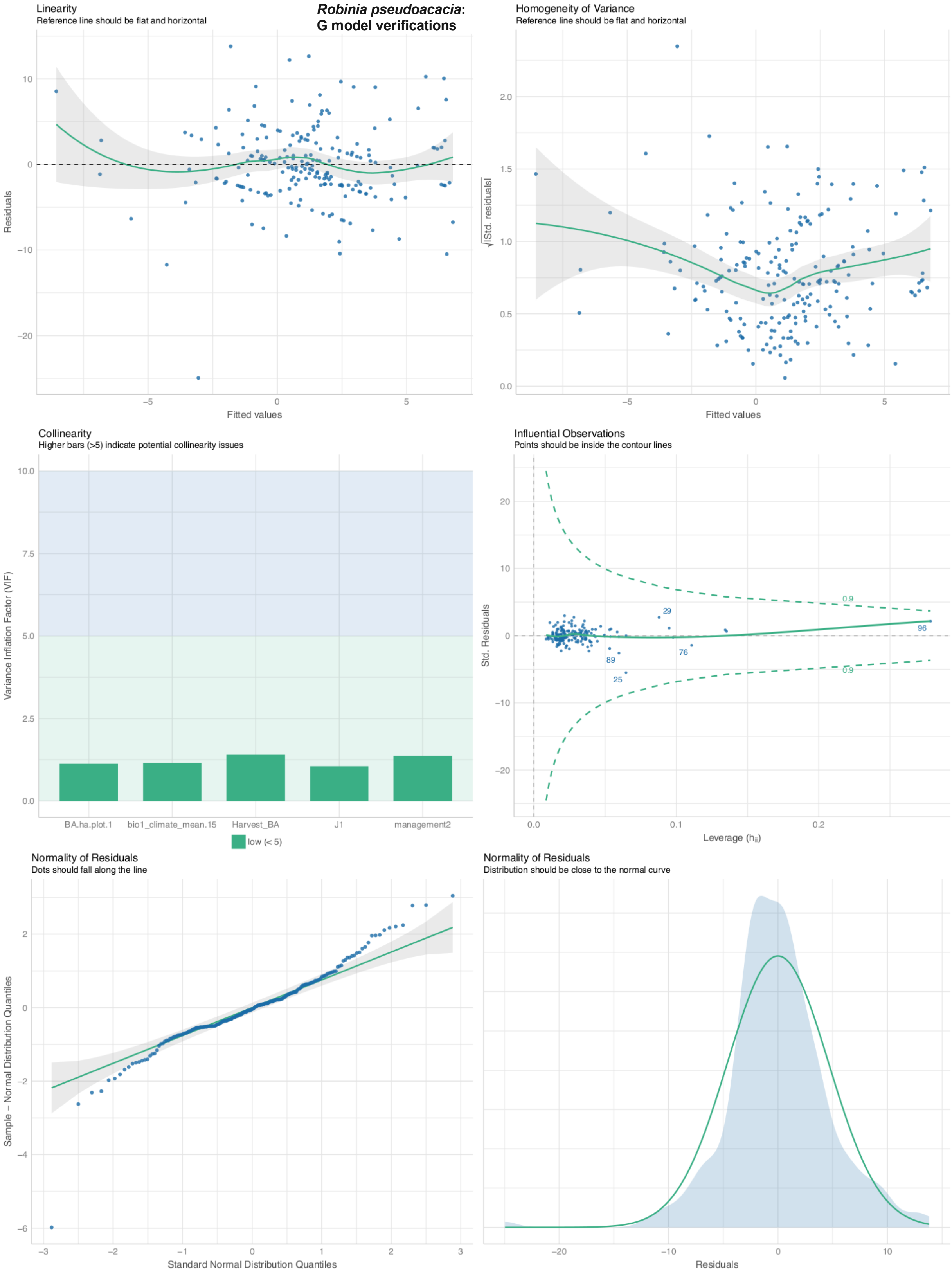


Figure S2: Model verification for the absolute stand basal area model, *Robinia pseudoacacia* with test of linearity,, homogeneity of variance, collinearity, outliers and normality of residuals

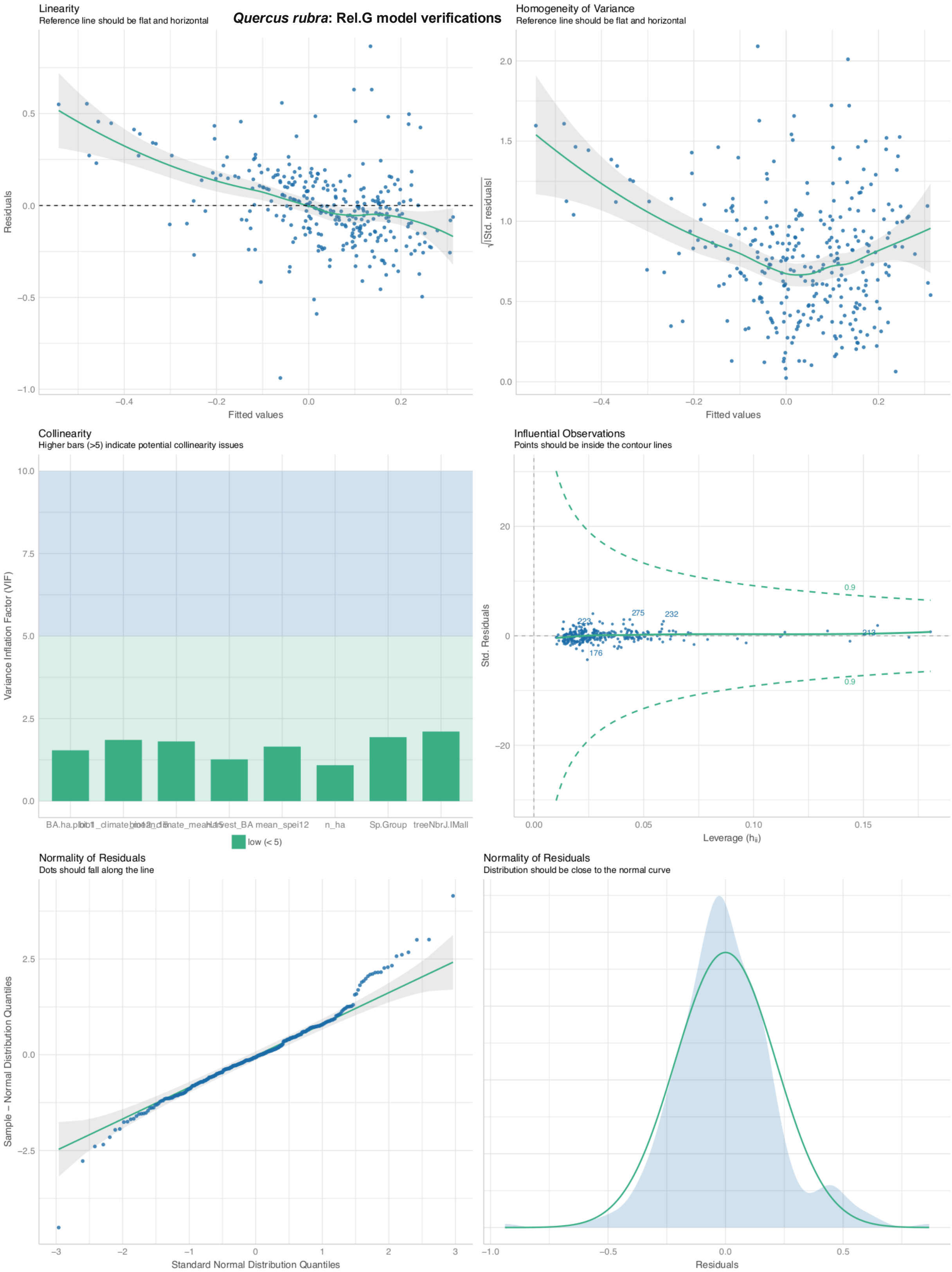


Figure S3: Model verification for the relative stand basal area model, *Quercus Rubra* with test of linearity,, homogeneity of variance, collinearity, outliers and normality of residuals

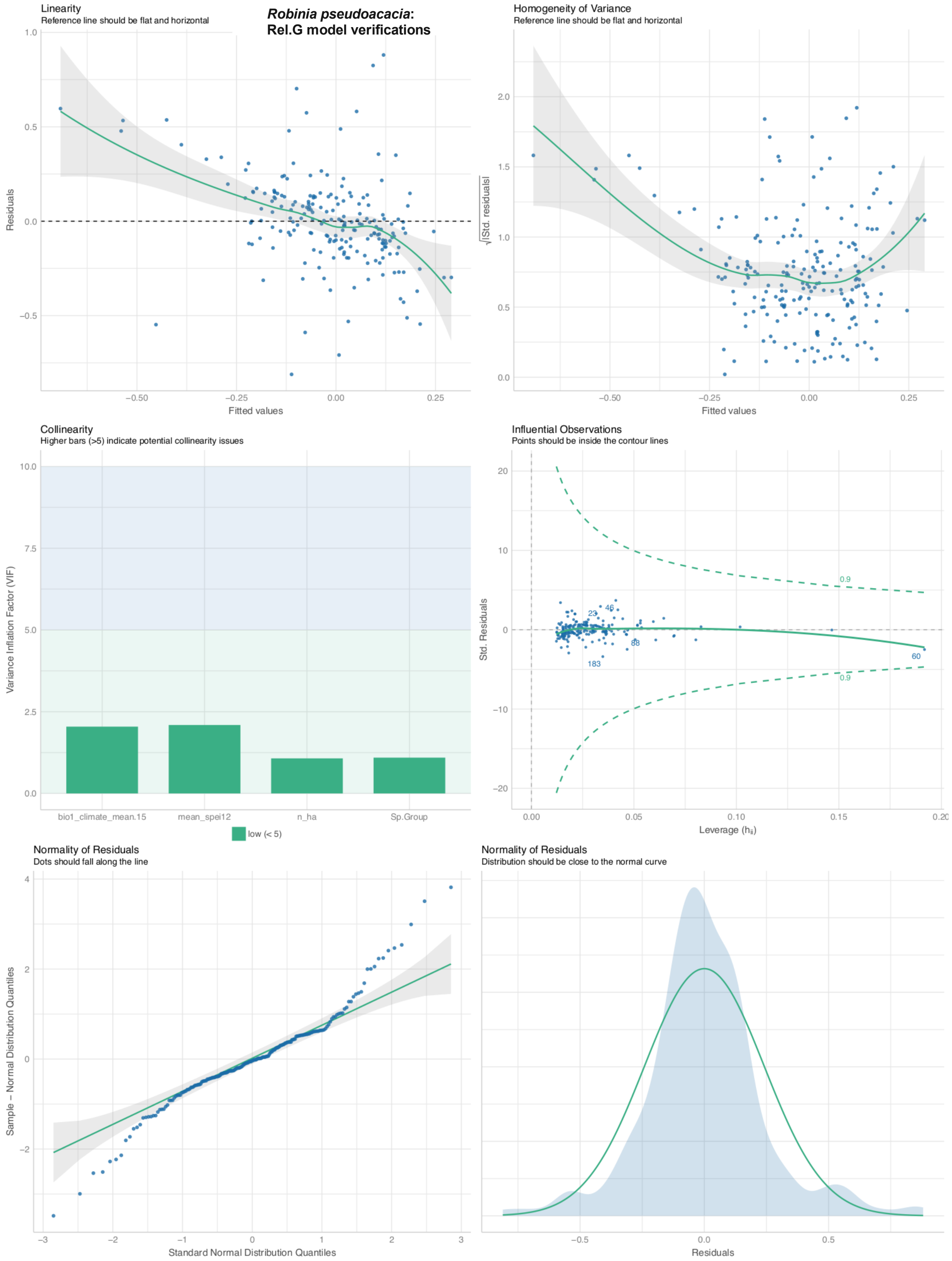


Figure S4: Model verification for the relative stand basal area model, *Robinia pseudoacacia* with test of linearity,, homogeneity of variance, collinearity, outliers and normality of residuals

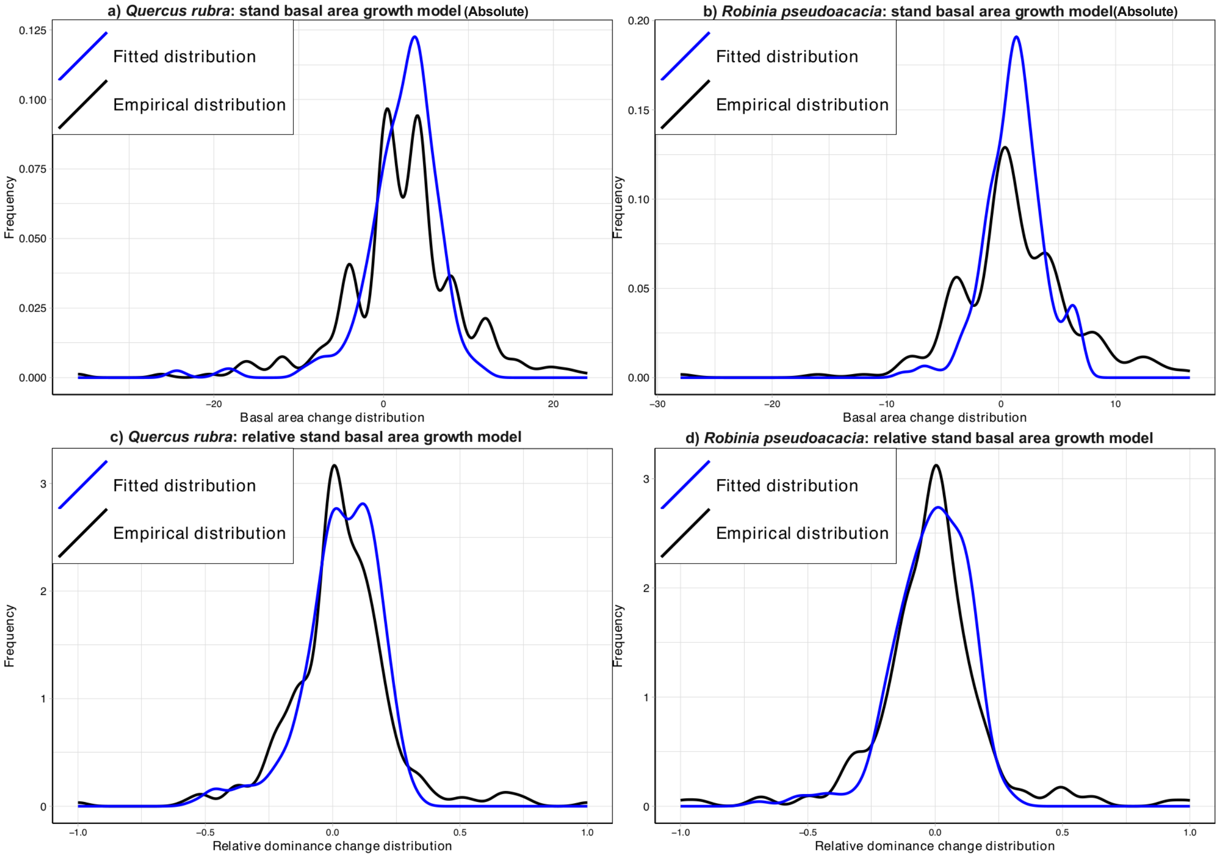


Figure S5: Distribution of observed VS fitted values of Absolute basal area growth for a) *Quercus rubra* and b)*Robinia pseudoacacia*; Relative basal area growth for c) *Quercus rubra* and d)*Robinia pseudoacacia*

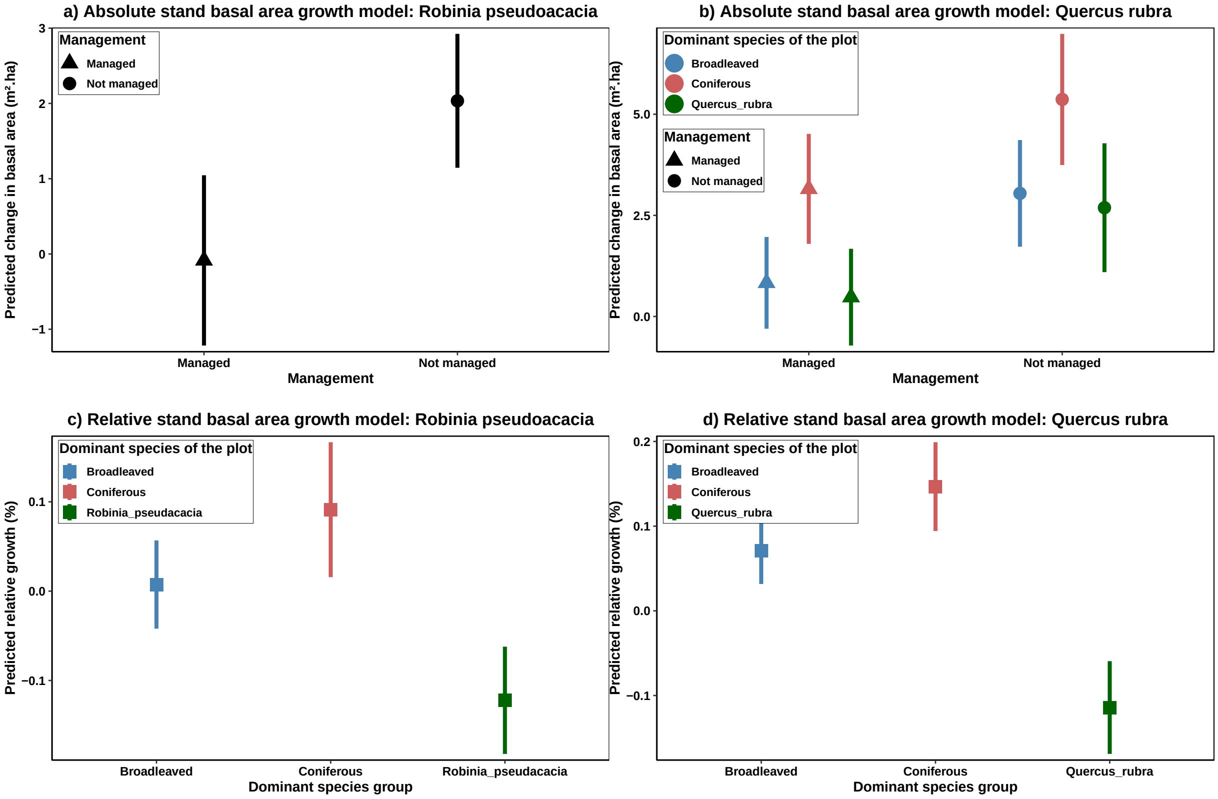


Figure S6: a) *Quercus rubra* and b) *Robinia pseudoacacia* absolute stand basal area response to management and dominant species of the plot. c) *Quercus rubra* and d) *Robinia pseudoacacia* relative stand basal area response to dominant species of the plot

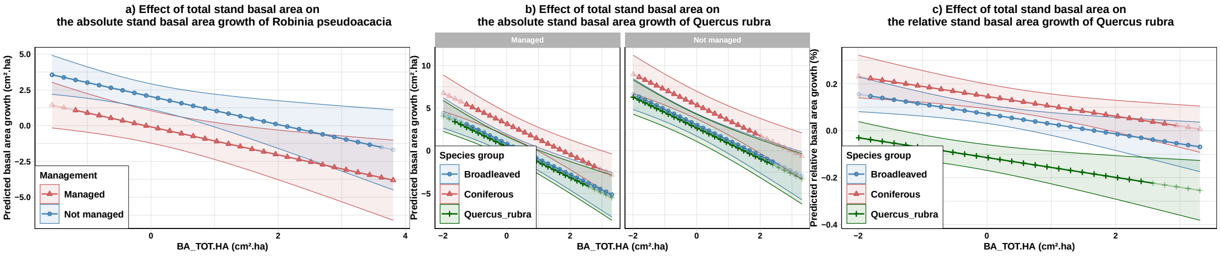


Figure S7: a) *Robinia pseudoacacia* and b) *Quercus rubra* absolute stand basal area response to the total basal area of the plot. c) *Quercus rubra* relative stand basal area response to total basal area of the plot

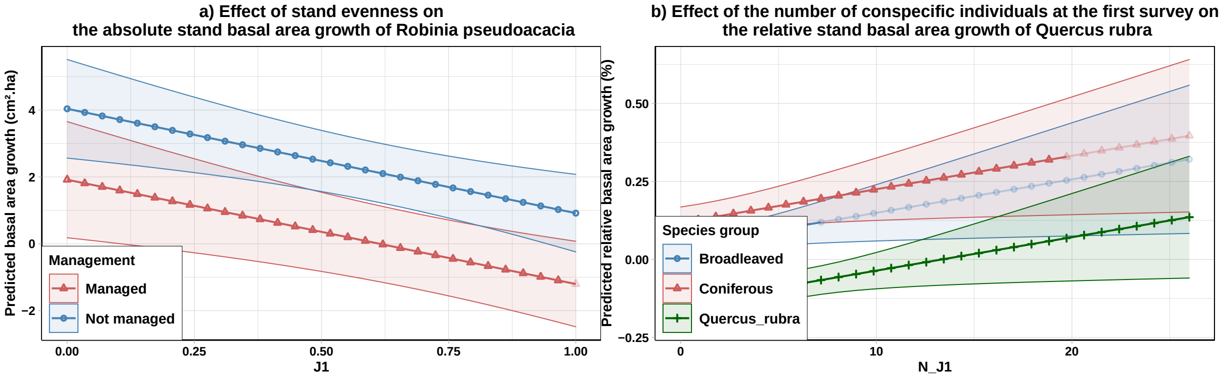


Figure S8: a) *Robinia pseudoacacia* absolute stand basal area response to evenness J1. b) *Quercus rubra* relative stand basal area response to the number of conspecific individual present in the plot at the first survey (SPEI)

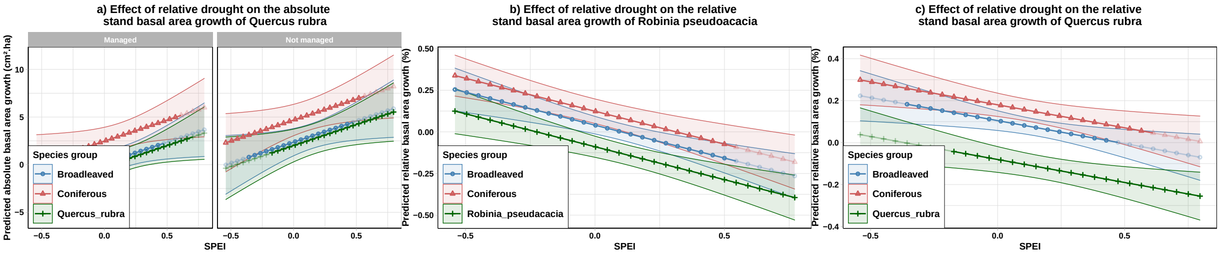


Figure S9: a) *Quercus rubra* absolute stand basal area response to drought index (SPEI). b) *Robinia pseudoacacia* and c) *Quercus rubra* relative stand basal area response to drought index (SPEI)

Annexes 8: Supplementary tables of chapter 5

Supplementary Information

National Forest Inventories harmonization

The sample plot design was different among countries. For instance, the Spanish National Inventory recorded single sample plots in a 1 km by 1 km grid whereas the Finnish National Inventory followed a cluster design, with number and grid size depending on location while the German NFI used a 4 x 4 km quadrangle grid where the samples lied on the intersection points. Most NFIs followed a nested circular subplot design whose radius differs among NFI and within which trees of different size classes were monitored. The main differences among inventories are summarized in Table S1.

Table S1: Summary of information of the NFI design for each country: Belgium (Wallonia), Finland, France, Germany, Spain and Sweden Inventories. We included the sampling dates; plot type: permanent plots (PP) the years indicate the two campaigns used in the analysis, for temporary plots (TP) the years used in the analysis are indicated. Grid size: indicates the grid dimension in km for each country. Distance between plots: indicates the distance between the plots within the grid. Plot radius: indicates the different radius (m) used within plots to sample trees. Sample tree DBH threshold: indicates the minimum DBH of the trees selected to sample a tree within a plot. N plot: number of plots per country. N trees: number of trees per country. Not managed plot: plot with evidence of management before the second census. Managed plot: plot with evidence of management before the second census. Ingrowth trees: trees present and alive in first and second census. Recruit trees: trees absent in the first census but present in the second census. Dead (managed): trees that were present at the first census but that were removed in the second census. (logging). Dead (natural): trees that were present at the first census but that were found dead in the second census.

Country	**Belgium-Wallonia**	**Finland**	**France**	**Germany**	**Spain**	**Sweden**
Sampling dates and plot type	1994-2003 2008-2011 PP	1985-1986 1995 PP	2005-2014 TP	1986- 1990, West Germany only 2001-2002 (West and East Germany)	1986-1996 1997-2007 PP	2005-2007 2008-2010 TP and PP
Grid size (km)	1x0.5	16x16 or 24x32 depending on the location.	1x1	4x4, 2.83x2.83 or 2x2 depending on region	1x1	Vary
Sampling design (Distance between plots)	Single sample plots	Cluster design (100 or 300)	Single sample plots	Cluster design (150)	Single sample plots	Cluster design (vary)
Radius (m)	2.25, 4.5, 9, 12, 18	5.64, 9.77	6, 9, 15	1, 2, 5, 10, 25	5, 10, 15, 25	3.5, 10
Sample tree DBH threshold (cm)	6.4	0	7.5	10 (1st) 7 (2nd)	7.5	1
N Plots	1238	2487	60782	29914	48133	11338
N Trees	16011	39263	637830	295029	813464	187561
Not managed plot	957	29783	84496	98464	627900	142665
Managed plot	15054	7292	299550	196565	164235	44896
Ingrowth trees	3607	13092	-	93148	230256	26680
Recruit trees	9746	23515	-	137772	496453	145625
Dead trees (managed)	2442	1963	-	57592	692	11342
Dead trees (natural)	216	490	63178	5725	68896	3136

Table S2: Number of plots for each species, by country. Species: species name. Code: code used for each species. NPlots: Total number of plots. DE, ES, FI, FR, SW, WA : number of plots by country with DE = Germany, ES = Spain, FI = Finland, SW = Sweden and WA = Wallonia.

Species	Code	Nplots	DE	ES	FR	FI	SW	WA
Quercus rubra L	QUERUB	348	272	43	368	0	0	33
Robinia pseudoacacia L.	ROBPSE	234	141	83	1901	0	0	10

Table S3: Mean, standard error, mininmum and maximum values of predictor and response variables by species.

Variable	*Quercus rubra*	*Robinia pseudoacacia*
Relative stand basal area growth	0.03 (0.21) -1-1	-0.02 (0.23) -1-1
Absolute basal area growth	2.14 (7.11) -36-24	1.19 (5.28) -28-16.48
Diversity index (Shannon) H1	0.67 (0.46) 0-1.7	0.77 (0.51) 0-1.83
Evenness index (Pieloud) J1	0.63 (0.37) 0-1	0.64 (0.35) 0-1
N.HA	633.32 (533.19) 19.24-2777.19	655.96 (566.45) 38.48-3871.99
Trees number at the first census	2.69 (3.73) 0-26	2.79 (4) 0-33
Total basal area of the plot (BA_TOT.HA)	24.8 (12.16) 0.6-65.03	23.58 (14.71) 0.72-79.59
Mean DBH of the plot	292.7 (119.03) 107-706.55	292.48 (101.07) 109-636
Removed basal area (BA_HARVEST)	0.14 (0.27) 0-1.83	0.06 (0.16) 0-1.19
mean_spei12	0.15 (0.19) -0.54-0.8	0.08 (0.26) -0.54-0.77
Temperature (BIO1)	10.45 (1.65) 7.47-15.46	11.9 (2.14) 8.04-18.08
Precipitation(BIO12)	843.72 (157.17) 579.05-1296.03	871.41 (189.03) 364.56-1541.4
Years between census (CI)	12.91 (2.23) 7-16	12.16 (2.32) 7-15

Table S4 VIF values calculated on the variables included in the best predictive model for each species. For each species, there is one column for each variable that are included in the model. The values reported are the VIF scores calculated.

Species	*Quercus rubra*				*Robinia pseudoacacia*			
Model	Prog.ha.model		Domin.model		Prog.ha.model		Domin.model	
Term	VIF	SE factor	VIF	SE factor	VIF	SE factor	VIF	SE factor
BA_TOT.HA	1.29	1.13	1.54	1.24	1.13	1.06	-	-
bio1_climate_mean.15	1.91	1.38	1.85	1.36	1.15	1.07	2.04	1.43
bio12_climate_mean.15	1.75	1.32	1.81	1.34	-	-	-	-
BA_HARVEST	4.26	2.07	1.26	1.12	1.40	1.18	-	-
J1	-	-	-	-	1.05	1.03	-	-
management2	1.39	1.18	-	-	1.36	1.17	-	-
mean_spei12	1.67	1.29	1.65	1.28	-	-	2.09	1.45
N_TOT.ha	1.09	1.04	1.09	1.04	-	-	1.07	1.04
Sp.Group	1.84	1.36	1.94	1.39	-	-	1.09	1.05
Sp.Group:Harvest_BA	5.49	2.34	-	-	-	-	-	-
N_J1	-	-	2.11	1.45	-	-	-	-

Table S5a: Model: model family; npar: number of parameter; AIC: Akaike information criterion, BIC: Bauesian information criteria; loglik: log-likelihood; deviance: deviance of the residuals; Chi-square: Statistic of the chi-square test between the most parsimonious model (M1) and the new fitted model; Df: degree of freedom; Pr: p-value associated with the chi sqrae test; RMSE: The RMSE is the square root of the variance of the residuals which indicates the absolute fit of the model to the data.; R2: The Pearson squared correlation between the model's actual and predicted response. R2adjusted: adjusted r-squared; R2C: Conditional r-squared. R2M: Marginal r-squared.

Quercus_rubra: Prog.ha.model	Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)	RMSE	Sigma	R2	R2_adjusted	R2_conditional	R2_marginal
M1	lm	13	1932.40	1980.85	-953.20	1906.40	NA	NA	NA	5.40	5.51	0.42	0.40	NA	NA
DBH	lm	14	1934.40	1986.57	-953.20	1906.40	0.00	0	NA	5.40	5.52	0.42	0.40	NA	NA
H1	lm	14	1933.64	1985.82	-952.82	1905.64	0.75	0	NA	5.39	5.51	0.42	0.40	NA	NA
J1	lm	14	1933.43	1985.61	-952.72	1905.43	0.21	0	NA	5.39	5.51	0.42	0.40	NA	NA
PRECIPxDENSITY	lm	14	1934.36	1986.54	-953.18	1906.36	0.00	0	NA	5.40	5.52	0.42	0.40	NA	NA
PRECIPxGROUP	lm	15	1930.58	1986.48	-950.29	1900.58	4.13	0	NA	5.35	5.47	0.43	0.41	NA	NA
PRECIPxHARVEST	lm	14	1933.88	1986.06	-952.94	1905.88	0.48	0	NA	5.39	5.51	0.42	0.40	NA	NA
SP.ID	lm	20	1941.66	2016.20	-950.83	1901.66	0.00	5	1.00	5.36	5.53	0.43	0.40	NA	NA
SPEIxGROUP	lm	15	1935.57	1991.48	-952.79	1905.57	0.52	1	0.47	5.39	5.52	0.42	0.40	NA	NA
TEMPxDENSITY	lm	14	1932.59	1984.77	-952.30	1904.59	1.29	0	NA	5.38	5.50	0.43	0.40	NA	NA
TEMPxGROUP	lm	15	1934.71	1990.61	-952.36	1904.71	0.86	0	NA	5.38	5.51	0.42	0.40	NA	NA
TEMPxHARVEST	lm	14	1933.59	1985.77	-952.80	1905.59	0.00	0	NA	5.39	5.51	0.42	0.40	NA	NA
N_J1	lm	14	1934.09	1986.26	-953.04	1906.09	0.00	0	NA	5.39	5.51	0.42	0.40	NA	NA
RE.COUNTRY	lmerMod	14	1934.40	1986.57	-953.20	1906.40	0.00	1	1.00	5.40	5.51	NA	NA	NA	0.41

Table S5b: Model: model family; npar: number of parameter; AIC: Akaike information criterion, BIC: Bauesian information criteria; loglik: log-likelihood; deviance: deviance of the residuals; Chi-square: Statistic of the chi-square test between the most parsimonious model (M1) and the new fitted model; Df: degree of freedom; Pr: p-value associated with the chi sqrae test; RMSE: The RMSE is the square root of the variance of the residuals which indicates the absolute fit of the model to the data.; R2: The Pearson squared correlation between the model's actual and predicted response. R2adjusted: adjusted r-squared; R2C: Conditional r-squared. R2M: Marginal r-squared.

Robinia_pseudacacia: Prog.ha. model	Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)	RMSE	Sigma	R2	R2_adjusted	R2_conditional	R2_marginal
M1	lm	7	1216.34	1239.57	-601.17	1202.34	NA	NA	NA	4.61	4.68	0.24	0.22	NA	NA
DBH	lm	8	1218.02	1244.57	-601.01	1202.02	0.32	0	NA	4.61	4.69	0.24	0.22	NA	NA
DENSITY	lm	8	1217.09	1243.63	-600.54	1201.09	0.94	0	NA	4.59	4.68	0.24	0.22	NA	NA
H1	lm	8	1218.34	1244.88	-601.17	1202.34	0.00	0	NA	4.61	4.69	0.24	0.21	NA	NA
HARVESTxJ1	lm	8	1218.11	1244.65	-601.05	1202.11	0.23	0	NA	4.61	4.69	0.24	0.21	NA	NA
PRECIP	lm	8	1217.17	1243.71	-600.58	1201.17	0.94	0	NA	4.60	4.68	0.24	0.22	NA	NA
SP.GROUP	lm	9	1217.37	1247.24	-599.69	1199.37	0.39	1	0.53	4.58	4.67	0.25	0.22	NA	NA
SP.ID	lm	15	1227.31	1277.08	-598.65	1197.31	2.06	6	0.91	4.55	4.72	0.26	0.21	NA	NA
SPEI	lm	8	1218.14	1244.69	-601.07	1202.14	0.00	0	NA	4.61	4.69	0.24	0.21	NA	NA
TEMPxHARVEST	lm	8	1216.04	1242.58	-600.02	1200.04	2.10	0	NA	4.58	4.66	0.25	0.22	NA	NA
TEMPxJ1	lm	8	1218.28	1244.82	-601.14	1202.28	0.00	0	NA	4.61	4.69	0.24	0.21	NA	NA
N_J1	lm	8	1215.76	1242.30	-599.88	1199.76	2.52	0	NA	4.58	4.66	0.25	0.22	NA	NA
RE.COUNTRY	lmerMod	8	1218.34	1244.89	-601.17	1202.34	0.00	1	1.00	4.61	4.68	NA	NA	NA	0.23

Table S5c: Model: model family; npar: number of parameter; AIC: Akaike information criterion, BIC: Bauesian information criteria; loglik: log-likelihood; deviance: deviance of the residuals; Chi-square: Statistic of the chi-square test between the most parsimonious model (M1) and the new fitted model; Df: degree of freedom; Pr: p-value associated with the chi sqrae test; RMSE: The RMSE is the square root of the variance of the residuals which indicates the absolute fit of the model to the data.; R2: The Pearson squared correlation between the model's actual and predicted response. R2adjusted: adjusted r-squared; R2C: Conditional r-squared. R2M: Marginal r-squared.

Quercus_rubra: Domin. model	Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)	RMSE	Sigma	R2	R2_adjusted	R2_conditional	R2_marginal
M1	lm	11	-54.20	-13.20	38.10	-76.20	0.00	0	NA	0.21	0.22	0.32	0.30	NA	NA
DBH	lm	12	-52.21	-7.49	38.10	-76.21	4.39	1	0.04	0.21	0.22	0.32	0.30	NA	NA
H1	lm	12	-54.93	-10.21	39.47	-78.93	2.72	0	NA	0.21	0.22	0.33	0.31	NA	NA
J1	lm	12	-55.64	-10.92	39.82	-79.64	0.71	0	NA	0.21	0.22	0.33	0.31	NA	NA
MANAGEMENT	lm	12	-54.87	-10.15	39.44	-78.87	0.00	0	NA	0.21	0.22	0.33	0.31	NA	NA
PRECIPxDENSITE	lm	12	-52.72	-8.00	38.36	-76.72	0.00	0	NA	0.21	0.22	0.32	0.30	NA	NA
PRECIPxHARVEST	lm	11	-44.33	-3.33	33.16	-66.33	0.00	0	NA	0.22	0.22	0.31	0.29	NA	NA
SP.ID	lm	17	-37.44	25.92	35.72	-71.44	0.00	5	1.00	0.22	0.22	0.32	0.28	NA	NA
SPEIxDENSITE	lm	12	-52.34	-7.62	38.17	-76.34	0.00	0	NA	0.21	0.22	0.32	0.30	NA	NA
SPEIxHARVEST	lm	11	-44.30	-3.30	33.15	-66.30	0.00	0	NA	0.22	0.22	0.31	0.29	NA	NA
TEMPxDENSITE	lm	12	-53.11	-8.39	38.55	-77.11	0.77	0	NA	0.21	0.22	0.33	0.30	NA	NA
TEMPxHARVEST	lm	11	-49.82	-8.83	35.91	-71.82	5.53	0	NA	0.22	0.22	0.32	0.30	NA	NA
RE.COUNTRY	lmerModLmerTest	11	-60.40	-19.40	41.20	-82.40	NA	NA	NA	0.21	0.21	NA	NA	0.48	0.09

Table S5d: Model: model family; npar: number of parameter; AIC: Akaike information criterion, BIC: Bauesian information criteria; loglik: log-likelihood; deviance: deviance of the residuals; Chi-square: Statistic of the chi-square test between the most parsimonious model (M1) and the new fitted model; Df: degree of freedom; Pr: p-value associated with the chi sqrae test; RMSE: The RMSE is the square root of the variance of the residuals which indicates the absolute fit of the model to the data.; R2: The Pearson squared correlation between the model's actual and predicted response. R2adjusted: adjusted r-squared; R2C: Conditional r-squared. R2M: Marginal r-squared.

Robinia_pseudacacia: Domin.model	Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)	RMSE	Sigma	R2	R2_adjusted	R2_conditional	R2_marginal
M1	lm	7	10.55	33.78	1.72	-3.45	NA	NA	NA	0.24	0.24	0.27	0.25	NA	NA
BATOTAL	lm	8	12.43	38.98	1.78	-3.57	0.00	0	NA	0.24	0.24	0.27	0.25	NA	NA
DBH	lm	8	12.52	39.06	1.74	-3.48	0.00	0	NA	0.24	0.24	0.27	0.25	NA	NA
H1	lm	8	11.98	38.52	2.01	-4.02	0.54	0	NA	0.24	0.24	0.28	0.25	NA	NA
HARVEST	lm	8	10.40	36.95	2.80	-5.60	1.57	0	NA	0.24	0.24	0.28	0.25	NA	NA
J1	lm	8	10.97	37.51	2.52	-5.03	1.46	0	NA	0.24	0.24	0.28	0.26	NA	NA
MANAGEMENT	lm	8	12.32	38.86	1.84	-3.68	0.00	0	NA	0.24	0.24	0.27	0.25	NA	NA
PRECIP	lm	8	10.86	37.41	2.57	-5.14	1.45	0	NA	0.24	0.24	0.26	0.24	NA	NA
SP.ID	lm	14	14.07	60.53	6.96	-13.93	9.25	6	0.16	0.23	0.24	0.29	0.25	NA	NA
SPEIxDENSITE	lm	8	6.59	33.14	4.70	-9.41	4.27	0	NA	0.24	0.24	0.30	0.28	NA	NA
TEMPxDENSITE	lm	8	12.49	39.03	1.76	-3.51	0.00	0	NA	0.24	0.24	0.27	0.25	NA	NA
N_J1	lm	8	11.33	37.87	2.34	-4.67	1.16	0	NA	0.24	0.24	0.27	0.25	NA	NA
RE.COUNTRY	lmerModLmerTest	8	8.48	35.03	3.76	-7.52	4.07	1	0.04	0.23	0.24	NA	NA	0.39	0.17