Spatio-temporal patterns and drivers of forest dynamics under global change:

Understanding the role of climate and forest-use legacies

PhD Thesis
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Programa de Doctorado en
Ecología, Conservación y
Restauración de Ecosistemas

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A todas las personas maravillosas
que he tenido la suerte de conocer y
aprender de ellas en el camino

Bidean ezagutu eta beraiengandik ikasteko
aukera izan dudan jende zoragarriari

Ítaca

Ten siempre a Ítaca en tu mente.
Llegar allí es tu destino.
Mas no apresures nunca el viaje.
Mejor que dure muchos años
y atracar, viejo ya, en la isla,
enriquecido de cuanto ganaste en el camino
sin aguantar a que Ítaca te enriquezca.

Ítaca te brindó tan hermoso viaje.
Sin ella no habrías emprendido el camino.
Pero no tiene ya nada que darte.

Aunque la halles pobre, Ítaca no te ha engañado.
Así, sabio como te has vuelto, con tanta experiencia,
entenderás ya qué significan las Ítacas.

Konstantino Kavafis

Content

Abstract

The impact of the drivers of global change (e.g. climate change and land-use change) on forests is increasing in recent years and a shift from a CO_2 and N fertilisation-dominated period to a climate-dominated period driving forest dynamics has been suggested. In addition, complex interactions between global change drivers are emerging, hindering our ability to predict future forest trajectories. Northern hemisphere forests have been managed by humans for centuries, but these centuries-old forest-uses have been rapidly abandoned since the mid-20th century, while its traces persist in the structure, distribution and species composition of today's forests (i.e. forest-use legacies). At the same time, the impacts of climate change on forest ecosystems are aggravating, but little is known about how forest-use legacies can interact with current climate change stressors to drive Northern Hemisphere forest dynamics. In this context, the main objective of the PhD thesis is to study how climate and forest-use legacies affect forest dynamics at multiple spatio-temporal scales. The thesis contains seven chapters. **Chapter 1** presents a general introduction of recent patterns and drivers of forest dynamics under global change across space and time. **Chapters 2-5** are four research chapters that address the overall objective of the thesis using a combination of continental to local data and decadal to centennial data. Finally, **Chapter 6** discusses the contribution of the four research chapters in the context of shifts in Northern Hemisphere forest dynamics, highlighting the key role of climate and forest-use legacies, and **Chapter 7** summarises the general conclusions of this thesis.

Northern Hemisphere forests are in transition in response to increased atmospheric CO_2 and N fertilisation, and climate change. The consequences of such changes in tree species are not well understood, largely because they are confounded by human-induced changes in forest succession. **Chapter 2** analyses Northern Hemisphere forests with national forest inventories from Europe and North America, and quantifies recent changes in species abundance as a function of climate and forest succession, while assessing the effect of species climatic affiliation, species traits and species range size. Even if past disturbances strongly alter the way in which Northern Hemisphere forests are influenced by climate, tree species are responding to climate change, increasing in abundance towards cold and wet regions of their climate range, and decreasing towards warm and arid regions. Although mainly warm-affiliated species with broad temperature niches increased in abundance in warm and arid regions of their climate range, we observed multiple directions in species responses to climate, highlighting different species climatic sensitivity. The observed species divergent responses to climate could help to select species that are best adapted to future climate change-related risks, while implementing conservation measures for those less well adapted.

Climate and forest succession – and hence, forest structure – are considered major drivers of forest demography and productivity as observed in **Chapter 2**. However, recent evidence suggests that the relationships between climate and tree growth are generally non-stationary (i.e., non-time stable), and therefore, it remains uncertain whether the relationships between climate, forest structure, demography and productivity are stationary or are being altered by recent climatic and structural changes. **Chapter 3** analyses three surveys from the Spanish Forest Inventory covering *c.* 30 years of information to assess temporal trends in forest structure, demography and above-ground productivity. It also quantifies whether the interactive effects of climate and forest structure on forest demography and aboveground forest

productivity were stationary over two consecutive time periods. Since the 1980s, Iberian forests are generally changing to denser and more homogeneous stands, with bigger trees, increased mortality and reduced ingrowth and growth. The temporal trends observed in forest structure and demography were driven by the interactive effects of climate and initial forest structure. However, the patterns of changes in forest demography and productivity and the effect of their underlying climate and structural drivers were non-stationary, observing changes in the magnitude and even in the direction of the effects. Despite increasing aboveground forest productivity over the last 30 years, we observed an aggravation of the negative effects of climate change and increased competition that led to decreased ingrowth and growth, and increased mortality. In most cases the direct and indirect effects of climate change on forest demography had opposite directions, suggesting that reducing tree competition could ameliorate the negative effects of climate change on forest demography.

Changes in forest structure can be the result of natural or human-induced disturbance regimes, and unravelling their causes remains a priority for adapting forests to an increasingly human-altered world. **Chapter 4** explicitly tests whether past forest-use can exacerbate climate change impacts on forests. For this aim, it analyses how forest-use legacies persisting in the structure, distribution and composition of forests can interact with climate change to heighten the probability of forest decline. Based on existing literature, we summarised hypotheses on the mechanisms leading to detrimental legacy effects and then, introduced a risk-based framework to identify forest-use legacies and quantify the impact of their interaction with climate-related stress on forest responses. Finally, we applied the framework to an existing dataset to show that detrimental forest-use legacy effects contribute to large-scale risk of tree mortality at the driest distribution edge of the Scots pine (*Pinus sylvestris* L.).

To understand the underlying drivers of forest-use legacies modulating forest ecosystems responses to climate change, we quantified tree growth synchrony in contrasting land- and forest-use legacies (**Chapter 5**). We sampled an area with similar biotic and abiotic conditions and a well-documented socio-ecological history, by mixing European beech (*Fagus sylvatica* L.) stands with different legacies located at the species rear edge analysing ~240 tree cores. We observed an increase in tree growth synchrony in response to reduced precipitation and increased heatwaves and late spring frosts in the period 1970-2020. However, land- and forest-use legacies modulated the magnitude of increases in growth synchrony through changes in forest structural diversity (i.e. mean tree size and tree size heterogeneity). We found that recently-established forests had the greatest tree growth synchrony, and that large trees and heterogeneous size distributions decreased growth synchrony.

Overall, this PhD thesis analyses recent dynamics of Northern Hemisphere forests at multiple spatio-temporal scales, highlighting the key role of the interactive effect of climate and forest-use legacies driving forest dynamics. For this aim, we used large inventory networks to detect patterns and major drivers of changes in forest dynamics, and intensive monitoring to understand the mechanistic relationship between drivers and forest responses. The combination of studies over different spatio-temporal extents is crucial to better assess the future climate risk of forests and assist in policies and management strategies to adapt forests to the increasing impacts of climate change.

Resumen

El impacto de los motores del cambio global (p. ej. el cambio climático y los cambios en los usos del suelo) en los bosques está aumentando en los últimos años y se ha sugerido el paso de un período dominado por la fertilización de CO_2 y N a un período dominado por el clima dirigiendo la dinámica forestal. Además, están surgiendo complejas interacciones entre los motores del cambio global, lo que dificulta nuestra capacidad para predecir las futuras trayectorias forestales. Los bosques del hemisferio norte han sido gestionados por los humanos durante siglos, pero estos usos forestales centenarios se han ido abandonando rápidamente desde mediados del siglo XX, mientras que sus huellas persisten en la estructura, distribución y composición de especies de los bosques actuales (i.e. legados del uso forestal). Al mismo tiempo, los impactos del cambio climático en los ecosistemas forestales se están agravando, aunque se desconoce cómo los legados del uso forestal pasado pueden interactuar con los actuales factores de estrés del cambio climático para determinar la dinámica de los bosques del hemisferio norte. En este contexto, el objetivo principal de la tesis doctoral es estudiar cómo el clima y los legados del uso de los bosques afectan a la dinámica forestal a múltiples escalas espaciotemporales. La tesis contiene siete capítulos. El **Capítulo 1** presenta una introducción general de los patrones recientes y los impulsores de la dinámica forestal bajo el cambio global a través del espacio y el tiempo. Los **Capítulos 2-5** son cuatro capítulos de investigación que abordan el objetivo general de la tesis utilizando una combinación de datos que van desde lo continental hasta lo local, espacialmente, y de décadas a siglos, temporalmente. Por último, el **Capítulo 6** discute la contribución de los cuatro capítulos de investigación en el contexto de los cambios en la dinámica forestal del hemisferio norte, destacando el papel clave del clima y los legados del uso forestal, y el **Capítulo 7** resume las conclusiones generales de la tesis.

Los bosques del hemisferio norte están en transición en respuesta al aumento de la fertilización del CO_2 atmosférico y N, y del cambio climático. Las consecuencias de estos cambios en las especies arbóreas siguen siendo inciertas, en gran medida porque se distorsionan con la sucesión forestal. El **Capítulo 2** analiza los bosques del hemisferio norte con inventarios forestales nacionales de Europa y Norteamérica, y cuantifica los cambios recientes en la abundancia de las especies en función del clima y la sucesión forestal, al tiempo que evalúa el efecto de la afiliación climática de las especies, sus rasgos y el tamaño de su rango de distribución. A pesar de que las perturbaciones pasadas alteran fuertemente la forma en que los bosques del hemisferio norte están influenciados por el clima, las especies arbóreas están respondiendo al cambio climático aumentando su abundancia hacia las regiones frías y húmedas de su rango climático, y disminuyendo hacia las regiones cálidas y áridas. Aunque principalmente la abundancia de las especies con nichos térmicos cálidos y amplios aumentó en las regiones cálidas y áridas de su rango climático, observamos múltiples direcciones en las respuestas de las especies al clima, lo que pone de manifiesto la diferente sensibilidad climática de las especies. Las respuestas divergentes de las especies observadas al clima podrían ayudar a seleccionar las especies mejor adaptadas a los futuros riesgos climáticos de los bosques, al tiempo que se aplican medidas de conservación para las no tan bien adaptadas.

El clima y la sucesión forestal – y por tanto, la estructura de los bosques – se consideran los principales impulsores de la demografía y la productividad de los bosques, tal y como se constata en el **Capítulo 2**. Sin embargo, la evidencia reciente

sugiere que las relaciones entre el clima y el crecimiento de los árboles son generalmente no estacionarias (i.e. no estables en el tiempo), y por tanto, sigue siendo incierto si las relaciones entre el clima, la estructura forestal, la demografía y la productividad son estacionarias o están siendo alteradas por los cambios en el clima y estructura forestal recientes. El **Capítulo 3** analiza tres censos del Inventario Forestal Nacional que cubren *c.* 30 años de información para evaluar las tendencias temporales en la estructura, demografía y productividad forestal aérea. También cuantifica si los efectos interactivos del clima y la estructura forestal sobre la demografía y la productividad aérea fueron estacionarios a lo largo de dos periodos de tiempo consecutivos. Desde la década de 1980, los bosques ibéricos están cambiando, en general, hacia masas más densas y homogéneas, con árboles más grandes, una mayor mortalidad y una reducción del reclutamiento y crecimiento. Las tendencias temporales observadas en la estructura y la demografía fueron impulsadas por los efectos interactivos del clima y la estructura inicial. Sin embargo, los patrones de los cambios en la demografía y la productividad de los bosques y el efecto de sus impulsores climáticos y estructurales subyacentes no fueron estacionarios, observándose cambios en la magnitud e incluso en la dirección de los efectos. A pesar de que la productividad aérea aumentó en los últimos 30 años, observamos un agravamiento de los efectos negativos del cambio climático y del aumento de la competencia, que provocó una disminución del reclutamiento y del crecimiento y un aumento de la mortalidad. En la mayoría de los casos, los efectos directos e indirectos del cambio climático sobre la demografía forestal tenían direcciones opuestas, lo que sugiere que reducir la competencia de los árboles podría reducir los efectos negativos del cambio climático sobre la demografía forestal.

Los cambios en la estructura de los bosques pueden ser el resultado de regímenes de perturbación naturales o antropogénicos, y desentrañar sus causas sigue siendo una prioridad para adaptar los bosques a un mundo cada vez más alterado por los humanos. El **Capítulo 4** comprueba explícitamente si los legados del uso forestal pueden incrementar los impactos del cambio climático en los bosques. Para ello, analiza cómo los legados del uso forestal que persisten en la estructura, distribución y composición de los bosques pueden interactuar con el cambio climático para aumentar la probabilidad de declive de los bosques. Basándonos en la bibliografía existente, resumimos las hipótesis sobre los mecanismos que conducen a los efectos perjudiciales del legado y, a continuación, introducimos un marco basado en el riesgo para identificar los legados del uso forestal y cuantificar el impacto de su interacción con el estrés climático en las respuestas de los bosques. Por último, aplicamos el marco a un conjunto de datos existente para demostrar que los efectos perjudiciales del legado de uso forestal contribuyen al riesgo de mortalidad de los árboles a gran escala en el límite de distribución más árido del pino silvestre (*Pinus sylvestris* L.).

Para comprender los factores subyacentes de los legados del uso forestal que modulan las respuestas de los ecosistemas forestales al cambio climático, cuantificamos la sincronía en el crecimiento de los árboles en distintos legados del uso del suelo y forestal (**Capítulo 5**). Muestreamos un área con condiciones bióticas y abióticas similares y una historia socioecológica bien documentada, mezclando rodales de haya (*Fagus sylvatica* L.) con diferentes legados situados en el límite meridional de la especie analizando ~240 cores de árboles. Observamos un aumento en la sincronía en el crecimiento de los árboles en respuesta a la reducción de las precipitaciones y al aumento de las olas de calor y de las heladas primaverales tardías en el periodo 1970-2020. Sin embargo, los legados del uso del suelo y forestal modularon la magnitud del aumento en la sincronía en el crecimiento a través de los cambios en la diversidad estructural del bosque (i.e. tamaño medio y la heterogeneidad del tamaño de los árboles). Encontramos que los bosques recientemente establecidos tenían la mayor sincronía en el crecimiento de los árboles, y que los árboles grandes y las distribuciones de tamaño heterogéneas disminuían la sincronía.

En general, esta tesis doctoral analiza la dinámica reciente de los bosques del hemisferio norte a múltiples escalas espaciotemporales, destacando el papel clave del efecto interactivo del clima y de los legados del uso de los bosques impulsando la dinámica forestal. Para ello, utilizamos grandes redes de inventarios para detectar los patrones y los principales impulsores de los cambios en la dinámica forestal, y un muestreo intensivo para comprender la relación mecanicista entre los impulsores y las respuestas de los bosques. La combinación de estudios a lo largo de diferentes extensiones espaciotemporales es crucial para evaluar mejor el futuro riesgo climático de los bosques y ayudar en las políticas y estrategias de gestión para adaptar los bosques a los crecientes impactos del cambio climático.

Chapter 1

General introduction

1.1. The dimensions of global change in forest ecosystems

Humans have altered ecosystems since they appeared on Earth, but the intensity of human impacts has intensified exponentially since the Industrial Revolution (Bowler et al., 2020; Steffen et al., 2007). Consequently, more than 75% of the Earth's ice-free land surface is currently altered by humans (Ellis & Ramankutty, 2008), having a direct impact on key Earth's biogeophysical processes and natural components such as, climate and biodiversity (Rockström et al., 2009). Forests play a fundamental role in these biogeophysical processes and components, for example, by providing refugees for biodiversity or regulating climate (Bonan, 2008; IPBES, 2019). However, forests are also subject to the multiple threats of global change which can lead to major changes in forest functioning (McDowell et al., 2020; Trumbore et al., 2015).

Multiple drivers affecting contemporary forest dynamics have been documented (McDowell et al., 2020), with CO_2 fertilisation and nitrogen deposition considered to be the main drivers of forest productivity over the last three decades (Zhu et al., 2016). However, other drivers of global change are increasing their impact in recent years, such as changes in climate and land-use (Fig. 1.1; IPCC, 2021; Song et al., 2018). Currently, the rate of warming that is affecting the whole planet (atmosphere, oceans and land) is unprecedented in the last 2000 years and extreme climatic events such as heatwaves, droughts, fires and pests are increasing in intensity and frequency worldwide (Forzieri et al., 2021; IPCC, 2021). In addition, although the global deforestation rate has decreased from 16 to 10 million ha annual rate from 1990-2000 to 2015-2020, forest area continues to be lost (FAO, 2020). Nevertheless, in the extratropical forests of the Northern Hemisphere since the middle of the 20th century, forest area and biomass are increasing due to reforestation and afforestation programs, and natural forest regrowth (Infante-Amate et al., 2022; McGrath et al., 2015; Song et al., 2018). These centuries-old human-impacts in extratropical countries have direct consequences on forest dynamics shaping current forest structure, distribution and species composition (Garbarino et al., 2022; Goring & Williams, 2017; Wason & Dovciak, 2017). For example, in Europe primary forests currently cover only 0.7% of the forest area (Sabatini et al., 2018). Furthermore, complex interactions between the drivers of global change are emerging (Gatti et al., 2021), and it has been suggested that there has been a shift from a CO_2 and N fertilisation-dominated period to a climate-dominated period in global carbon sinks that can offset the positive effects of CO_2 and N fertilisation observed in the 20th century (Hubau et al., 2020; Peñuelas et al., 2017a).

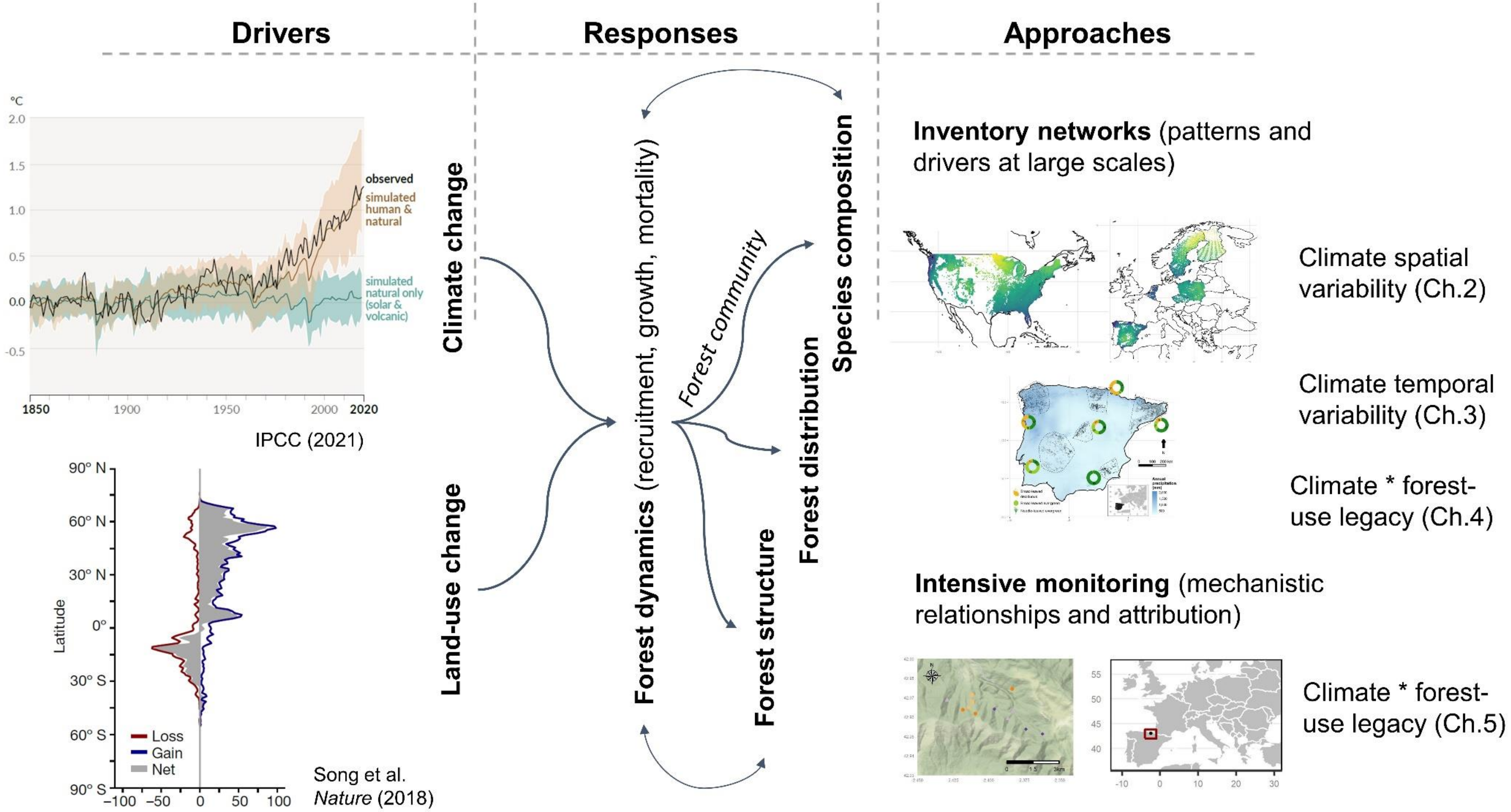


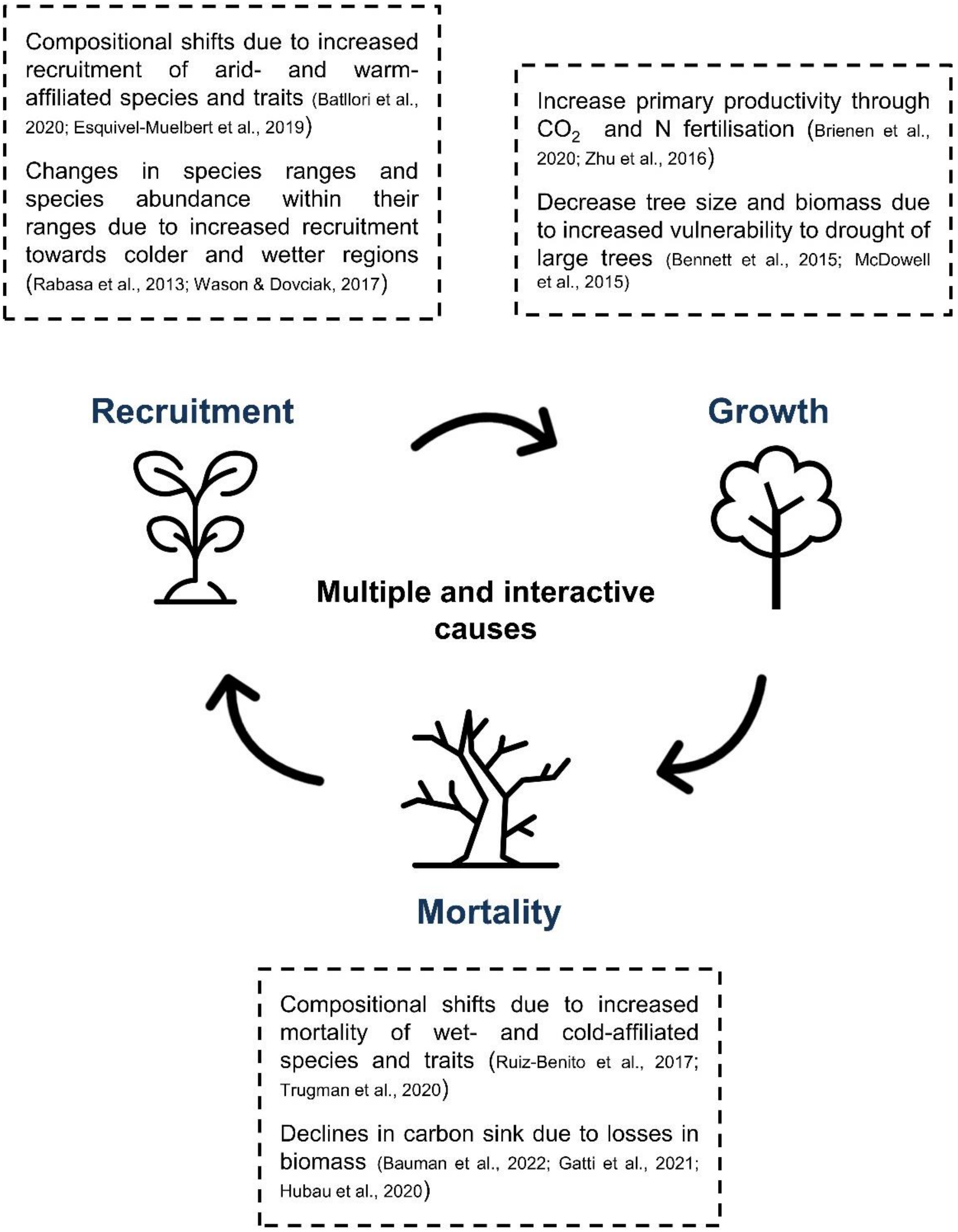
Figure 1.1. Framework representing the main drivers, forest responses and approaches to analyse the relationships between drivers and responses used in the PhD thesis. Climate change and land-use change interact driving forest dynamics. Forest dynamics shape forest structure, distribution and species composition. At the same time, changes in forest structure, distribution and composition might affect forest dynamics (e.g. by increasing tree competition). Inventory networks allow detecting patterns and drivers of shifts in forest dynamics. Intensive monitoring at local scales allows clarifying mechanistic relationships and attributing the causes of changes in forest dynamics. In Chapters 2-5 of the PhD thesis (Ch.2-5) we used large inventory networks and local intensive monitoring to better understand the effect of climate and forest-use legacies on forest dynamics.

Vegetation trajectories remain uncertain mainly due to the unknown future socioeconomic path of humans and our still limited ability to understand and predict future forest responses to global change. On the one hand, antagonistic impacts of global change are being documented (e.g. increase tree mortality due to climate and land-use changes vs. increase tree growth due to CO_2 fertilisation; Peñuelas et al., 2017a). On the other hand, little is known about how past land- and forest-use can shape current forest dynamics (Perring et al., 2016), and the thresholds of forest ecosystem responses to global change are not completely understood (Cooper et al., 2020; Hillebrand et al., 2020). However, at the same time, research on the impacts of global change on forests is achieving the capacity to conduct global-scale analyses over an increasingly wide range of time scales and is greatly improving the ability to disentangle the human and natural contributions of these impacts (Anderegg et al., 2022; Zhu et al., 2016). The combination of studies over different spatio-temporal extents will be crucial to better assess the climate and land-use risk of the Earth's forests in the coming decades (Fig. 1.1 and see section *1.4. Forest responses to climate and forest-use across space and time: The role of large-scale and long-term data in understanding the impacts of global change*).

1.2. The study of forest dynamics through demography: Recent changes under global change

The interplay between demographic processes of tree recruitment, growth and mortality, and global change gives rise to forest dynamics. To adequately understand and forecast future forest dynamics we need to first understand the spatio-temporal trends in forest demography. In this sense, there is ample evidence that mortality rates are increasing in all the biomes (see e.g. Bauman et al. (2022) in tropical forests, Peng et al. (2011a) in boreal forests and Senf et al. (2021) in temperate forests). However, tree recruitment and growth show contrasting patterns, potentially due to the antagonistic effects that the drivers of global change might have. For example, warming can increase forest productivity through CO_2 fertilisation and elimination of photosynthesis limitations due to low temperatures, but excess warming may reduce tree growth due to reduced water availability and increased carbon respiration costs (Adams et al., 2009; D'Orangeville et al., 2018; Peñuelas et al., 2017a). In addition, although increased warming and droughts could increase tree recruitment in wetter and colder regions, other drivers, such as changes in land-use, could hinder tree recruitment in these regions (Goring & Williams, 2017).

Changes in demographic rates underlie changes in forest structure, distribution and species composition (Fig. 1.1 and 1.2). There is mounting evidence that increased warming and disturbances are causing changes in forest structure over time towards smaller and more abundant individuals (McDowell et al., 2020; McIntyre et al., 2015; Zhou et al., 2013). At the same time, globally, more arid- and warm-affiliated species are being favoured due to climate change (Batllori et al., 2020; Esquivel-Muelbert et al., 2019; Trugman et al., 2020). These structural and compositional changes are altering species ranges and species abundance within their ranges, causing shifts in forest biomass (García-Valdés et al., 2021; Zhang et al., 2018). However, multiple directions in species demographic responses to climate have been documented but little is known about the causes of these divergent responses to climate (Kunstler et al., 2021; Rabasa et al., 2013; Wason & Dovciak, 2017; Zhu et al., 2014), hindering our ability to predict how species will respond to the increasing impacts of climate change.



Compositional shifts due to increased recruitment of arid- and warm-affiliated species and traits (Batllori et al., 2020; Esquivel-Muelbert et al., 2019)

Changes in species ranges and species abundance within their ranges due to increased recruitment towards colder and wetter regions (Rabasa et al., 2013; Wason & Dovciak, 2017)

Increase primary productivity through CO_2 and N fertilisation (Brienen et al., 2020; Zhu et al., 2016)

Decrease tree size and biomass due to increased vulnerability to drought of large trees (Bennett et al., 2015; McDowell et al., 2015)

Compositional shifts due to increased mortality of wet- and cold-affiliated species and traits (Ruiz-Benito et al., 2017; Trugman et al., 2020)

Declines in carbon sink due to losses in biomass (Bauman et al., 2022; Gatti et al., 2021; Hubau et al., 2020)

Figure 1.2. Changes in demographic processes of tree recruitment, growth and mortality[1] underlie changes in forest structure, distribution and species composition. Forest life cycle, including tree recruitment, growth and mortality is shown. The boxes show key processes that changes in each demographic rate cause in forest functioning. Although tree

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[1] Image credits:
-Recruitment: Plant by omeneko from Noun Project
-Growth: Tree by ani rofiqah from Noun Project
-Mortality: Dead tree by Dooder from Noun Project

regeneration (i.e. from seed production to germination and establishment) is a critical process in the life cycle of trees, it is not included in the figure because throughout the PhD thesis we focus on tree recruitment, growth and mortality.

Shifts in forest structure, distribution and species composition influence the ecosystem contributions that forests provide to society (Anderegg et al., 2013; Brodribb et al., 2020). For example, in relation to changes in species composition, higher levels of biodiversity have been associated with greater multifunctionality (Ruiz-Benito et al., 2014a; van der Plas et al., 2016) or increased tree mortality rates have been related to the decline of major carbon sinks such as tropical forests (Bauman et al., 2022; Gatti et al., 2021; Hubau et al., 2020). Thus, the analysis of spatio-temporal trends in tree demographic rates could help to anticipate structural, distributional and compositional changes that may occur in forest ecosystems in the long-term and their effects on human well-being. Once we understand the trends in tree demographic rates and their consequences on forest ecosystems, the next frontier is to unravel the underlying causes of the observed patterns. Driver attribution is a major challenge, as multiple drivers act synergistically and could have compounding or counteracting effects across space and time (i.e. effect of drivers in the same directions or opposite directions, respectively; Goring & Williams, 2017; Guo et al., 2018). Moreover, the interactive effects of global change drivers on forest dynamics may be scale-dependent, with complex interplays between processes occurring at global and local scales, and their impacts persisting long after they occur in ecosystems (Trugman et al., 2021; Trumbore et al., 2015).

1.3. The interaction between changes in climate and forest-use underlies forest dynamics

Reforestation and afforestation programs, together with natural forest regrowth, are leading to an increase in forest area in the extratropics. For example, temperate forest cover has increased more than 30% over the last three decades (Song et al., 2018). In addition, in industrialised countries tree cover and biomass are increasing over the last decades, largely due to the abandonment of agricultural activities and traditional forest management (see example of Fig. 1.3; Infante-Amate et al., 2022). These increases in tree cover and biomass might alter forest structure by increasing tree density or reducing tree size heterogeneity (Jump et al., 2017; Poyatos et al., 2003; Seijo et al., 2018). Furthermore, tree plantations often use fast-growing species with direct effects on species distribution through species selection (Holl & Brancalion, 2020) and, therefore, planted forests might expand tree species distributions outside species climatic niche (Ruiz-Benito et al., 2012; Vilà-Cabrera et al., 2019). These changes in forest structure, distribution and species composition could interact with climate change shaping forest dynamics (Zhang et al., 2015).

Changes in forest structure might interact with climate change driving shifts in forest productivity (Ruiz-Benito et al., 2014b) and survival (Ruiz-Benito et al., 2013; Young et al., 2017). At the same time, tree plantations often alter the natural distribution of species, which could increase climatic stress and lead to a decrease in tree recruitment (Ruiz-Benito et al., 2012). Furthermore, shifts in species composition towards aridaffiliated species could decrease forest biomass by filtering more arid-tolerant but slower-growing species (García-Valdés et al., 2021; Zhang et al., 2018). In addition to climate change, changes in forest structure, distribution and species composition are mainly due to changes in land- and forest-use. Land-use changes imply a complete change in forest cover (e.g. deforestation, afforestation or natural regrowth; Song et al. (2018)) while forest-use changes occur without a complete change in forest cover (Jump et al., 2017). For instance, changes in forest-use might happen through the abandonment of traditional forest exploitation techniques (e.g. abandonment of firewood extraction, see Fig. 1.3) or the abandonment of forest plantations once planted. Furthermore, the impacts of changes in land- and forest-use might persist long after they have occurred (Johnstone et al., 2016).

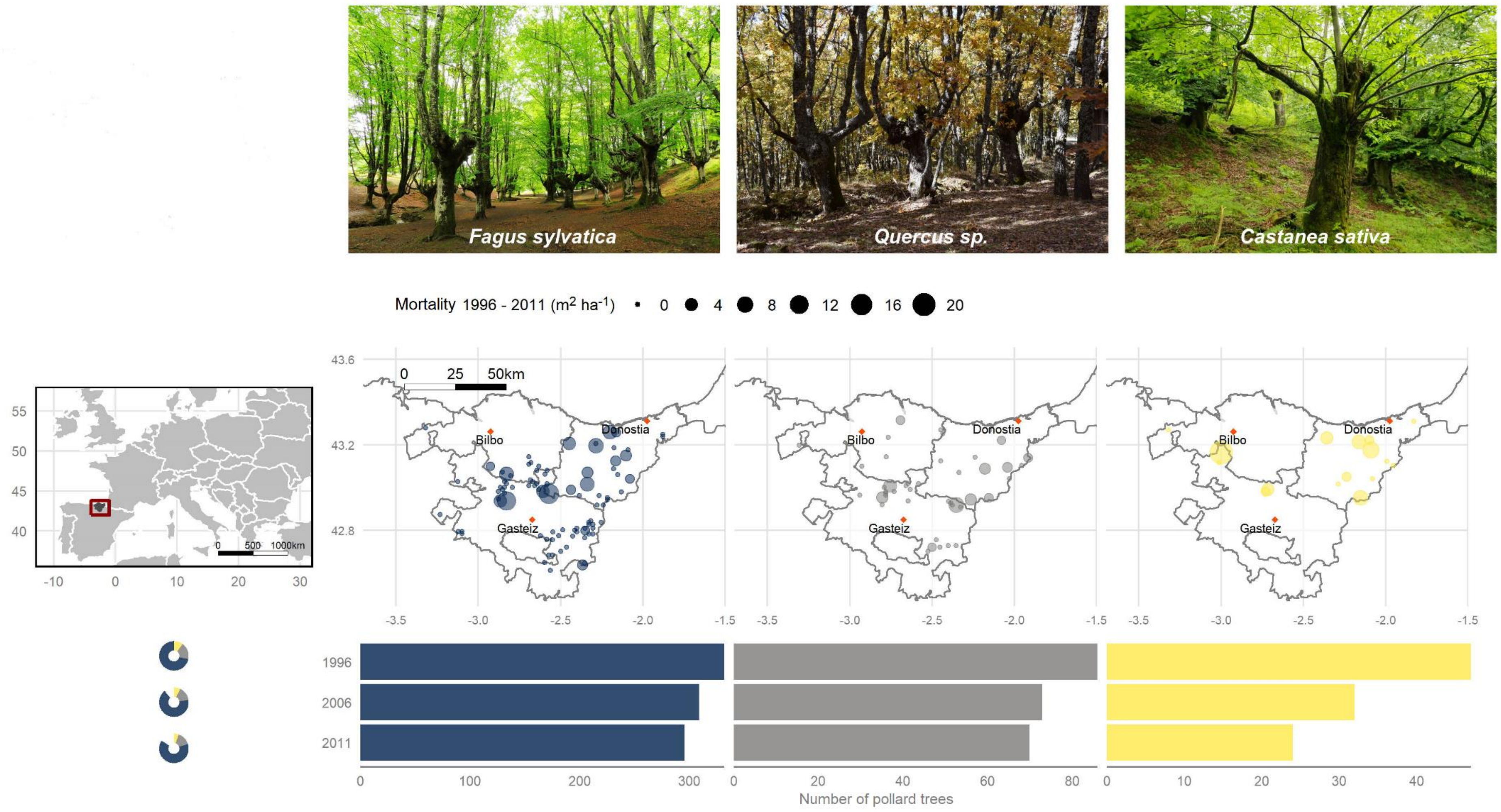

Figure 1.3. Increased mortality and reduced density of different species of pollard trees has accelerated since the introduction of fossil fuels and the abandonment of charcoal and firewood (adapted from Herrero, Astigarraga, & Cruz-Alonso, 2021). Maps depicting the mortality rates of beech (*Fagus sylvatica*), oak (*Quercus sp.*) and chestnut (*Castanea sativa*) pollard trees (points) and the evolution of their numbers (barplots) in Araba, Bizkaia and Gipuzkoa according to data from the second, third and fourth forest inventories of the Basque Autonomous Community (1996-2011). Pie charts show the percentages of pollard trees sorted by species for each inventory, with missing trees leaving gaps in the pie charts of the most recent inventories.

Past modifications of an ecosystem shape current ecological processes (Peterson, 2002). This mechanism, known as legacy effects, suggests that following a disturbance, information (i.e. species adaptive responses to disturbances) and materials (i.e. biotic and abiotic structures produced by disturbances) can be transmitted in ecosystems as legacies (Johnstone et al., 2016). Multiple evidence of legacy effects has been documented, including climate legacy effects (i.e. persistent effect of past climatic impacts on current forest dynamics; Anderegg et al., 2015) or land-use legacy effects (persistent effect of past land-use impacts on current forest dynamics; Berenguer et al., 2021). For example, recent evidence suggests that recently-established forests in former agricultural lands might be more sensitive to climate change than long-established forests (Alfaro-Sánchez et al., 2019; Mausolf et al., 2018). However, much less attention has been paid to investigate how forest-use legacies might alter forest responses to climate change (Perring et al., 2016). It has been found that increased forest biomass due to management abandonment could alter ecosystem carrying capacity and potentially expose forests to increased climate vulnerability (Jump et al., 2017), or that forest understory diversity might vary depending on forest management legacies and climate change (Perring et al., 2018). Yet, our knowledge of the interactive effects of climate change and forest-use legacy effects remains limited. In addition, while warming and extreme climatic events are expected to increase globally – albeit at different levels depending on the region – changes in land- and forest-use are more context-dependent (Marqués et al., 2022), highlighting the importance of analysing changes in forest dynamics across multiple spatial and temporal extents.

1.4. Forest responses to climate and forest-use across space and time: The role of large-scale and long-term data in understanding the impacts of global change

Forests are complex ecosystems (Messier et al., 2013) formed by sessile and long-lived organisms with a limited dispersion capacity that can hamper the adaptation to rapid changes in climate and forests-use (Jump & Peñuelas, 2005). Furthermore, forest responses to changes in climate and forest-use might vary across different spatial and temporal extents. Spatially, forest responses can range from changes in demographic rates at individual or population scales (Herrero et al., 2016) to changes in structure and composition at community level (Thom & Seidl, 2021) or even changes in forest productivity and carbon sink capacity at ecosystem level (Hubau et al., 2020). Temporarily, forests responses to global environmental change can range from rapid responses (Guo et al., 2018) to delayed responses long after the impact has occurred (Perring et al., 2018). Therefore, to understand forest dynamics multiple forest responses analysed at different spatial (from population to ecosystem) and temporal (from annual to decadal) extents are needed.

Several studies have used space-for-time substitution to predict future forest dynamics but their main assumption that spatial species responses to climate will match temporal species responses to climate change is under dispute (Blois et al., 2013; Johnson & Miyanishi, 2008). In a rapidly changing world where the pace of vegetation change is unprecedented in recent millennia (Mottl et al., 2021), where the impacts of climate change on forests are expected to increase (Anderegg et al., 2022) and where novel ecosystems are emerging (Filgueiras et al., 2021), the use of space-for-time substitution should be viewed with caution. In addition, predictions based solely on spatial data may underestimate the plasticity in species-climate responses or the potential existence of thresholds of species responses to climate change (D'Orangeville et al., 2018; Goring & Williams, 2017). Local conditions, such as, favourable microclimatic and forest-use conditions, might also allow species to persist in unfavourable regional climates (Dobrowski, 2011; Jump et al., 2017), resulting in deviations from the expected overall predictions of species responses to climate change. Therefore, observational data with a broad spatial and temporal resolution are needed to accurately predict how species will respond to changing climatic conditions.

Systematic forest inventories provide an important data source due to their wide spatial extents covering large environmental gradients and detailed information on forest structure, composition and demography (Ruiz-Benito & García-Valdés, 2016). These characteristics allow forest inventories to quantify from changes in forest dynamics to multifunctionality (Ruiz-Benito et al., 2020) and gives them a fundamental role in understanding the impacts of global change on forests (Kunstler et al., 2021; Purves, 2009; Ruiz-Benito et al., 2017). However, forest inventories might underestimate species resilience to environmental changes due to their relatively limited temporal scope (Goring & Williams, 2017) and spatially discontinuous sampling design. For example, the 25-metre radius plots of the Spanish Forest Inventory are systematically distributed on a 1 km^2 grid and may not capture local biotic and abiotic processes, such as microclimatic refugia (Vilà-Cabrera et al., 2019). Yet, the Spanish Forest Inventory is one of the most spatially intensive forest inventory surveys worldwide (see Fig. 1.4).

The temporal and local information provided by forest inventories can be complemented with long-term and locally detailed data provided by other data sources. On the one hand, linking forest inventories with dendrochronological data allows combining the large spatial extents covered by inventories with long-term data provided by tree cores, which allows for a better understanding of temporal changes in tree growth and mortality over a wide spatial extent (Gazol et al., 2022). On the other hand, linking forest inventories with detailed local information on forest-use improves our understanding of the underlying drivers of forest dynamics (Ruiz-Benito et al., 2012). In this sense, databases containing detailed historical information available on a local scale, such as forest management archives, aerial photographs or local knowledge can provide more accurate information on the historical processes that have shaped forest ecosystems, allowing better attribution between global change drivers and forest dynamics (Cruz-Alonso et al., 2019; Madrigal-González et al., 2015). Thus, the complementary information provided by supplementary data sources is key to understanding and predicting how forest ecosystems will respond to novel climatic conditions across space and time (Ruiz-Benito et al., 2020).

Throughout the chapters of this PhD thesis, we used a variety of spatio-temporal scales and data types to analyse multiple forest responses to climate and forest-use legacies (see Fig. 1.1, 1.4 and Table 1.1). In terms of spatial extent, we used data from continental to local extents, using information from forest inventories covering Northern Hemisphere forests (Chapter 2: Ch.2) and Spanish forests (Chapter 3 and 4: Ch.3 and Ch.4) to tree-ring data, forest management archives, aerial photographs and local interviews (Chapter 5: Ch.5). In terms of temporal extent, we used data ranging from decades to centuries. In Ch.2 and Ch.4 we used decadal data to analyse recent forest dynamics and unravel the human and climatic attribution of the underlying drivers. Next, in Ch.3 we extend the time scale to three decades by analysing the temporal stability of climate impacts on forests and finally, in Ch.5 we compiled centennial information that allowed us to test both human and climatic attribution of changes in forest dynamics and the temporal stability of climatic impacts on forests. Hence, the combination of local and centennial information with continental and decadal information is a key aspect of this thesis which allows a better assessment of the spatio-temporal patterns and drivers of forest dynamics under global change.

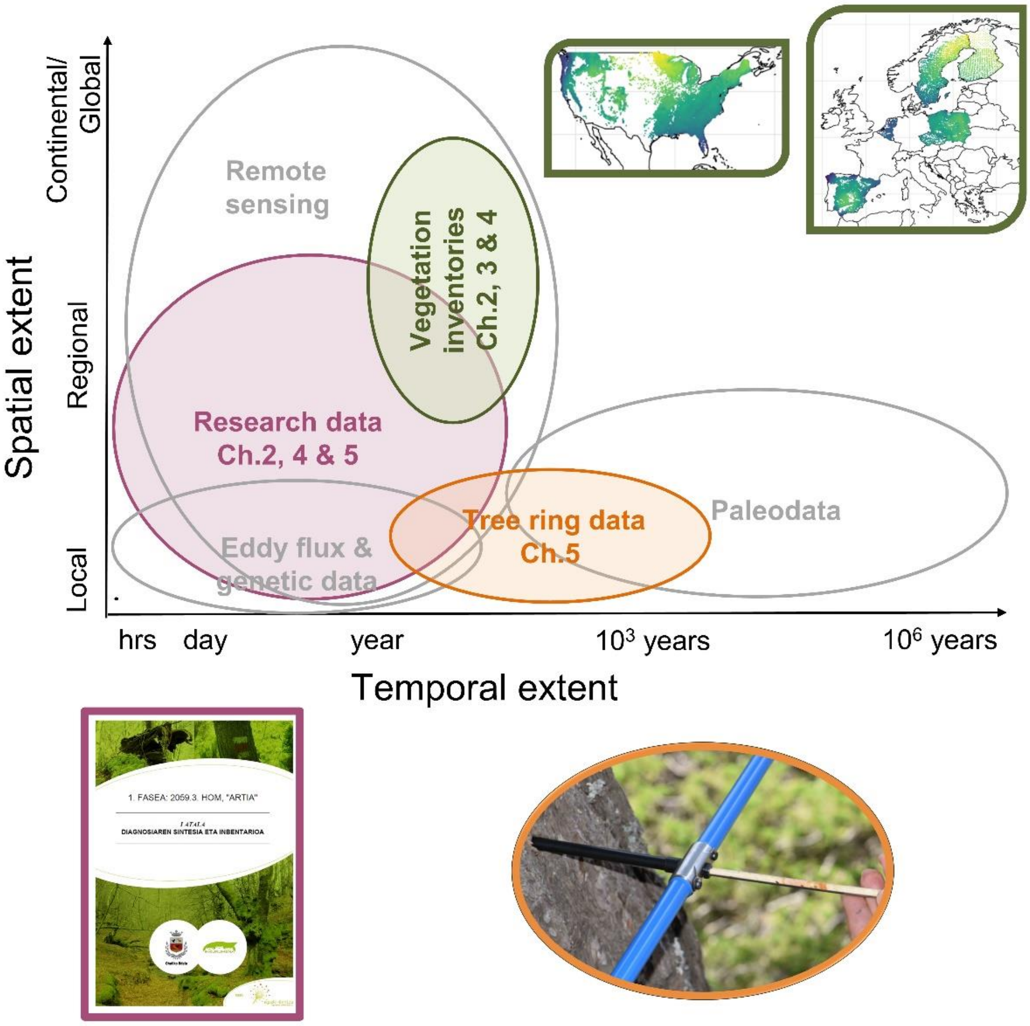

Figure 1.4. Data types to monitor changes in forest dynamics according to the spatial and temporal extents in which they are generally collected (adapted from Ruiz-Benito et al., 2020). To analyse forest responses to climate and forest-use legacies we used forest inventory data (Ch.2, 3 & 4), tree-ring data (Ch.5) and research data (i.e. species traits data and chorological maps in Ch.2, regions of provenance information in Ch.4**,** and forest management archives, aerial photographs and local interviews in Ch.5). Note that the book with the pink border is a forest management plan used in Ch.5.

Observational and open data are key to understanding the impacts of global environmental change in forests (Ruiz-Benito et al., 2020; Sagarin & Pauchard, 2012). The increasing amount of observational data has led ecology to embrace big data (Farley et al., 2018; Hampton et al., 2013). However, there are several risks in the use of millions of observational data related to the scientific pillar of reproducibility (Gibney, 2022). Reproducibility can be understood as the ability to independently recreate results from the same data and code used by the original team (The Turing Way Community, 2021), but currently many studies are completely unreproducible (Peng, 2011b; Yong, 2013). In this sense, open data and open source code are gaining importance as tools related to project traceability (from preparation to publication) and reproducibility (Astigarraga & Cruz-Alonso, 2022; Rodríguez-Sánchez et al., 2016). In addition, given that the impacts of global change range from epigenetic to planetary changes (Peñuelas et al., 2017b), the collaboration of scientists from multiple fields in large collaborative teams is essential, making traceability and reproducibility increasingly necessary. Thus, reproducible and collaborative science is key to generate robust and useful knowledge (Peng, 2011b). In this sense, all the analyses in the chapters of this thesis have been developed in different programming languages (mainly R Statistical Software (R Core Team 2022)), almost all the articles have been written in the RStudio environment and we have created open-source software freely available for possible contributions and modifications (*easyclimate,* https://github.com/VeruGHub/easyclimate and *trini,* https://zenodo.org/record/7193360).

1.5. PhD thesis objectives and structure

The main objective of the PhD thesis is to investigate the effects of climate and forest-use on Northern Hemisphere forest dynamics at multiple spatio-temporal scales. The main objective is achieved through specific research chapters ranging from Ch.2 to Ch.5 (Table 1.1). Specifically, we analyse how forest dynamics are altered by climate and forest structure (Ch.2 and Ch.3) and by climate and forest-use legacies (Ch.4 and Ch.5). Our spatio-temporal extent ranges from continental but temporally decadal data (Ch.2) to local but temporally over 50-years data (Ch.5). To understand the role of forest-use legacies on forest dynamics, we use local observational data collected in the field together with observational data available at a broad spatial scale. Considering the trade-offs between data types available at different spatio-temporal scales (i.e. local but temporally broad vs. spatially broad but temporally shorter data), the research questions and the nature of the data analysed, several methodological approaches are used ranging from generalised additive models and structural equation models to network analyses (see Table 1.1).

The thesis is structured in seven chapters. After this introductory chapter, Chapters 2, 3, 4 and 5 reproduce the contents of published (Ch.3), under review (Ch.4) and to be submitted (Ch.2 and Ch.5) works. Chapters from 2 to 5 have the structure of a scientific manuscript, both in long (i.e. abstract, introduction, materials and methods, results, discussion and references) and short format (i.e. main text containing introduction, results and discussion together, followed by materials and methods and references). Ch.6 contains a general discussion of the results of the thesis, and Ch.7 the general conclusions. An updated curriculum vitae is attached at the end, following the supporting information from Ch.2-5.

In Ch.2 “Recent dynamics of Northern Hemisphere tree species along climatic and successional gradients”, we analysed Northern Hemisphere forests with national forest inventories from Europe and North America, using ~80 widely-distributed species across more than 125000 forest inventory plots, and quantified recent changes in species abundance as a function of climate and forest succession, while assessing the effect of species climatic affiliation, species traits and species range size. We found that even if past disturbances strongly alter the way in which Northern Hemisphere forests are influenced by climate, tree species are responding to climate change, increasing in abundance towards cold and wet regions of their climate range, and decreasing in warm and arid regions. In addition, we quantified species climatic sensitivity which is key to selecting the species best adapted to future climate change-related risks, while implementing conservation measures for those less well adapted.

Then, in Ch.3 “Evidence of non-stationary relationships between climate and forest responses: Increased sensitivity to climate change in Iberian forests”, we quantified whether climatic and structural changes were altering the time stability of climate-forests relationships in Iberian forests. To analyse the time stability between climate, forest structure, demography and aboveground productivity we used three consecutive Spanish Forest Inventory censuses covering *c.* 30 years. We observed that despite increasing aboveground productivity over time, there has been an aggravation of the negative effects of climate change and increased competition on forest demography, reducing ingrowth and growth, and increasing mortality. In addition, we found that forest structure was the main driver explaining shifts in forest demography, opening a window of opportunity to reduce climate change impacts on forest ecosystems through forest management by reducing tree competition.

In Ch.4 “Anthropogenic legacies underpin climate change-related risks to forests”, we explicitly tested how forest-use legacies persisting in the distribution, structure, and composition of forest ecosystems can interact with climatic stressors to increase the probability of forest decline. For this aim, we first summarised hypotheses on the processes and drivers leading to detrimental legacy effects based on existing literature, and then introduced a risk-based framework to identify forest-use legacies and quantify the impact of their interaction with climate-related stress on forest responses. Finally, we applied the framework to an existing dataset to show that detrimental forest-use legacy effects contribute to large-scale risk of tree mortality at the driest distribution edge of the Scots pine (*Pinus sylvestris* L.).

Finally, in Ch.5 “Land- and forest-use legacies modulate tree growth synchrony in response to climate change through changes in forest structural diversity”, we sought to better understand the mechanistic relationship between forest-use legacies and European beech (*Fagus sylvatica* L.) tree growth synchrony in response to climate change by intensively monitoring an area with similar biotic and abiotic conditions and a well-documented socio-ecological history. We observed an increase in tree growth synchrony in response to increasing climate change impacts in the period 1970-2020. However, land- and forest-use legacies modulated the magnitude of increases in growth synchrony through changes in forest structural diversity, with recently-established forests having the greatest tree growth synchrony and large trees and heterogeneous size distributions decreasing growth synchrony.

It is worth mentioning that this thesis has an important collaborative component between scientists, managers and decision makers. An example of this is that Ch.5 has been funded by a project funded by the municipality of Oñati (Gipuzkoa, Spain) where I had the opportunity to be PI of the project (see in Table 1.1 some contributions directly related to each chapter and the curriculum vitae for further information). Another component to which we have been committed throughout the thesis has been the transfer of knowledge, as evidenced by the publication of a book on the state of Spanish forests as natural solutions to climate change or the scientific seminars and informative talks given during the thesis. I also had the opportunity to do a 3-month international stay at the University of Birmingham and a 3-month national stay at the Universidad de Sevilla, strengthening links with various research groups and fostering collaboration between scientists from different institutions that is yielding results in the form of scientific articles. Furthermore, since it is a thesis with heavy use of big data and computational skills, the thesis has also provided results in the form of R packages and related publications and workshops, as well as being one of the coordinators of the Ecoinformatics group of the Spanish Ecological Association of Terrestrial Ecology (AEET). I have also been part of evaluation committees for the evaluation of official degrees and a reviewer of several scientific articles. Finally, I had the chance to actively support in teaching activities and co-supervised two bachelor’s thesis.

Table 1.1. Overview of the main objectives, processes, drivers, spatio-temporal extents, data sources and main analyses in parentheses, and publication status of the Chapters 2-5 of the PhD thesis. The numbers in parentheses following each chapter show some contributions directly related to that chapter.

	Objective	Processes	Drivers	Spatio-temporal extents	Data sources (main analyses)	Publication status
Chapter 2 (1,2)	Quantify recent changes in species abundance (i.e. changes in population density) as a function of climate and forest succession, and assess the effect of species climatic affiliation, species traits and species range size	Tree recruitment and mortality	Climate change & forest structure	*Spatial:* Continental (Northern Hemisphere) *Temporal*: Decadal	Forest inventory data, species trait data and chorological maps (Generalised Additive Models and Linear Mixed Models)	To be submitted (*PNAS*)
Chapter 3 (3)	Examine whether climatic and structural changes are altering the time stability of climate-forests relationships	Tree recruitment, growth and mortality	Climate change & forest structure	*Spatial*: Regional (Iberian Peninsula) *Temporal*: 30 years	Forest inventory data (Structural Equation Models and Linear Mixed Models)	Published (*Global Change Biology)*
Chapter 4 (4)	Analyse how forest-use legacies persisting in the distribution, structure, and composition of forest ecosystems can interact with climate to increase the probability of forest decline	Forest structure, composition and distribution (conceptual) Tree mortality (data)	Climate change & forest-use legacies	*Spatial*: Regional (Iberian Peninsula) *Temporal*: Decadal	Forest inventory data and regions of provenance for forest species information (Generalised Linear Models)	Submitted (*Trends in Plant Science*)
Chapter 5 (5,6)	Understand how land- and forest-use legacies modulate tree growth synchrony in response to climate change	Tree growth	Climate change & forest-use legacies	*Spatial*: Local (Oñati, Gipuzkoa) *Temporal*: 50 years	Tree-ring data, aerial photographs, forest management archives and local interviews (Network analyses and Linear Mixed Models)	To be submitted (*Ecosystems / Agricultural and Forest Meteorology*)

1. International 3-months stay at the University of Birmingham (UK) with D. Thomas Pugh and D. Adriane Esquivel-Muelbert
2. National 3-months stay at the Universidad de Sevilla with D. Francisco Rodríguez-Sánchez
3. *Effect of climate change on the structure and dynamics of Iberian forests* (Project funded by Becas Leonardo a Investigadores y Creadores Culturales 2018. Fundación BBVA; 2018-2020; PI: P. Ruiz-Benito; 38,989.67€)
4. *Data-driven models of forest drought vulnerability and resilience across spatial and temporal scales: application to the Spanish climate change adaptation strategy (DARE)* (Coordinated project funded by Ministerio de Ciencia, Innovación y Universidades. Proyecto Retos Coordinados; 2019-2022; PI: Miguel A. Zavala; 96,000€)
5. *Forest management legacies as a modulator of tree growth responses to climate change* (Project funded by the Municipality of Oñati; 2020-2023; PI: J. Astigarraga; 4,155.72€)
6. Create *trini* R package: https://zenodo.org/record/7193360

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Chapter 2

Recent dynamics of Northern Hemisphere tree species along climatic and successional gradients

Astigarraga, J., Esquivel-Muelbert, A., Ruiz-Benito, P., Rodríguez-Sánchez, F., Zavala, M. A., Gazol, A., Vilà-Cabrera, A., Schelhaas, M. J., Cienciala, E., Dahlgren, J., Govaere, L., König, L., Kunstler, G., Lehtonen, A., Talarczyk, A., Woodall, C. W., & Pugh, T. A. M. Recent dynamics of Northern Hemisphere tree species along climatic and successional gradients

Abstract

Northern Hemisphere forests are in transition in response to increased atmospheric CO_2 and N fertilisation, and climate change. The consequences of such changes in tree species are not well understood, largely because they are confounded by human-induced changes in forest succession. Here, we analysed changes in species abundance across Northern Hemisphere forests and quantified a dominant trend of increasing abundance towards cold and wet regions of the species ranges, and decreasing towards warm and arid regions, even controlling for forest succession. Although mainly warm-affiliated species with broad temperature niches increased in abundance in warm and arid regions of their climate range, we observed multiple directions in species responses to climate, highlighting different species climatic sensitivity. We observed strong interactive effects of climate and forest succession driving changes in species abundance for *c.* 70% of species, but the relative contribution of forest succession was two times greater than the contribution of climate. Our results show that, even if past disturbances strongly alter the way in which Northern Hemisphere forests are influenced by climate, tree species are responding to climate change increasing in abundance towards cold and wet regions of their climate range. The observed species divergent responses to climate could help to select species that are best adapted to future climate change-related risks, while implementing conservation measures for those less well adapted.

Resumen

Los bosques del hemisferio norte están en transición en respuesta al aumento de la fertilización del CO_2 atmosférico y N, y del cambio climático. Las consecuencias de estos cambios en las especies arbóreas siguen siendo inciertas, en gran medida porque se distorsionan con la sucesión forestal. Aquí, analizamos los cambios en la abundancia de especies en los bosques del hemisferio norte y cuantificamos una tendencia dominante de aumento en la abundancia hacia las regiones frías y húmedas del área de distribución de las especies, y de disminución hacia las regiones cálidas y áridas, incluso controlando por la sucesión forestal. Aunque principalmente la abundancia de las especies con nichos térmicos cálidos y amplios aumentó en las regiones cálidas y áridas de su rango climático, observamos múltiples direcciones en las respuestas de las especies al clima, lo que pone de manifiesto la diferente sensibilidad climática de las especies. Observamos fuertes efectos interactivos entre el clima y la sucesión forestal impulsando los cambios en la abundancia de especies para el *c.* 70% de las especies, pero la contribución relativa de la sucesión forestal fue dos veces mayor que la contribución del clima. Nuestros resultados muestran que, a pesar de que las perturbaciones pasadas alteran fuertemente la manera en que los bosques del hemisferio norte están influenciados por el clima, las especies arbóreas están respondiendo al cambio climático aumentando su abundancia hacia las regiones frías y húmedas de su rango climático. Las respuestas divergentes de las especies observadas al clima podrían ayudar a seleccionar las especies mejor adaptadas a los futuros riesgos climáticos de los bosques, al tiempo que se aplican medidas de conservación para las no tan bien adaptadas.

2.1. Main text

Humans are strongly altering forest dynamics worldwide, reducing forest age, simplifying their structure and altering their composition by changing disturbance regimes and land-use change (McDowell et al., 2020). Human-induced shifts in tree demography have direct implications for ecosystem functioning by driving key ecosystem components such as species distribution, forest composition and carbon dynamics (Batllori et al., 2020; Fei et al., 2017; Zhang et al., 2018). In Northern Hemisphere forests, forest productivity and extension has increased substantially since the 1980s mainly due to CO_2 and N fertilisation and legacies of past disturbances, respectively (Song et al., 2018; Zhu et al., 2016). In addition, intensive forest harvesting has decreased tree age and increased tree density and biomass (McGrath et al., 2015; Pugh et al., 2019; Rautiainen et al., 2011). Such alterations in forest succession influence forest demographic responses to climate by modifying tree competition (Bradford & Bell, 2017; Young et al., 2017). Recent evidence suggests that the interactive effect of forest succession and climate drive forest dynamics, with a larger effect of forest succession (Astigarraga et al., 2020; Zhang et al., 2015). However, temperature and water availability also play a key role in shaping forest dynamics (Babst et al., 2013; Hampe & Petit, 2005), and since temperature and water deficit are increasing due to climate change, shifts in species abundance towards colder and wetter regions are expected (Lenoir & Svenning, 2015). Thus, to predict how Earth's forests will respond to global environmental change, it is essential to quantify the extent to which changes in species abundance are affected by climate (i.e. tree species climatic sensitivity). However, there are still large uncertainties about how species demography is changing along climatic gradients (Fei et al., 2017; Kunstler et al., 2021; Rabasa et al., 2013; Wason & Dovciak, 2017; Zhu et al., 2014), in part because the effect of human-driven shifts in forest succession has not been elucidated. Assessing large-scale demographic responses to climate is crucial, as demographic changes underlie changes in tree distribution and species turnover and therefore, ecosystem functioning and Earth system feedbacks (Bonan, 2008).

Here, we analysed Northern Hemisphere forests with national forest inventories from Europe and North America, considering 74 widely-distributed species across 127,707 plots over the period 1985-2019 (Table 2.S1). We quantified recent changes in species abundance (i.e. changes in population density) as a function of climate and forest succession, and assessed the effect of species traits, species range size and the climatic affiliation of species to specific temperature and aridity niches. We anticipated that species demography will be more affected by forest succession than by climate. Nonetheless, we expected to find decreases in species abundance in warm and arid regions of species climate ranges and increases in cold and wet regions, particularly in late successional stage forests due to the greater vulnerability of large trees to climate (Bennett et al., 2015; McDowell & Allen, 2015). Furthermore, we hypothesised that species climatic affiliation might play an important role shaping species climatic sensitivity because shifts in forest composition towards arid- and warm-affiliated species have been documented in multiple regions of the world (Batllori et al., 2020; Esquivel-Muelbert et al., 2019; Gottfried et al., 2012; Trugman et al., 2020). Finally, we expected that species demographic responses to climate will also differ according to seed size and wood density, which are critical to tree recruitment and mortality, respectively (Díaz et al., 2016; Greenwood et al., 2017), and that species with larger ranges (i.e. temperature and aridity niche width) will be less affected by climate, as they may have greater genotypic and phenotypic plasticity (Bussotti et al., 2015).

Species abundance changes over the time window differed according to the position of the population in the temperature and aridity range of its species (Fig. 2.1A, B). For over half of the species the lowest values of changes in species abundance occurred in warmest regions of their climate range (54% of the species, see cells on the right named as “warm” in Fig. 2.1A, B; Table 2.S4.1, Fig. 2.S4.1 and Fig. 2.S4.2) while half of the species had the largest values of changes in species abundance in coldest regions (46% of the species, see cells on the left named as “cold” in Fig. 2.1A, B; Table 2.S4.1, Fig. 2.S4.1 and Fig. 2.S4.2). From the species with the lowest values of changes in species abundance in warm regions, 72% decreased in abundance and from the species with the largest values in cold regions, 88% increased in abundance. Shifting species abundance toward colder regions could be an early signal of a shift in species ranges towards colder regions, which is consistent with the expected pattern under increased warming (Lenoir et al., 2020).

Species abundance increased in Northern Hemisphere forests with greater increases for European species than U.S. species (Fig. 2.1C, D). The overall increase in species abundance on both continents agrees with the observed trend in tree productivity in Northern Hemisphere forests, especially in Europe (Zhu et al., 2016). Interestingly, we found that south European species showed the greatest increases in species abundance. This result might be due to agricultural abandonment followed by natural regrowth that is leading to an increase in tree density in south Europe (Astigarraga et al., 2020), suggesting an interaction between climate and land-use change affecting tree demography (Goring & Williams, 2017). Thus, the balance between different species leading and trailing edge drove an increase in species abundance in warm regions in Europe. On the contrary, warm and arid regions of the U.S. had the lowest values in species abundance (Fig. 2.1D, cell id 9), highlighting a general negative effect of increased warming and aridity on tree abundance (Bradford & Bell, 2017).

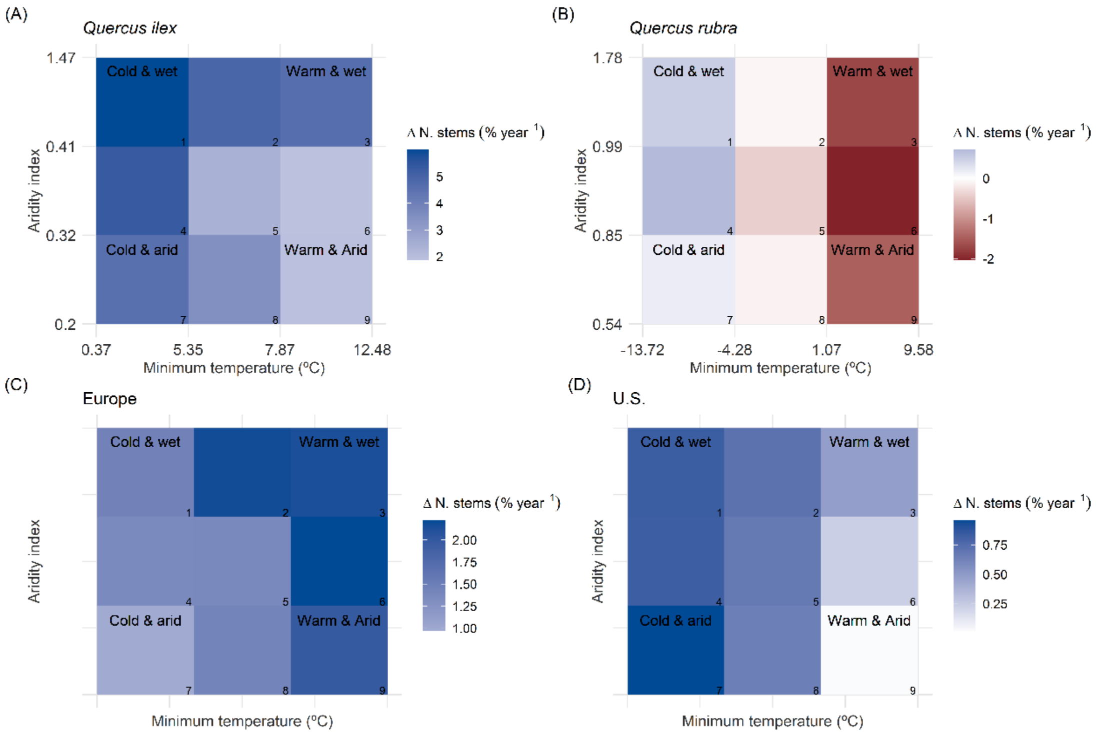

Figure 2.1. Changes in species abundance across climate range. Mean changes in species abundance (i.e. annual changes in the number of stems, %) across the climate range of (A) *Quercus ilex* and (B) *Quercus rubra*, showing the lowest values in the number of stems in warm regions and the largest values in cold regions. Mean changes in species abundance for (C) all European species and (D) all U.S. species. The climate range is quantified dividing minimum temperature and aridity index into the first, second and third terciles. Note that legends are on different scales and (C) and (D) minimum temperature and aridity index are dimensionless because it is the mean of all species in the climate range of each species. The number in the bottom-right corner in each cell corresponds to each cell id.

Both climate and forest succession drove changes in species abundance. Of all the species analysed, 69% of species showed changes greater than ± 1% year^{-1} due to climate and forest succession, with 5% of the species due to climate and 24% of the species due to forest succession (see e.g. in Fig. 2 *Quercus robur* and *Pinus echinata* affected more than ± 1% year^{-1} by both climate and forest succession; Table 2.S4.2), Climate had an effect of ± 1.4% year^{-1} in changes in species abundance while the effect of forest succession was two times higher (± 3% year^{-1}; Table 2.S4.2). These findings are consistent with previous studies suggesting that mainly forest succession followed by climate drive forest dynamics (Astigarraga et al., 2020; Zhang et al., 2015). In general, species abundances decreased in warm and arid regions of their ranges compared to cold and wet regions. For instance, when setting forest succession in observed, early or late forest succession values, over 61% of the species had greater values in cold and wet regions than in warm and arid regions (Fig. 2.2, Fig. 2.S4.5 and Fig. 2.S4.6). We inferred that increasing abundance in cold and wet regions of species climate range and decreasing in warm and arid region, whilst controlling for forest succession, was a result of climate change as no other driver could explain such a pattern for so many species on two different continents. We observed the greatest increases in species abundance in early successional forests following the expected pattern in early stages of forest succession where recruitment is higher than mortality. For example, when setting minimum temperature and aridity index in cold and wet, median climate, or warm and arid regions of each species climate range, 97% of the species had greater values in early successional stage than in late successional stage (Fig. 2.2, Table 2.S4.2, Fig. 2.S4.3 and Fig. 2.S4.4; Westoby, 1984). In contrast, late successional stage forests showed mainly declines in species abundance as large trees might be more vulnerable to climate (Bennett et al., 2015; McDowell & Allen, 2015) and the increment of climate-driven forest disturbances in recent years (Fig. 2.2, Table 2.S4.2, Fig. 2.S4.3 and Fig. 2.S4.4) (Allen et al., 2010; Forzieri et al., 2021; Senf et al., 2020). The combination of decreasing species abundance in warm and arid regions of species ranges in late successional stage forests with increasing abundance in early successional stage forests, indicates that past human disturbances that alter forest succession have a strong effect on how the current dynamics of Northern Hemisphere forests are influenced by climate.

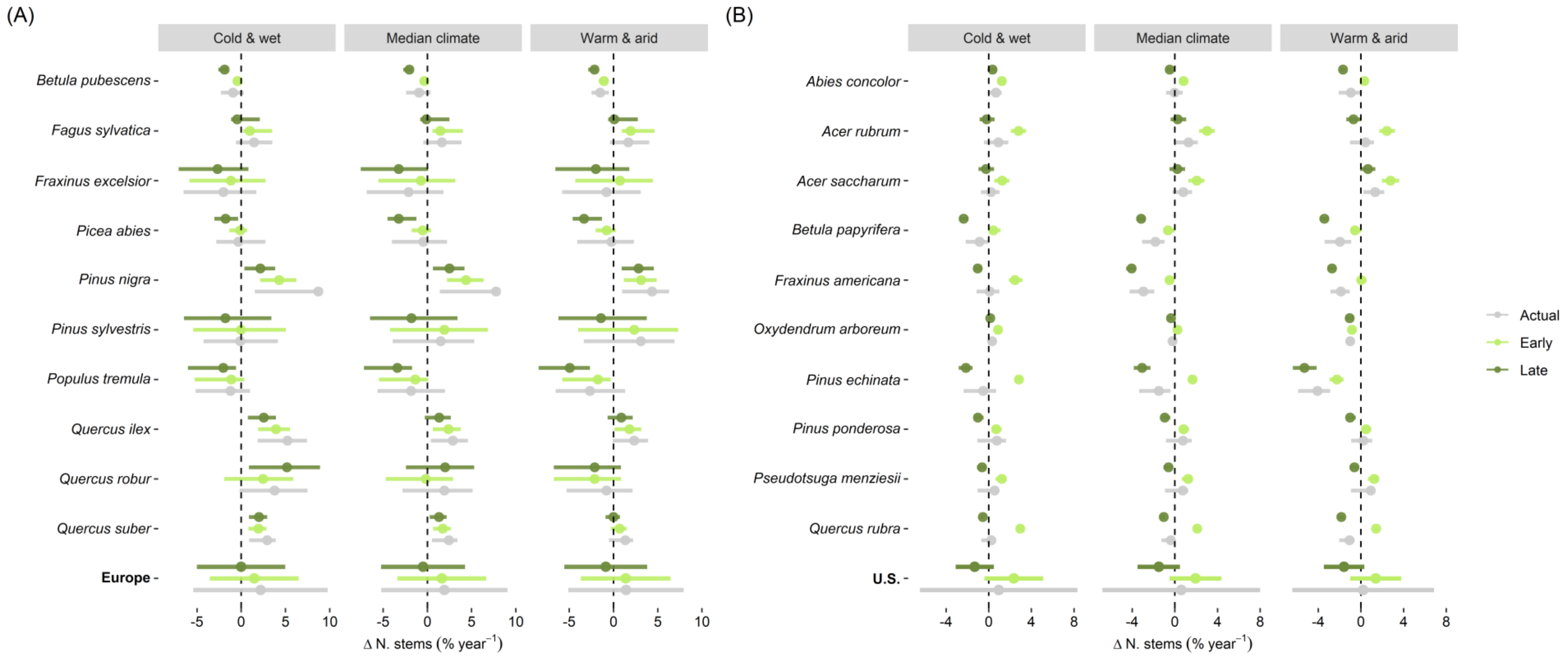

Figure 2.2. Climatic and successional gradients determine changes in species abundance. Changes in species abundance (i.e. annual changes in the number of stems, %) as predicted by species-level models when setting minimum temperature and aridity index in cold and wet, median climate, and warm and arid regions of each species climate range, and setting forest succession in actual (i.e. forest succession observed in the plot), early and late forest succession values (see *Methods*). Points indicate mean changes in species abundance and intervals 50% uncertainty, negative values indicate decreases in abundance and positive values increases. The selection of species for representation was made by covering climate gradients of Europe and the U.S. and selecting species that were affected by more than ± 1% year^{-1} by both climate and forest succession, only by climate and only by forest succession. (A) European species and the general pattern when all European species are considered together (in bold); and (B) U.S. species and the general pattern when all U.S. species are considered together (in bold). Mean changes and uncertainty in species abundance for Europe and the U.S. are weighted means and weighted standard deviation of changes in species abundance, respectively, with weights set as the inverse of sampling frequencies, so that all species have equal weight. Note that the plots are on different scales.

Species niche and traits determine the climatic sensitivity of tree species with a stronger effect on European species than North American species (Fig. 2.3). Warm-affiliated species with broad temperature niche width increased species abundance in warm and arid regions of their climate range, while cold-affiliated species with narrow temperature niche width increased species abundance in cold and wet regions. These results indicated that warm-affiliated species with broad minimum temperature niche width might be favoured under future scenarios of increased warming, consistent with previous results in mountain regions (Gottfried et al., 2012). In addition, in the U.S. wet-affiliated species increased in cold and wet regions in early successional stage forests suggesting a poleward species movement (Sharma et al., 2022). In contrast, in Europe wet-affiliated species with low seed dry mass increased in warm and arid regions which could be a response to past disturbance legacies, such as agricultural abandonment (Sánchez de Dios et al., 2021). Species with high wood density also increased species abundance in warm and arid regions of Europe in late successional stage forests which is consistent with previous studies indicating a greater ability of wood-dense species to cope with increased warming and aridity (Ruiz-Benito et al., 2017).

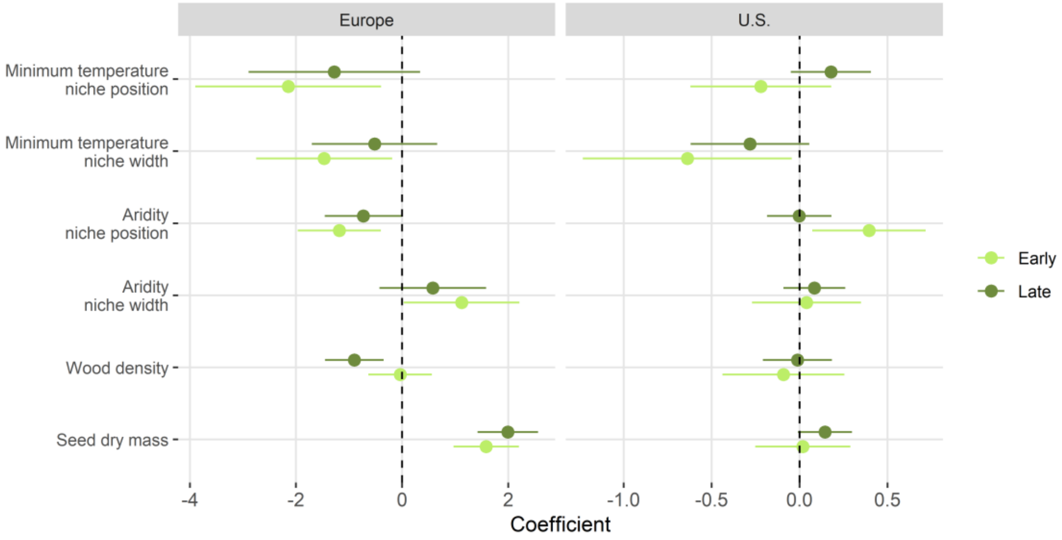

Figure 2.3. Drivers of species climatic sensitivity depending on successional gradient. Estimated coefficients ± 1 standard error for the regression of species climatic sensitivity on minimum temperature niche position and niche width, aridity niche position and niche width, wood density and seed dry mass. Positive coefficients indicate a greater increase in species abundance in cold and wet regions than in warm and arid regions when predictor X increases, and negative coefficients indicate a greater increase in warm and arid regions when predictor X increases. Note that the plots are on different scales.

Our results indicated that, although past human disturbances have a strong impact driving current dynamics of Northern Hemisphere forests, tree species are already responding to climate change increasing in abundance towards cold and wet regions of their climate range, addressing a big knowledge gap at the scale of two continents. The next frontier to better understand how species will respond to novel climatic conditions is to include further vital rates that that are critical in tree life cycle (e.g. fecundity and seedling establishment; Sharma et al. (2022)) and incorporate the impact of biotic interactions, as new assemblages may emerge due to increased human disturbances in the coming decades (Filgueiras et al., 2021; Paquette & Hargreaves, 2021). In addition, by showing evidence of recent shifts in species abundance in Northern Hemisphere forests, we tested with observational data the expected changes in forest dynamics reviewed by previous studies (McDowell et al., 2020). Finally, our findings quantifying species climatic sensitivity while considering previous anthropogenic changes at the stand level, have major implications for forest managers and policymakers to select species that are best adapted to future climate change-related risks, while implementing conservation measures for those less well adapted. These quantifications are a crucial step towards reducing the uncertainty over the future climate risk of forests (Anderegg et al., 2022), helping to anticipate reversing forest loss and contributing to tackle climate change, as set out in the first goal of the United Nations Strategic Plan for Forests 2030 (United Nations, 2017).

2.2. Materials and Methods

2.2.1. Forest inventory data

We analysed changes in species abundance using forest inventory data from extensive areas of Europe and the United States spanning between 1985-2019 (Table 2.S1.1). We used a total of 127,707 plots and analysed two consecutive forest inventory censuses with a census interval $\geq$ 4 years, $\geq$ 1 stem per plot in the first census and we excluded plots where all stems were removed between censuses. In the U.S. we also excluded macroplots (i.e. optional plots originating at the centre of the standard design subplots with a radius of 58.9 feet each). In plots where not all trees were measured in all subplots (e.g. variable radius plots) we randomly generated a truncated poisson distribution of tree abundance with λ equal to the number of trees extrapolated to the plot to add stochasticity. We calculated changes in species abundance as changes in the number of stems between two consecutive forest inventory censuses relative to the initial number of stems in the stand and the time elapsed between censuses. To select the most widely-distributed species, we extrapolated the number of stems to the hectare and aggregated the data into 0.1º × 0.1º grid cells (i.e. ~11.1 km at equator) and we only considered native species to Europe and the U.S. that have a good coverage in our dataset (i.e. species with $\geq$ 50,000 individuals of $>$ 12.7 cm in diameter at breast height and that were present in $\geq$ 500 cells and $>$ 1000 plots in our dataset). In total we selected 74 species (Table 2.S1.1).

2.2.2. Climate data

Since temperature and water availability are major constraints on tree demography, we quantified a climate range composed of minimum temperature and aridity index. To characterise minimum temperature, we used the mean temperature of the coldest quarter obtained from WorldClim 2 (Fick & Hijmans, 2017). Aridity was obtained from Global Aridity Index and Potential Evapo-Transpiration (ET0) Climate Database v2 (Trabucco & Zomer, 2019). This variable is based on the Global Aridity Index and it is calculated by dividing the mean annual precipitation by the mean annual reference evapo-transpiration, with its values increasing for wetter conditions. Both datasets provide 30 arc-seconds spatial resolution (~ 1km at equator) for the 1970-2000 period.

2.2.3. Species niche and traits data

To characterize species minimum temperature niche position and niche width, and species aridity niche position and niche width, we used species chorological maps for European species (Caudullo et al., 2018) and Little's range maps for U.S. species (Conservation Biology Institute; Prasad & Iverson, 2003). To quantify species minimum temperature niche position and niche width, we used the mean and standard deviation of minimum temperature across the whole species range, respectively. To quantify aridity niche position and niche width, we applied the same procedure to aridity as to minimum temperature. Trait data was downloaded from TRY Database (Kattge et al., 2020) and we used the mean of the standardised value of each species for each trait.

2.2.4. Analyses

First, we analysed how changes in species abundance varied across each species climate range. For this aim, we generated a climate range of minimum temperature and aridity index, dividing each climate variable into the first, second and third terciles (i.e. populations located between the 0-33%, 33-66% and 66-100% of each species distribution in our data set) and generating a climate range composed of 9 cells in total ranging from cold and wet to warm and arid regions.

Then we quantified the effect of climate and successional gradient on changes in species abundance across each species climate range by fitting generalised additive models (GAM; Pedersen et al. (2019)) to each species separately using *mgcv* R package (Wood, 2022). We modelled the number of stems in the second census as a function of the interaction of aridity, minimum temperature and forest succession of each plot, assuming a negative binomial family conditional distribution of the response with a *log* link function. We calculated forest succession based on the basal area of each plot with respect to the maximum basal area found in plots with similar climate and soil characteristics (Appendix 2.S2). We used a tensor product of aridity, minimum temperature and forest succession with cubic regression splines. We also included as fixed effects the interaction of the natural logarithm of the number of stems in the first census and census interval to control for the initial number of stems in the plot and the time elapsed between censuses, respectively. In addition, we included as an additive effect the country in which each plot was measured to control for different sampling methods and spatial autocorrelation of the plots, and an offset of the natural logarithm of stand area to control the different areas of the stands. We checked the covariation of the climate variables included in the model and diagnosed each species *gam* fit, checking the residuals plots with *mgcv*, *gratia* and *DHARMa* R packages (Hartig, 2022; Simpson, 2022; Wood, 2022). We also checked the relationship between the response and main effects with *visreg* R package (Breheny & Burchett, 2020), estimated smooths with *gratia* R package (Simpson, 2022), the performance of the model using *performance* R package (Lüdecke et al., 2022) and evaluating predictions on the observed data (Appendix 2.S3). All analyses were performed using R Statistical Software (v4.2.0; R Core Team 2022).

To quantify the sensitivity to climate and forest succession of species we used predictive comparisons (Gelman & Pardoe, 2007). To calculate the impact of climate on changes in species abundance, we made one prediction by setting minimum temperature in the first quartile and aridity index in the third quartile (i.e. cold and wet), another prediction by setting minimum temperature and aridity index in the second quartiles (i.e. median climate), and another by setting minimum temperature in the third quartile and aridity index in the first quartile (i.e. warm and arid) of each species climate range. Each of these three predictions was repeated three times: (i) using the observed forest succession values in the plot (i.e. actual); (ii) setting forest succession values to the first quartile when considering all species together (i.e. early forest succession); and (iii) setting forest succession values to the third quartile when considering all species together (i.e. late forest succession). Then we obtained changes in species abundance as the difference between the predictions of each model and the number of stems in the first census, relative to the initial number of stems in the stand and the time elapsed between censuses. The climatic sensitivity of each species was calculated as the difference in percentage between cold and wet regions, and warm and arid regions in actual, early and late successional stage forests. To test the effect of forest succession, we calculated the difference in percentage between early and late successional stage forests in cold and wet, median climate and warm and arid regions.

Finally, we analysed the effect of species niche and traits on species climatic sensitivity. To quantify climatic sensitivity, we also used the difference in percentage between cold and wet regions, and warm and arid regions. We fitted linear mixed effects models assuming a normal distribution of errors with *lme4* package (Bates et al., 2022). We used species minimum temperature niche position and niche width, aridity niche position and niche width, wood density and seed dry mass as additive fixed effects, and we included species identity and plot identity as random effects. We fitted the same model in early and late successional stage forests for climate sensitivities of $\pm$ 6% year^{-1} (i.e. data between 1st and 99th quantiles). All fixed predictors were standardised before being included in the models. We diagnosed each model fit, checking the residuals plots with *DHARMa* R package (Hartig, 2022) (Appendix 2.S3).

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Chapter 3

Evidence of non-stationary relationships between climate and forest responses: Increased sensitivity to climate change in Iberian forests

This chapter reproduces the article:

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Abstract

Climate and forest structure are considered major drivers of forest demography and productivity. However, recent evidence suggests that the relationships between climate and tree growth are generally non-stationary (i.e., non-time stable), and it remains uncertain whether the relationships between climate, forest structure, demography and productivity are stationary or are being altered by recent climatic and structural changes. Here, we analysed three surveys from the Spanish Forest Inventory (SFI) covering *c.* 30 years of information and we applied mixed and structural equation models to assess temporal trends in forest structure (stand density, basal area, tree size and tree size inequality), forest demography (ingrowth, growth and mortality) and aboveground forest productivity. We also quantified whether the interactive effects of climate and forest structure on forest demography and aboveground forest productivity were stationary over two consecutive time periods. Since the 1980s, density, basal area and tree size increased in Iberian forests, and tree size inequality decreased. In addition, we observed reductions in ingrowth and growth, and increases in mortality. Initial forest structure and water availability mainly modulated the temporal trends in forest structure and demography. The magnitude and direction of the interactive effects of climate and forest structure on forest demography changed over the two time periods analysed indicating non-stationary relationships between climate, forest structure and demography. Aboveground forest productivity increased due to a positive balance between ingrowth, growth and mortality. Despite increasing productivity over time, we observed an aggravation of the negative effects of climate change and increased competition on forest demography, reducing ingrowth and growth, and increasing mortality. Interestingly, our results suggest that the negative effects of climate change on forest demography could be ameliorated through forest management, which has profound implications for forest adaptation to climate change.

Resumen

El clima y la estructura forestal se consideran los principales impulsores de la demografía y la productividad de los bosques. Sin embargo, la evidencia reciente sugiere que las relaciones entre el clima y el crecimiento de los árboles son generalmente no estacionarias (i.e. no estables en el tiempo), y sigue siendo incierto si las relaciones entre el clima, la estructura forestal, la demografía y la productividad son estacionarias o están siendo alteradas por los cambios en el clima y estructura forestal recientes. Aquí, analizamos tres censos del Inventario Forestal Nacional que cubren *c.* 30 años de información y aplicamos modelos mixtos y de ecuaciones estructurales para evaluar las tendencias temporales en la estructura forestal (densidad del rodal, área basal, tamaño de los árboles y desigualdad de tamaño de los árboles), la demografía forestal (reclutamiento, crecimiento y mortalidad) y la productividad forestal aérea. También cuantificamos si los efectos interactivos del clima y la estructura forestal sobre la demografía y la productividad aérea fueron estacionarios a lo largo de dos periodos de tiempo consecutivos. Desde la década de 1980, la densidad, el área basal y el tamaño de los árboles aumentaron en los bosques ibéricos, y la desigualdad en el tamaño de los árboles disminuyó. Además, observamos reducciones en el reclutamiento y en el crecimiento, y aumentos en la mortalidad. La estructura forestal inicial y la disponibilidad de agua modularon principalmente las tendencias temporales de la estructura forestal y la demografía. La magnitud y la dirección de los efectos interactivos del clima y la estructura forestal sobre la demografía de los bosques cambiaron a lo largo de los dos periodos de tiempo analizados, lo que indica relaciones no estacionarias entre el clima, la estructura forestal y la demografía. La productividad forestal aérea aumentó debido al balance positivo entre el reclutamiento, el crecimiento y la mortalidad. A pesar del aumento de la productividad a lo largo del tiempo, observamos un agravamiento de los efectos negativos del cambio climático y del aumento de la competencia en la demografía forestal, reduciendo el reclutamiento y el crecimiento y aumentando la mortalidad. Curiosamente, nuestros resultados sugieren que los efectos negativos del cambio climático sobre la demografía forestal podrían reducirse mediante la gestión forestal, lo que tiene profundas implicaciones para la adaptación de los bosques al cambio climático.

3.1. Introduction

The increase in atmospheric CO_2 and the subsequent climate change are compromising human well-being (Costello et al., 2009; Jacobson et al., 2019) and could cause a major disruption in Earth's functioning (Rothman, 2019). Forests play a critical role in the world's functioning and climate change mitigation (IPBES, 2019; Millennium Ecosystem Assessment, 2005). Since the 1980s, forest productivity and carbon storage are increasing in the Northern Hemisphere (Pan et al., 2011) primarily due to forest regrowth in forest stands less than 140-years-old (Pugh et al., 2019). Previous studies have extensively documented the importance of climate and tree competition as drivers of forest demography and productivity (e.g., Vayreda, Martinez-Vilalta, Gracia, & Retana, 2012; Young et al., 2017; Zhang, Huang, & He, 2015), but recent evidence suggests that the relationships between climate and tree growth are non-stationarity (i.e., non-time stable, Wilmking et al., 2020). Forests are facing rapid demographic shifts in response to climate change and increased stand density worldwide (Allen et al., 2010; Jump et al., 2017; McIntyre et al., 2015; Zhou et al., 2013), and it remains uncertain whether the relationships between climate and forest responses are stationary or are being modulated by recent changes in both climate and forest structure.

In the last decades, climate change has translated into widespread increases in temperature and more frequent and intense droughts, particularly in water limited areas (IPCC, 2018). Warming and extreme droughts directly alter forest demographic responses (Fig. 3.1; Allen, Breshears, & McDowell, 2015; Anderegg, Kane, & Anderegg, 2013; Frank et al., 2015). However, climate change could also have indirect effects on forest demography modulated by forest structure (Fig. 3.1; Ruiz-Benito et al., 2017), given that management legacy effects and secondary succession can lead to high-density stands highly vulnerable to climate change (Jump et al., 2017; McDowell & Allen, 2015). Therefore, recent changes in climate and structure could underlie shifts in forest demography and aboveground productivity (Fig. 3.1). The quantification of the relative contribution of such drivers is a major challenge to understand and predict forest responses to global change.

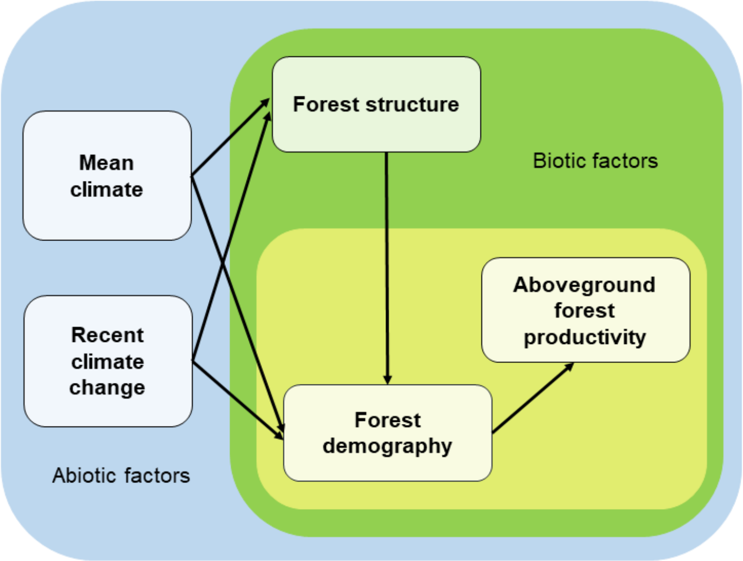

Figure 3.1. Theoretical flow diagram showing the relationships between climate (i.e., abiotic factors, blue box), forest structure (i.e., biotic factors, green box), forest demography and aboveground forest productivity (yellow box). Mean climate and recent climate change have direct and indirect effects on forest demography, the latter being modulated by forest structure. In turn, forest structure has a direct effect on forest demography, and, finally, forest demography has a direct effect on aboveground forest productivity.

Currently, the temporal trends observed in forest demography suggest a worldwide increase in tree mortality (Brienen et al., 2015; Peng et al., 2011; Senf et al., 2018; van Mantgem et al., 2009), while recruitment shows contrasting trends depending on the functional group analysed (Carnicer et al., 2014; Vayreda, Gracia, Martinez-Vilalta, & Retana, 2013). Tree growth has increased in temperate forests, while in drought-induced Mediterranean forests tree growth has generally decreased (Charru, Seynave, Hervé, Bertrand, & Bontemps, 2017; Ruiz-Benito et al., 2014). However, since the beginning of the 20th century forest density has increased in the Northern Hemisphere (McIntyre et al., 2015; Rautiainen, Wernick, Waggoner, Ausubel, & Kauppi, 2011; Zhou et al., 2013) and in high-density stands undergoing intense competition, decreased recruitment and growth (Linares, Camarero, & Carreira, 2009; Zhang et al., 2015) and increased mortality have been observed (Carnicer et al., 2011; Vilà-Cabrera, Martínez-

Vilalta, Vayreda, & Retana, 2011). Furthermore, the effects of changing climate and forest structure on forest demography might not be stationary due to stabilizing processes (Lloret, Escudero, Iriondo, Martínez-Vilalta, & Valladares, 2012; Valladares et al., 2014) and legacy effects of droughts, natural disturbances and management (Anderegg et al., 2015; Johnstone et al., 2016; Jump et al., 2017; Perring et al., 2018). Thus, further observational and modelling studies considering consecutive time periods are needed to better understand the time stability of the interactive effects of climate and forest structure on forest demography.

Functional traits of species determine contrasting strategies to cope with changing climate and forest structure (Carnicer, Barbeta, Sperlich, Coll, & Peñuelas, 2013; Díaz et al., 2016). Gymnosperms have shown a higher sensitivity to increased density than angiosperms mainly due to their lower competitive ability and shade-tolerance (Zavala, Espelta, & Retana, 2000). However, the greater sensitivity of gymnosperms to increased temperature and droughts than angiosperms is still under debate, because non-significant differences in gymnosperm and angiosperm forest responses to droughts have been obtained in some studies (Anderegg et al., 2016; Greenwood et al., 2017). Nonetheless, high wood density and low specific leaf area have been related to slower maximum growth and high competitive tolerance (Kunstler et al., 2016); alongside lower drought-induced mortality than species with opposite strategies (Anderegg et al., 2015; Greenwood et al., 2017). Thus, the underlying drivers of forest demography in response to changes in climate and forest structure could change depending on the forest type (Chen & Luo, 2015).

Here, we examined whether climatic and structural changes were altering the time stability of climate-forests relationships. Specifically, we analysed how forest demographic responses were altered by the direct effects of climate but also by the indirect effects modulated by forest structure over two consecutive time periods. To analyse changes over time, we focused on permanent forest plots (i.e., not recently established due to land-use changes or extreme disturbances) with three consecutive surveys from the Spanish Forest Inventory data set spanning *c.* 30 years (1986-2017). These plots cover from temperate to Mediterranean biomes, ranging from broad-leaved evergreen and deciduous forests to needle-leaved evergreen forests. Our specific aims were to: (i) analyse temporal changes in forest structure and demography in Iberian forests since the 1980s; (ii) quantify the underlying drivers of temporal changes in forest structure and demography; and (iii) unravel whether climate, forest structure, demography and productivity relationships were stationary over the two consecutive time periods. Our findings show how changes in forest structure can buffer the negative effects of climate change on a regional scale which has important implications for forest management and climate change adaptation.

3.2. Materials and Methods

3.2.1. Spanish Forest Inventory (SFI)

The study area covers the entire climatic gradient of peninsular Spain (43º 47’ 25’’ N – 36º 00’ 38’’ N, 3º 19’ 20’’ E – 9º 18’05’’ W), from oceanic climate in the north to semi-arid climate in the southeast (De Castro, Martin-Vide, & Alonso, 2005). Furthermore, multiple mountain ranges with treeline reaching up to *c.* 2400 m a.s.l., contrasting soil types principally composed by siliceous, limestone and clay soils (Instituto Geográfico Nacional, 2019) and great anthropogenic influence (Blondel, 2006), have led to large environmental heterogeneity and high forest diversity (Sainz Ollero, Sánchez, & García-Cervigón, 2010).

We used data from the second (1986-1996), third (1997-2007) and fourth (2008-2017) Spanish Forest Inventory (2SFI, 3SFI, and 4SFI, respectively) composed by plots systematically distributed on a 1-km^2 cell in all forests (i.e., forest cover over 5%, Villaescusa & Díaz, 1998). The SFI plots have a variable radius design with 5, 10, 15 and 25 m radius subplots where trees with a diameter at breast height (d.b.h.) of 7.5-12.4 cm, 12.5-22.4 cm, 22.5-42.4 cm and > 42.4 cm are measured, respectively. Tree height, d.b.h., species identity, distance to the centre of the plot, the position of the tree and tree status (alive or dead) are recorded for each adult tree (d.b.h. $\geq$ 7.5, Villaescusa & Díaz, 1998).

We used 10533 permanent plots with at least one adult tree in the 2SFI, 3SFI and 4SFI (236061 trees of *c.* 96 species, see Fig. 3.2 and Table 3.S1.1). We classified each plot as broad-leaved deciduous (2601 plots), broad-leaved evergreen (2346 plots), needle-leaved deciduous (nine plots), needle-leaved evergreen (5312 plots) and mixed forests (265 plots) if more than 50% of the basal area belonged to those functional groups or to a mix of them, and considered those forest types with at least 1000 plots (Fig. 3.2 and Table 3.S1.2). We also classified each plot as managed if there was any evidence of clear-cut or thinning observed during consecutive inventories.

In each SFI plot, we quantified forest structure, changes in forest structure, forest demography and aboveground forest productivity. Forest structure was characterised by stand density (i.e., Dens, No. trees ha^{-1}), stand basal area (i.e., BA, m^2 ha^{-1}), tree size (i.e., mean d.b.h., Size, mm) and tree size inequality (i.e., the coefficient of variation in d.b.h. calculated as the ratio of the standard deviation to the mean d.b.h., Ineq, dimensionless). Changes in forest structure were characterised considering the time between consecutive SFIs surveys to calculate changes in density (i.e., *Δ*Dens, No. trees ha^{-1} yr^{-1}), basal area (i.e., *Δ*BA, m^2 ha^{-1} yr^{-1}), tree size (i.e., *Δ*Size, mm yr^{-1}) and tree size inequality (i.e., *Δ*Ineq, yr^{-1}). We characterised forest demography through ingrowth (i.e., annual increase in basal area due to the incorporation of adult trees over consecutive inventories, m^2 ha^{-1} yr^{-1}), growth (i.e., annual increase in basal area of living trees over consecutive inventories, m^2 ha^{-1} yr^{-1}) and mortality (i.e., basal area lost annually by dead trees over consecutive inventories, only when mortality > 0, m^2 ha^{-1} yr^{-1}). Finally, aboveground forest productivity was characterised through net annual basal area changes per plot (m^2 ha^{-1} yr^{-1}, see correlations between basal area, aboveground biomass and carbon storage $\geq$ 0.82 in Fig. 3.S2.1).

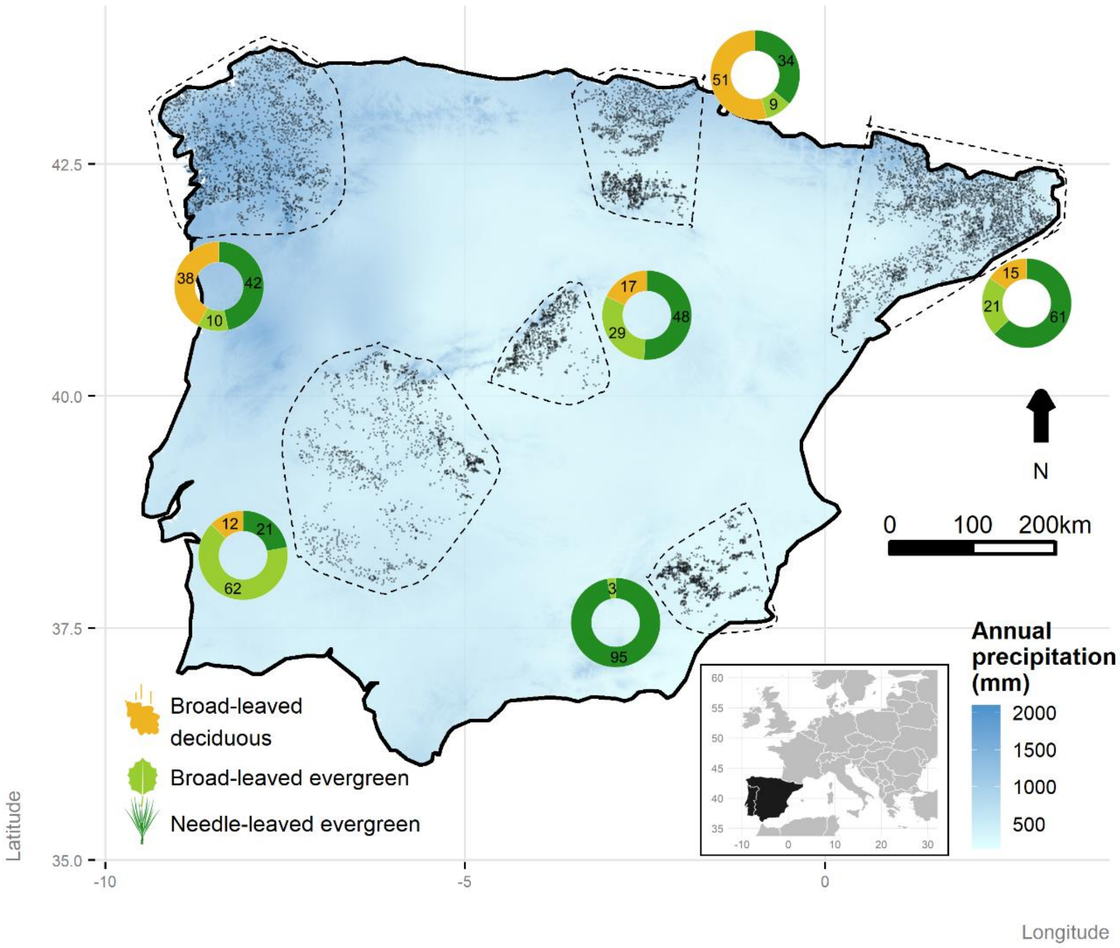

Figure 3.2. Spatial distribution of permanent plots (grey dots) of the second, third and fourth Spanish Forest Inventory over annual precipitation. Doughnut charts indicate the proportion of broad-leaved deciduous (orange slices), broad-leaved evergreen (light green slices) and needle-leaved evergreen (dark green slices) forest for each region. Annual precipitation data were obtained from WorldClim (Fick & Hijmans, 2017).

3.2.2. Climate data

We used high spatial (1 km^2) and temporal (weekly) resolution data created from complete observations from the Spanish National Meteorological Agency from 1961 to 2016 (Vicente-Serrano et al., 2017). From these data, first, we calculated water availability (WAI) through the relationship between annual precipitation (P) and atmospheric evaporative demand (AED) (i.e., WAI = (P - AED) / AED, %). Hence, water availability characterises the spatial climate variability. Negative WAI corresponds to arid regions and positive to wet regions. Moreover, we quantified recent climate change by temperature anomalies (TA) and the Standardised Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano, Beguería, & López-Moreno, 2009). Temperature anomalies were the absolute difference between the mean temperature of the study period of each plot (i.e., years between consecutive inventories) and the reference period (i.e., 1961-2016, see Ruiz-Benito et al., 2014). In the case of SPEI, we calculated the 18-months SPEI values of August because it considers the vegetative growth of the current and previous year (spring and summer). Afterwards, for the period between SFIs (i.e., between 2SFI and 3SFI, and between 3SFI and 4SFI) the minimum August SPEI (hereafter SPEImin) was selected to account for the potential influences of severe droughts episodes on forests (Pasho, Camarero, Luis, & Vicente-Serrano, 2011).

3.2.3. Statistical analyses

3.2.3.1. Temporal trends in forest structure and demography

To analyse temporal trends in forest structure and demography, we carried out an exploratory analysis of temporal changes using the mean changes over consecutive SFIs and the dispersion of variables related to forest structure and demography. In addition, we performed paired samples Wilcoxon test ($P < 0.05$) to analyse differences over consecutive SFIs for all forest types jointly, each forest type separately and each management status (i.e., managed and unmanaged) using R 3.6.0 (R Core Team, 2019).

3.2.3.2. Effect of climate and initial forest structure on changes in forest structure and demography

To quantify the effect of climate and initial forest structure on changes in forest structure and demography, we fitted linear mixed models (LMM, Pinheiro & Bates, 2006). Growth and mortality were ln-transformed (ln(growth) and ln(mortality+1), Fig. 3.S2.2) prior to the analyses. We used an identity link function with a normal distribution of residuals (Fig. 3.S2.3). Plot identity was used as a random term to account for temporal dependency resulting from repeated inventories (Fig. 3.S2.4). The fixed terms were initial forest structure (i.e., density, basal area, tree size and tree size inequality), climate (i.e., water availability, temperature anomalies and SPEImin) and the interactions between structural and climate variables. However, we did not consider interactions among structural variables and among climate variables because we chose depth rather than breadth in the conducted analyses. The fixed terms were standardised (Schielzeth, 2010), not strongly collinear ($r < 0.5$, Fig. 3.S2.5) and the linearity of each predictor with each response variable was checked (see partial residual plots in Fig. 3.S2.4).

Thereafter, the most parsimonious model was selected using Bayesian Information Criterion (BIC, Schwarz, 1978) considering both parsimony and likelihood (i.e., ΔBIC > 2 provides support to select the most complex model, Burnham & Anderson, 2002). To disentangle the effects of climate and structural variables and their pairwise interactions, we compared the most parsimonious model obtained from model comparison using BIC with models were each interaction or main effect was removed. As a measure of goodness of fit, we explored the distribution of the residuals along each explanatory variable and we obtained marginal and conditional R^2 (i.e., for the fixed and fixed plus random effects, respectively, Nakagawa & Schielzeth, 2013). We used *lme4* (Bates, Mächler, Bolker, & Walker, 2015), *MuMIn* (Barton, 2019) and *visreg* packages (Breheny & Burchett, 2017) in R 3.6.0 (R Core Team, 2019).

3.2.3.3. Climate, forest structure, demography and productivity relationships over two consecutive time periods: structural equation models (SEM)

To test whether the relationships between climate, forest structure, demography and productivity were stationary, we used structural equation models (SEM, Bollen, 1989). SEM allow combining multiple causal relationships between variables from multiple separate linear models into a single causal network (Grace, 2006; Shipley, 2000). We created a theoretical model to analyse the relationships between climate, forest structure, demography and aboveground productivity (see Fig. 3.1). Climate, structural and demographic variables were exogenous variables (i.e., explanatory variables in linear models). Endogenous variables (i.e., response variables in linear models) were those related to structure, demography and aboveground productivity. As the correlations between all exogenous and endogenous variables were high and we were not interested in explaining their effects, we considered correlations between the errors of structural and demographic variables in our SEM model.

Based on the theoretical model (Fig. 3.1), we tested whether recent changes in climate and forest structure were altering climate-forests relationships over time differentiating two data groups according to the SFI period: from 2SFI to 3SFI (23SFI) and from 3SFI to 4SFI (34SFI). To analyse causal relationships and their variances for two groups simultaneously, we fitted SEM using a multigroup analysis (Gazol & Camarero, 2012; Grace, 2006). If the pathways of the SEM held constant from 23SFI to 34SFI (Chi-Square (χ^2) test, $P > 0.05$), the effect was time stable over the two consecutive periods (i.e., stationary effect). To evaluate the SEM fits, we used the Comparative Fit Index (CFI $\geq$ 0.90), the Root Mean Square Error of Approximation (RMSEA < 0.08) and the Standardised Root Mean Square Residual (SRMR < 0.08, see Table 3.S4.1). SEM analysis was performed using *lavaan* package (Rosseel, 2012) in R 3.6.0 (R Core Team, 2019).

3.3. Results

3.3.1. Temporal trends in forest structure and demography in Iberian forests over the last three decades

The main trends in forest structure from 1986 to 2017 were towards decreases in mean tree size inequality and increases in mean density, basal area and tree size (Fig. 3.3), showing similar trends for all forest types and management status (Fig. 3.3, Fig. 3.S3.1 and Fig. 3.S3.2). All changes in structure were greater in 23SFI (1986-1996, 1997-2007) than 34SFI (1997-2007, 2008-2017; Fig. 3.3, Fig. 3.S3.1 and Fig. 3.S3.2). In forest demography, we observed trends of decreasing ingrowth and growth while mortality increased (Fig. 3.3). Those trends were maintained in each forest type, but needle-leaved forests had the greatest temporal differences in ingrowth, growth, mortality and aboveground forest productivity. Moreover, the highest values of temporal changes in forest demography were found in northern Spain (Fig. 3.S3.3).

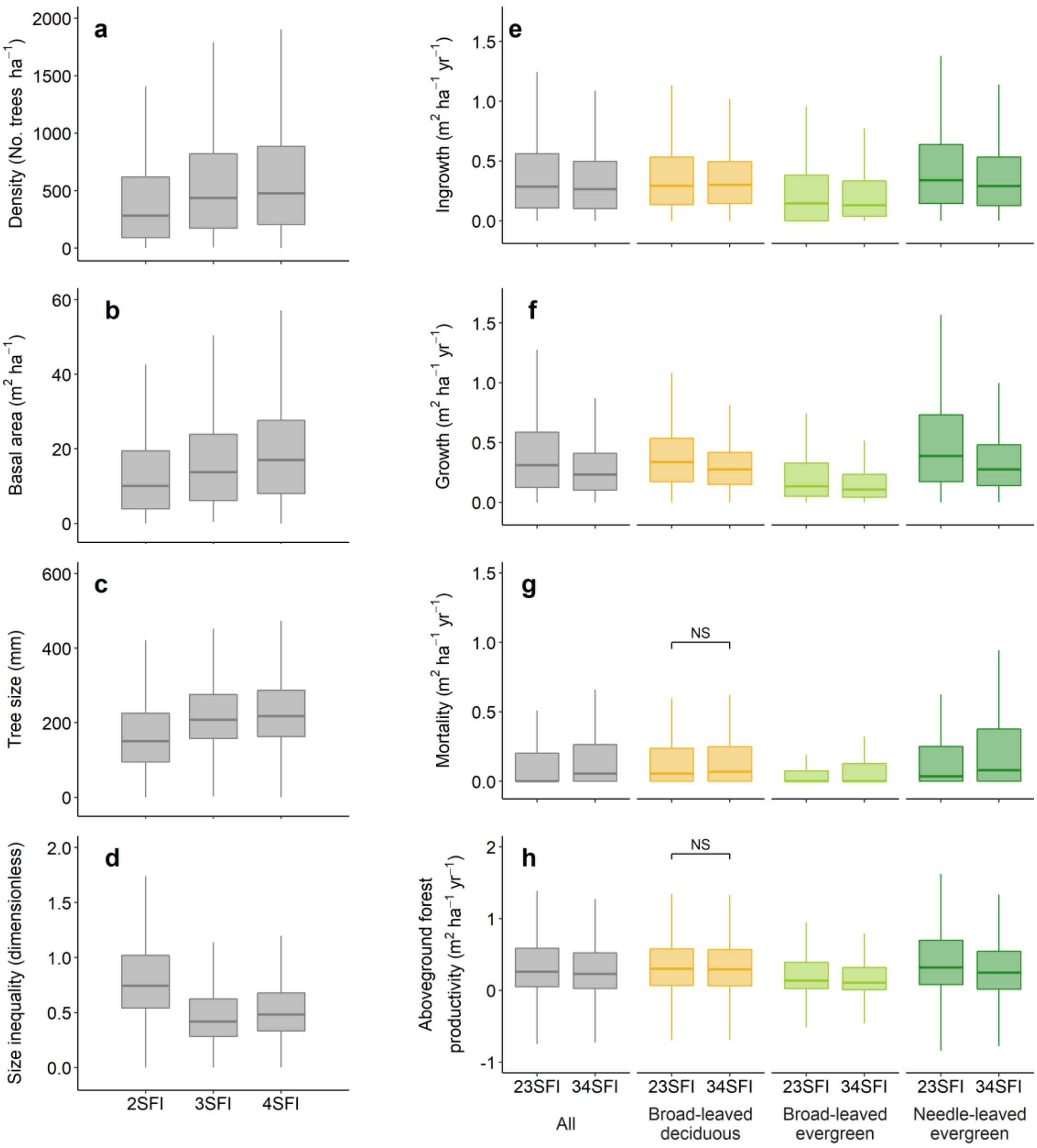

Figure 3.3. Forest structure and demography over three consecutive forest inventories. Box plots of forest structure over the second (2SFI), third (3SFI) and fourth (4SFI) Spanish Forest Inventory include (a) density, (b) basal area, (c) tree size, and (d) tree size inequality. Forest demography from 23SFI to 34SFI includes (e) ingrowth, (f) growth, (g) mortality and (h) aboveground forest productivity. Trends for all forests (grey box plots) and broad-leaved deciduous (orange box plots), broad-leaved evergreen (light green box plots) and needle-leaved evergreen (dark green box plots) forests are shown. NS indicate non-significant differences from 23SFI to 34SFI according to paired samples Wilcoxon test.

3.3.2. Interactive effects of climate and initial forest structure on changes in forest structure and demography

Through a mixed modelling analysis, we found that climate and initial structure underlay changes in forest structure and demography, with a greater relative importance of initial forest structure than climate (see *Δ*BIC in Table 3.1, with a bigger increase in BIC when removing structural than climate variables, and not strong differences depending on forest types in Table 3.S2.1). However, interactions between climate and structural variables strongly modulated temporal changes in forest structure and demography (see *Δ*BIC > 2 for interactions in Table 3.1). Analysing all forests jointly, the proportion of variance explained varied between 32% and 84% (see models of changes in tree size and tree size inequality, respectively in Table 3.1). Moreover, the interactive effects of water availability and basal area were especially strong underlying changes in forest structure and demography in all forest types analysed (see *Δ*BIC in Table 3.1 and Table 3.S2.1). Particularly, the interaction between water availability and basal area modulated changes in growth and mortality (Table 3.1, Fig. 3.4 and Table 3.S2.1). The highest growth and mortality rates were found in forests with high water availability and basal area (Fig. 3.4). Furthermore, water availability and density also played an important role, but to a lesser extent, underlying shifts in forest structure and demography (Table 3.1 and Table 3.S2.1).

Table 3.1. Comparisons of alternate models of changes in forest structure and demography to test the degree of support of the main effects and the interactions. Comparisons between models of changes in density, basal area, tree size, tree size inequality, ingrowth, growth and mortality based on Bayesian Information Criterion (BIC). The best models include the main effects and interactions between structural and climate variables supported in terms of *Δ*BIC (only the numbers of the variables that are included in the best model are shown). Structural variables are density (Dens), basal area (BA), tree size (Size), tree size inequality (Ineq); climate variables are water availability (WAI), temperature anomalies (TA) and SPEImin (SPEImin). The BIC of the best fitting model is compared with models in which each main effect and interaction is dropped (i.e., “No”). Therefore, the positive *Δ*BIC are shown if removing explanatory variables is not supported by BIC comparison. The combined effect of BIC when dropping all structural or climate variables and its interactions is also shown. Marginal and conditional R^2 (i.e., for the fixed and fixed plus random effects, respectively) are indicated for the best fitting model.

Models	Density	Basal area	Tree size	Size inequality	Ingrowth	Growth	Mortality
Best model	0	0	0	0	0	0	0
No Dens × WAI	231	18	12	-	20	320	-
No Dens × TA	-	-	-	-	46	-	-
No Dens × SPEImin	5	-	-	-	22	-	-
No BA × WAI	74	202	-	-	-	94	198
No BA × TA	5	45	-	-	-	6	16
No BA × SPEImin	-	-	-	-	-	-	-
No Size × WAI	107	19	26	-	-	-	38
No Size × TA	-	-	22	-	-	-	-
No Size × SPEImin	-	-	-	-	-	-	-
No Ineq × WAI	-	-	49	96	48	-	-
No Ineq × TA	-	-	-	-	-	-	-
No Ineq × SPEImin	-	-	-	-	-	-	-
No Dens	6395	1492	59	33	3748	2254	-
No BA	2669	1332	131	266	315	1221	3056
No Size	1000	136	342	14	86	330	93
No Ineq	595	9	1731	15784	251	1083	12
No WAI	246	397	93	369	1484	1031	606
No TA	27	39	63	26	43	1	40
No SPEImin	14	-	-	-	13	30	30
No interactions	227	229	64	96	225	430	195
No structure	12020	3652	6546	23276	7932	7084	3553
No climate	69	175	100	275	1510	663	416
R^2 marginal	0.51	0.23	0.32	0.75	0.48	0.51	0.30
R^2 conditional	0.51	0.41	0.32	0.84	0.60	0.74	0.41

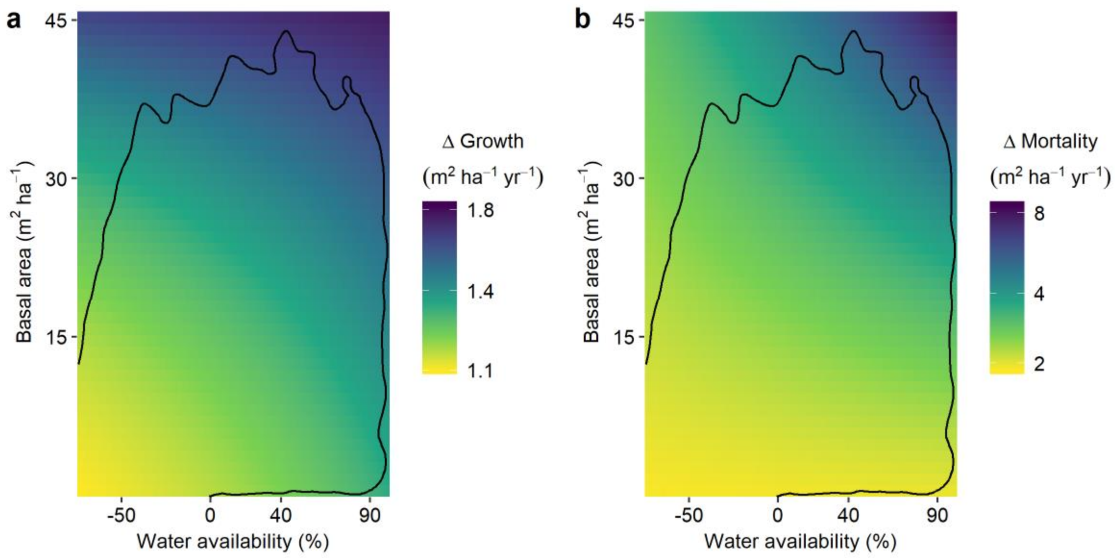

Figure 3.4. Interactive effects of stand basal area and water availability in (a) growth and (b) mortality. Yellow, green and blue colours show the magnitude of changes and black lines illustrate 95% of data used to generate the models.

3.3.3. Time stability of the relationships between climate, forest structure, demography and productivity

Using multigroup structural equation models based on the theoretical framework in Fig. 3.1, we found that climatic and forest structural changes were altering the relationships between climate, forest structure, demography and productivity over the two consecutive time periods analysed (i.e., 7 out of 36 paths were stationary from 23SFI to 34SFI, Table 3.S4.2). None of the structural variables considered in the analyses (stand density, basal area, tree size and tree size inequality) maintained their effects stationary on forest demography from 23SFI to 34SFI (Fig. 3.5 and Table 3.S4.2). Interestingly, tree size changed its effect on ingrowth from positive to negative from 23SFI to 34SFI (βSize in 23SFI = 0.275 and in 34SFI = -0.099, Table 3.S4.2), whereas stand density changed its effect on mortality from negative to positive (βDens in 23SFI = -0.072 and in 34SFI = 0.083, Table 3.S4.2). Moreover, even if other structural variables did not change the sign of their effects from one period to another, their effects decreased or increased considerably. In the period 23SFI, stand density had positive effects on growth (βDens = 0.480, Table 3.S4.2) and particularly on ingrowth (βDens = 0.865, Table 3.S4.2), but these positive effects decreased sharply in 34SFI (βDens in Growth = 0.156 and βDens in Ingrowth = 0.234, Table 3.S4.2). The effect of size inequality on ingrowth also decreased greatly (βIneq in 23SFI = 0.342 and in 34SFI = 0.076, Table 3.S4.2). On the contrary, the effect of basal area on growth increased substantially (βBA in 23SFI = 0.243 and in 34SFI = 0.490, Table 3.S4.2).

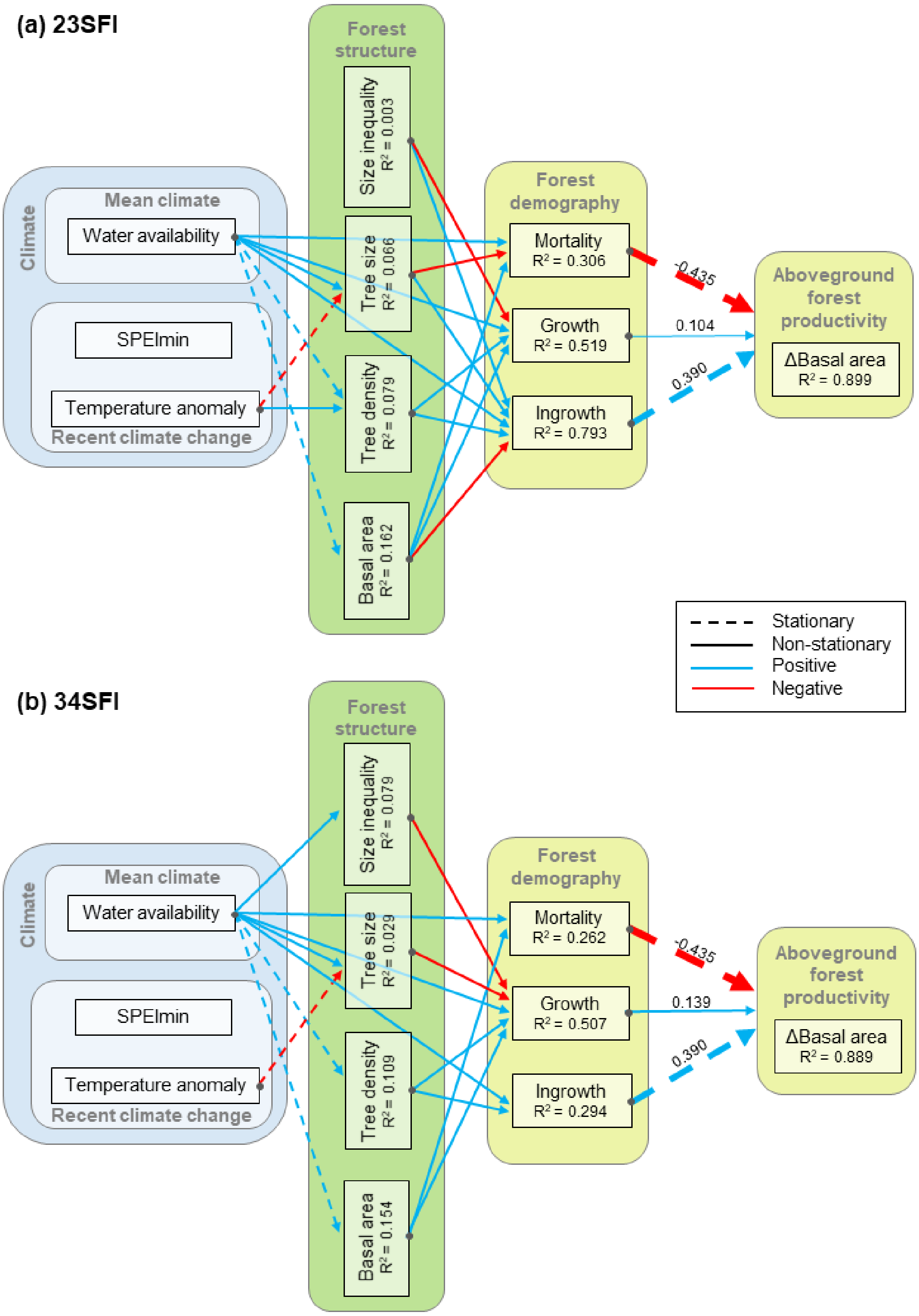

Figure 3.5. Multigroup structural equation models representing the relationships between climate, forest structure, demography and aboveground productivity over two consecutive time periods: (a) 23SFI (b) 34SFI. Variables are grouped in four categories characterising climate (blue box), forest structure (green box), forest demography and aboveground forest productivity (yellow boxes). Arrows indicate causal relationships between variables based on the theoretical model (Fig. 3.1) for parameter $\beta \geq 0.10$ (see all parameter values in Table 3.S4.2). Dashed lines illustrate stationary effects (i.e., time stable effects from 23SFI to 34SFI) and continuous lines indicate the opposite. Blue lines show positive effects

and red lines show negative effects. The estimated coefficients for ingrowth, growth and mortality are provided above their corresponding arrows and the thickness of these arrows have been scaled based on those magnitudes. The R^2 of the models in each period are shown below each response variable.

Climate variables had both direct and indirect effects (the latter modulated by forest structure) on forest demography (Fig. 3.6 and Table 3.S4.3). Water availability was the most influential variable with a positive effect on structural changes and forest demography (see positive βWAI in Table 3.S4.3). The effects of temperature anomalies and SPEImin were low but relevant and changed from 23SFI to 34SFI (Fig. 3.6 and Table 3.S4.3). In the case of temperature anomalies, direct effects changed from positive to negative (i.e., positive effects of temperature anomalies on ingrowth and growth in 23SFI, while negative effects in 34SFI), except in mortality in which we detected the opposite pattern (Fig. 3.6 and Table 3.S4.3). However, considering the total effects (i.e., the sum of direct and indirect effects) temperature anomalies had a positive effect on all demographic rates in 23SFI (Fig. 3.6 and Table 3.S4.3). In 34SFI the positive effect of temperature anomalies on ingrowth decreased (βTA in 23SFI = 0.106 and in 34SFI = 0.017, Fig. 3.6 and Table 3.S4.3) and the positive effect on mortality increased (βTA in 23SFI = 0.021 and in 34SFI = 0.074, Fig. 3.6 and Table 3.S4.3). The effect of temperature anomalies on growth changed from positive to negative over the two consecutive time periods (βTA in 23SFI = 0.202 and in 34SFI = -0.017, Fig. 3.6 and Table 3.S4.3).

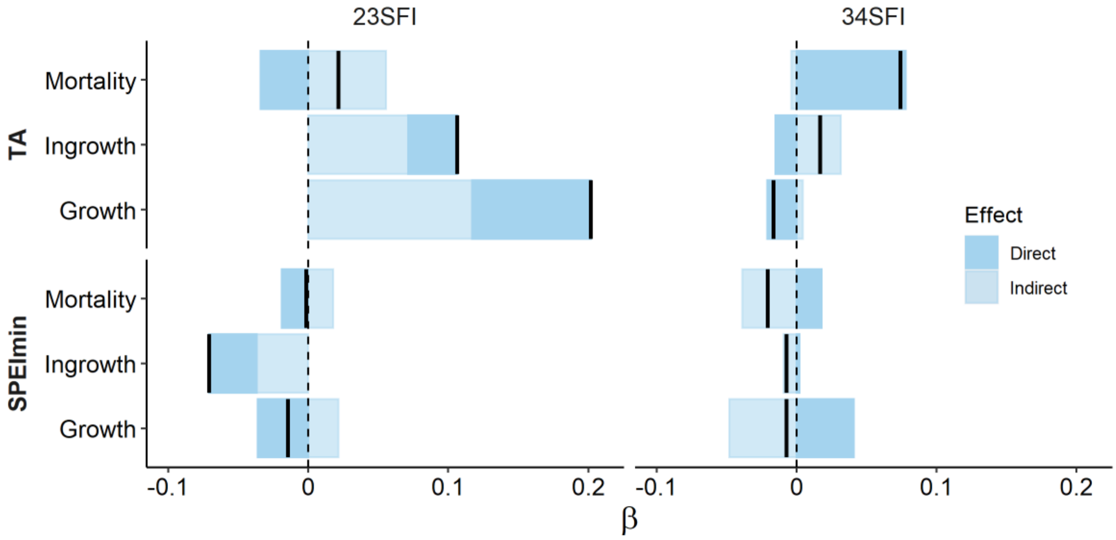

Figure 3.6. Effects of temperature anomalies (TA) and 18-month minimum SPEI (SPEImin) on mortality, ingrowth and growth over two consecutive time periods: 23SFI and 34SFI. β estimates of the direct (dark blue), indirect (light blue) and total (black continuous line) effects are shown. The indirect effects are modulated by forest structure and the total effects for each period are the sum of the direct and indirect effects.

The direct effect of SPEImin on forest demography changed from negative to positive (i.e., decreasing SPEImin or more severe droughts increased ingrowth, growth and mortality in 23SFI, but in 34SFI decreasing SPEImin decreased ingrowth, growth and mortality (Fig. 3.6 and Table 3.S4.3)). Nevertheless, the total effect of SPEImin on forest demography had negative effects in 23SFI and 34SFI. The negative effect on ingrowth decreased from one time period to another (βSPEImin in 23SFI = -0.071 and in 34SFI = -0.007, Fig. 3.6 and Table 3.S4.3), as well as in growth (βSPEImin in 23SFI = -0.014 and in 34SFI = -0.007, Fig. 3.6 and Table 3.S4.3). In contrast, the negative effect of SPEImin on mortality increased (βSPEImin in 23SFI = -0.001 and in 34SFI = -0.021, Fig. 3.6 and Table 3.S4.3). In summary, considering the total effects of temperature anomalies and SPEImin, warmer temperatures and more severe droughts increased mortality, decreased their positive effects on ingrowth and reduced growth from 23SFI to 34SFI.

Analysing the effect of forest demography on aboveground forest productivity we found that mortality was the most influential variable followed by ingrowth and growth explaining aboveground forest productivity (see parameter magnitude: βMortality = -0.435; βIngrowth = 0.390; βGrowth in 23SFI = 0.104 and in 34SFI = 0.139, Fig. 3.5 and Table 3.S4.2). Mortality had a negative effect on aboveground forest productivity, whereas ingrowth and growth had positive effects (Fig. 3.5 and Table 3.S4.2). However, the combined effect of ingrowth and growth was greater than the effect of mortality, which caused aboveground forest productivity to increase from 1980s to the present (see Fig. 3.3b). In addition, we observed that mortality and ingrowth maintained their effects stationary from 23SFI to 34SFI, while growth increased its effect over the study period (βGrowth in 23SFI = 0.104 and in 34SFI = 0.139, Fig. 3.5 and Table 3.S4.2).

Different numbers of paths were stationary in each forest type (15 paths in broad-leaved deciduous, 10 paths in broad-leaved evergreen and 7 paths in needle-leaved forests out of 36 paths in each case, Table 3.S4.2). Analysing the effect of forest demography on aboveground forest productivity, each forest type followed the same pattern observed for all forest types together, except for an increased mortality effect on aboveground forest productivity in needle-leaved forests and decreased in broad-leaved forests (Table 3.S4.2 and Fig. 3.S3.4). Furthermore, in broad-leaved evergreen and needle-leaved forests in the 23SFI period the effect of density on ingrowth and water availability on forest structure and demography was particularly strong (see βDens and βWAI in Table 3.S4.2). Water availability had a strong effect on density and tree size inequality in broad-leaved evergreen forests, and on density and basal area in needle-leaved forests (Table 3.S4.2). In the end, considering climate, forest structure and demography, the R^2 of the models of aboveground forest productivity was $\approx$ 0.9 in all forest types (Fig. 3.5 and Fig. 3.S3.4). To sum up, these results showed that in the last 30 years the relationships between climate, forest structure, demography and productivity were mostly non-stationary, in some cases even changing the sign of their effects.

3.4. Discussion

We found that since the 1980s Iberian forests are generally changing to denser and more homogeneous stands, with bigger trees, increased mortality and reduced ingrowth and growth. The temporal trends observed in forest structure and demography were driven by the interactive effects of climate and forest structure.

However, the patterns of changes in forest demography and productivity and the effect of their underlying climate and structural drivers were non-stationary, observing changes in the magnitude and even in the direction of the effects. Aboveground forest productivity increased over the last 30 years due to the positive balance between tree ingrowth, growth and mortality. Yet, we observed an aggravation of the negative effects of climate change and increased competition that led to decreased ingrowth and growth, and increased mortality. In most cases the direct and indirect effects of climate change on forest demography had opposite directions suggesting that changes in forest structure could ameliorate the negative climate change effects on forest demography and providing further evidence of the potential of forest management for climate change adaptation.

3.4.1. Temporal trends in forest structure and demography of Iberian forests follow similar trends of Northern Hemisphere forests

We observed increases in mean stand basal area and density together with decreases in size inequality over the last three decades. This finding suggests that Iberian forests are still relatively young forests in developing stages (Ruiz-Benito et al., 2014; Westoby, 1984), with a very low representation of old-growth forests in our data set (less than 3.4% and 1.3% of plots could be classified as old-growth forests by applying thresholds of 500 and 610 mm in d.b.h., respectively, according to Braumandl & Holt, 2000; McIntyre et al., 2015, see Fig. 3.S3.4). The increases in forest density and basal area over time could also be due to the abandonment of forest management (Seijo, Cespedes, & Zavala, 2018; Vayreda, Martinez-Vilalta, Gracia, Canadell, & Retana, 2016) and agricultural activities (Cruz-Alonso, Ruiz-Benito, Villar-Salvador, & Rey-Benayas, 2019; Poyatos, Latron, & Llorens, 2003; Vilà-Cabrera, Espelta, Vayreda, & Pino, 2017), and the subsequent large scale afforestations that increased tree density (McGrath et al., 2015; Villar-Salvador, 2016). The increase in aboveground forest productivity is consistent with trends previously reported in Northern Hemisphere forests (Pan et al., 2011; Pugh et al., 2019; Sarmiento et al., 2010). Furthermore, ingrowth and growth decreased, whereas tree mortality increased over time in Iberian forests (Fig. 3.3). Similar trends in forest demography have been observed in European (Carnicer et al., 2011; Senf et al., 2018) and North American forests (Luo, Chen, McIntire, & Andison, 2019; Peng et al., 2011; van Mantgem et al., 2009; Zhang et al., 2015), and have been related to increased competition and higher dependence of growth on water availability due to climate change.

We found that temporal changes in forest demography were greatest in northern Spain and needle-leaved forests. The faster dynamics of northern forests suggests that forest demography is strongly dependent on water availability (see steep gradient of water availability in Iberian forests in Fig. 3.2 and effects in Fig. 3.4). The high water availability of northern Spain could be promoting tree ingrowth, growth and mortality rates (Lecina-Diaz et al., 2018; Ruiz-Benito et al., 2014). On the other hand, the greatest temporal changes in needle-leaved gymnosperms could be due to their lower shade tolerance and competitive ability (Zavala, Espelta, Caspersen, & Retana, 2011).

We did not find any effect of recent management on forest demography in contrast with previous studies (Senf et al., 2018; Vayreda et al., 2012). This could be because Northern Hemisphere forests have been historically managed (FAO, 2015), which makes it difficult to disentangle recent management effects. In addition, the lack of detailed management or legacy data at large spatial scales in Europe is an additional difficulty to detect recent management effects (Ruiz-Benito et al., 2020). However, the greatest growth and mortality rates found in needle-leaved forests might be due to the lower competitive ability of gymnosperms than angiosperms (Vayreda et al., 2016; Zavala et al., 2000), but also to management legacies, such as afforestations in high-density stands (Ruiz-Benito, Gómez-Aparicio, & Zavala, 2012; Villar-Salvador, 2016).

3.4.2. Interactions between climate and forest structure drive forest demography

Initial forest structure and its interaction with climate were the main factors explaining changes in forest structure and demography, highlighting the key role of the interactive climate and forest structure effects on demography (Jump et al., 2017; Ruiz-Benito et al., 2017). We observed a greater relative importance of forest structure than climate in accordance with previous studies (Vayreda et al., 2012; Vilà-Cabrera et al., 2011; Zhang et al., 2015).

We found that especially the interaction between basal area and water availability underlay changes in forest structure and demography, with the highest growth and mortality rates at high basal area and water availability. The positive effect of basal area on tree growth and mortality depending on water availability could be explained through the self-thinning rule (Brunet-Navarro, Sterck, Vayreda, Martinez-Vilalta, & Mohren, 2016; Westoby, 1984). Increased basal area could be due to the abandonment of forest management (Vayreda et al., 2016), which generates stronger competition for resources than in non-abandoned forests and, therefore, increases climate change impacts (Bradford & Bell, 2017; Jump et al., 2017). At the same time, when water availability does not suppose a limitation for tree productivity, basal area might have a positive effect on tree growth and mortality in temperate forests (Ruiz-Benito et al., 2014).

3.4.3. Climate, forest structure, demography and productivity relationships are non-stationary

Our results showed that the relationships between climate, forest structure, demography and productivity were non-stationary due to climatic and forest structural changes. This result is in line with Wilmking et al. (2020) in which they observed that tree growth responses to climate are generally non-stationary. We found that 80% of all SEM paths changed from 23SFI to 34SFI, including changes in magnitude but also changes in the direction of the effect; from positive to negative in the effect of tree size on ingrowth, and from negative to positive in the effect of density on mortality. The decreasing effect of tree size on ingrowth and the increasing effect of density on mortality could be due to forest development and the self-thinning rule (see also the increasing effect of basal area on tree growth over time and trends of increasing density and basal area in Fig. 3.3; Brunet-Navarro et al., 2016; Westoby, 1984). Consequently, asymmetric competition and drought vulnerability might increase (Bradford & Bell, 2017; Young et al., 2017) leading to a decrease in ingrowth (Carnicer et al., 2014; Zhang et al., 2015) and increased mortality (Carnicer et al., 2011; Ruiz-Benito, Lines, Gómez-Aparicio, Zavala, & Coomes, 2013).

Forest demographic responses were modified by the direct effects of climate change but also by indirect effects. We observed that the direct and indirect effects of climate change on ingrowth, growth and mortality worked in opposite directions in 75% of all SEM paths (i.e., sign of β coefficients in 23SFI and 34SFI, see Fig. 3.6). This finding suggests that the direct negative effects of climate change could be buffered through changes in forest structure highlighting the key role of forest management for climate change adaptation (Vilà-Cabrera, Coll, Martínez-Vilalta, & Retana, 2018). Analysing the total effects of climate change (i.e., the sum of direct and indirect effects), we found that warmer temperatures and more severe droughts increased mortality and reduced growth from 23SFI to 34SFI. This finding could also be a consequence of forest development in which forests are getting older and bigger in size, and thus, their sensitivity to temperature might increase (Bennett et al., 2015; McIntyre et al., 2015; Olson et al., 2018; Zhou et al., 2013). In addition, beyond surpassing a temperature and drought severity and frequency threshold, positive climate change effects on demography (e.g., CO_2 fertilisation, longer growing seasons and increased water-use efficiency) could be offset by the negative effects of climate extremes (Allen et al., 2015).

Regarding the effect of forest demography on aboveground forest productivity over time, we observed a net increment due to the combined effect of ingrowth and growth. However, mortality was the most important variable explaining aboveground forest productivity, in accordance with a previous study showing that changes in functional composition in European forests were mainly driven by tree mortality (Ruiz-Benito et al., 2017). The effects of ingrowth and mortality on aboveground forest productivity did not change from 23SFI to 34SFI, whereas growth increased its effect over time. This finding agrees with the fact that ingrowth in 23SFI determines growth in 34SFI and suggests that forests are still growing and, therefore, increasing aboveground forest productivity.

Analysing by forest type we found that broad-leaved forests maintained more paths stationary than needle-leaved forests. These unstable responses of gymnosperms might be responding to increased competition, temperature and droughts during the study period (Gazol et al., 2018; Ruiz-Benito et al., 2017). Water availability had the strongest effect on forest structure and demography in needle-leaved and broad-leaved evergreen forests. In broad-leaved evergreen forests water availability had a particularly positive effect on tree density, basal area and tree size inequality. The observed effect of water availability could be related to the presence of open forests, agroforestry systems or *dehesas*, which are mainly located in southern Spain (low water availability) and have low density and tree size inequality (Plieninger, Pulido, & Konold, 2003; Pulido, Díaz, & Hidalgo De Trucios, 2001). In needle-leaved forests we found that water availability is especially critical for density and basal area increases, which might be due to highly dense and competitive afforestations in wet regions as northern Spain (Ruiz-Benito et al., 2014; Vayreda et al., 2012).

3.4.4. Temporal trends and drivers of Iberian forest demography and aboveground productivity: Implications for natural climate solutions

Forests have a considerable potential for climate change mitigation and a critical role as natural climate solutions, which aim to reduce and store carbon emissions in natural systems (Doelman et al., 2019; Griscom et al., 2017). Therefore, it is crucial to assess trends in forest demography and productivity, and to quantify the relative contribution of their climatic and structural drivers. Nevertheless, examining the stationarity of the effects of these drivers is also of paramount importance since climate change impacts on forests might not be time stable. In this sense, we found an increase in aboveground forest productivity of Iberian forests since the 1980s mainly driven by forest development and relatively benign climate conditions. However, since the beginning of the 21st century we observed an aggravation of the negative effects of climate change and increased competition, suggesting that forest management might play a key role (e.g. by decreasing tree competition) to mitigate these negative effects.

Our results suggest that past reconstructions and future projections of forest demography and productivity made under stationary assumptions could lead to misleading results since the relationships between climate, forest structure, demography and productivity are changing over time. Disturbances are also likely to amplify in the future and interact with drought and temperature stress which could further lead to non-stationary forest responses (Seidl et al., 2017). Old-growth or young forests may have different responses to climate (Ruiz-Benito et al., 2015; Stephenson et al., 2014). Nonetheless, due to the long-lasting human legacy on Iberian forests old-growth forests are very scarce (Blondel, 2006; FAO, 2013; Sabatini et al., 2018, see also Fig. 3.S3.4). In the present study we used permanent forest plots already established in the 1980s and we did not include new forests given that our objective was to examine whether climatic and structural changes were altering the time stability of climate-forests relationships. We suggest that future studies should further investigate the potential consequences of space-for-time substitutions (Johnson & Miyanishi, 2008) and consider key aspects as age-mediated forest responses to climate (Chen & Luo, 2015), non-linear growth-climate relationships (Lloret et al., 2012; Wilmking et al., 2020) and legacy effects (Anderegg et al., 2015; Johnstone et al., 2016; Jump et al., 2017; Perring et al., 2018).

Data Availability

Spanish Forest Inventory data were provided by the Spanish Ministry of Agriculture, Fisheries and Food (MAPA) and climate data were provided by the Spanish National Meteorological Agency.

Contributions by the authors

JA, EA, AG and PRB conceived and planned the research. JA, EA and PRB processed data and JA, EA, AG and PRB analysed them. JA, VCA and PRB design and performed the graphical representation. All authors contributed to the final version through several revisions.

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Chapter 4

Anthropogenic legacies underpin climate change-related risks to forests

This chapter reproduces the article sent for publication[2]:

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[2] The citation style language of this chapter is as required *by Trends in Plant Science*. Since we conducted a literature review and added the main references in Table 4.1, the numerical format allows for more space and therefore differs from the format of the other references in the thesis.

Abstract

Forest ecosystems with long-lasting human imprints are emerging worldwide as forest exploitation for extractive uses is abandoned. However, whether these anthropogenic legacies can exacerbate climate change impacts on forests is not well understood. Here, we set out how anthropogenic legacies of past forest exploitation that persist in the distribution, structure, and composition of forest ecosystems can interact with climate change stressors. We propose a risk-based framework to identify anthropogenic legacies in forest ecosystems and quantify the impact of their interaction with climate-related stress on forest responses. Considering anthropogenic legacies alongside environmental drivers of forest ecosystem dynamics will improve our predictive capacity of climate-related risks to forests and our ability to promote ecosystem resilience in regions dominated by human-modified forests.

Resumen

En todo el mundo están emergiendo ecosistemas forestales con huellas humanas duraderas a medida que se abandona la explotación forestal para usos extractivos. Sin embargo, no se conoce bien si estos legados antropogénicos pueden agravar los impactos del cambio climático en los bosques. Aquí, exponemos cómo los legados antropogénicos de la explotación forestal del pasado que persisten en la distribución, estructura y composición de los ecosistemas forestales pueden interactuar con los factores de estrés del cambio climático. Proponemos un marco basado en el riesgo para identificar los legados antropogénicos en los ecosistemas forestales y cuantificar el impacto de su interacción con el estrés climático en las respuestas de los bosques. La consideración de los legados antropogénicos junto a los impulsores ambientales de la dinámica de los ecosistemas forestales mejorará nuestra capacidad de predicción de los riesgos climáticos de los bosques y nuestra habilidad para promover la resiliencia de los ecosistemas en regiones dominadas por bosques modificados por los humanos.

4.1. Do anthropogenic legacies of past forest exploitation exacerbate climate-related risks to forests?

Humans have exploited forest ecosystems for millennia [1–3]. Given the magnitude of land-use changes, forest management practices, and plantation establishment over the last few centuries, recent humanity's footprint today shapes > 70% of the world's forests [4]. While the intensity of **forest exploitation** (*see glossary*) for extractive uses is still high in many regions [5,6], its abandonment has been also spreading since the post-1950's **great acceleration** [7]. As a consequence, forest exploitation and its subsequent abandonment is leading to the emergence of forest ecosystems with long-lasting human impacts (i.e., **human-modified forests**) worldwide [8,9] (Fig. 4.1). Although often assumed to influence forest dynamics, there is still a lack of understanding on how these human imprints may exacerbate the vulnerability of forest ecosystems to climate change [10–12]. However, such understanding is essential to better predict **climate-related impacts on forests** and define mitigation and adaptation priorities.

The response of forest ecosystems to climate change strongly depends on historical factors [13]. Past forest exploitation alters the stability of relationships between forest ecosystems and climate by modifying forest distribution [14], structure [10], and composition [15] (Fig. 4.1). These alterations may impact forest ecosystems at different ecological levels (population, community, functional, and genetic). Despite their relevance, the effects of past forest exploitation are rarely considered alongside environmental drivers, often hindering our ability to predict climate-related impacts on forests [16]. Given that climate change stressors and other anthropogenic perturbations interact and today strongly impact biological communities [17], quantifying the relative influence of climate and past forest exploitation is essential to understand future dynamics of forest ecosystems [10,16]. This understanding might, in turn, support the anticipation of large-scale disturbances, such as the occurrence of abrupt forest die-off events, mega-fires and forest degradation [10,18–20]. Consequently, a research agenda focused on identifying hotspots of increased vulnerability in areas dominated by human-modified forests is of critical importance if we are to develop and adopt mitigation and adaptation strategies to improve forest **resilience** [9,21,22]. A risk-based framework using the concept of **anthropogenic legacy** could provide such an approach.

Legacies are persistent patterns and processes that result from the ecological impacts of past disturbance, potentially leading to lagged alterations of ecosystem dynamics [23]. Although disturbance legacies may have beneficial effects and enhance forest resilience, the concept also acknowledges the chance of increasing ecosystem vulnerability to environmental stressors. In the latter case, legacy effects of disturbance become detrimental [10]. The effective study of anthropogenic legacies depends on a deep knowledge of the history, ecological dynamics, and environmental factors that will ultimately determine forest ecosystem responses to climate change [24]. However, the lack of guidelines to quantify how anthropogenic legacies alter climate-related risks to forests makes it difficult to anticipate the outcomes of this interaction.

Here, we set out how anthropogenic legacies of past forest exploitation that persist in the distribution, structure, and composition of human-modified forests can heighten the probability of, or exacerbate the impact of climatic stressors on forest ecosystems. Based on existing literature, we first summarise hypotheses on the processes that can lead to detrimental legacies of forest exploitation and how these might interact with climate-related stress. We then introduce a risk-based framework to first identify human-modified forests and then quantify impacts of anthropogenic legacies on forests and their interaction with climate change. We then apply the framework in an example to show that detrimental anthropogenic legacies contribute to large-scale risk of tree mortality at the driest distribution edge of the Scots pine (*Pinus sylvestris* L.). The proposed framework provides scientists, managers, and policymakers with an approach to anticipate climate-related risks to forests and promote ecosystem resilience in regions dominated by human-modified forests.

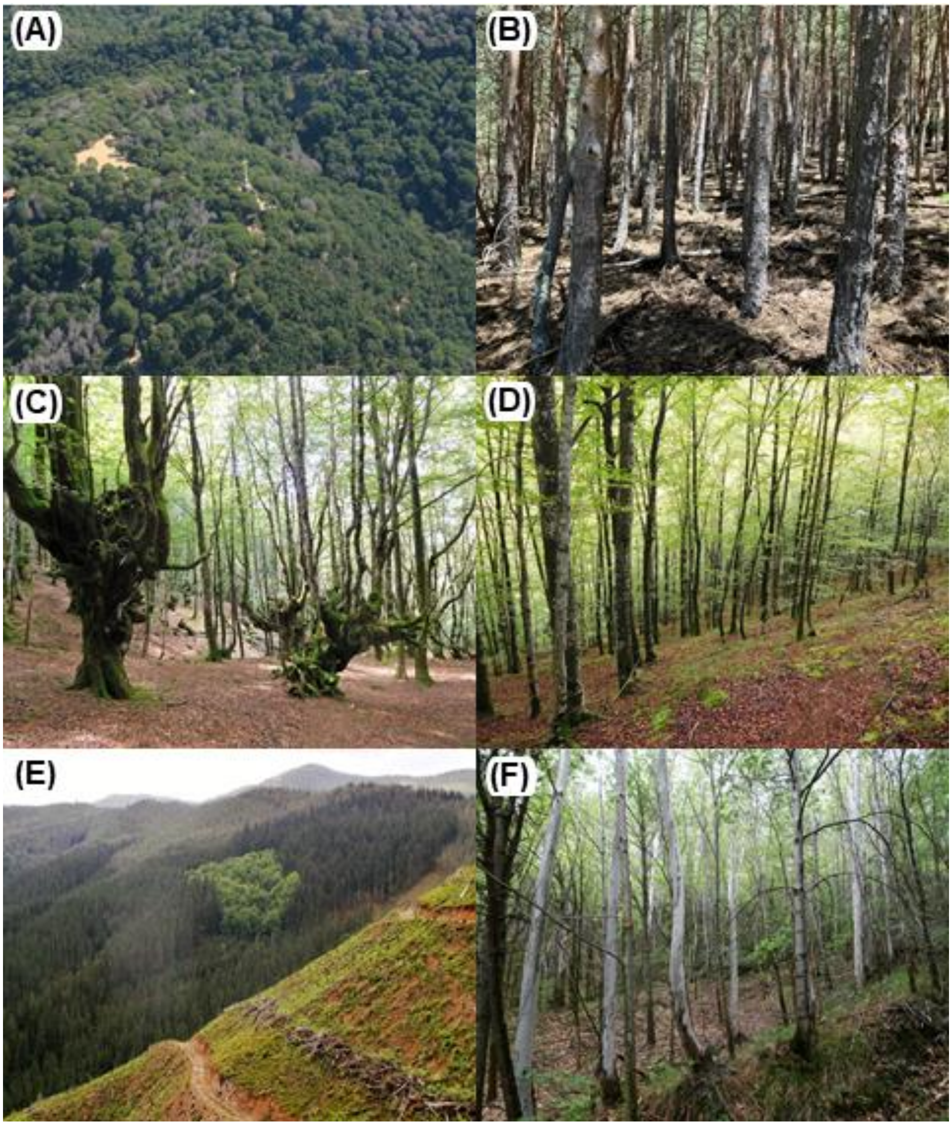

Figure 4.1. Examples of Iberian human-modified forests emerging from alterations in forest distribution, structure, and composition. Description of photos: (A) Forest landscape with stands of reforested and afforested Stone pines (*Pinus pinea*). Pines are today declining in response to drought and biotic stressors (photo: F. Vilà-Carbonell. Maresme, Catalonia, Spain). (B) Over-dense and structurally homogeneous Scots pine (*Pinus sylvestris*) abandoned plantation in a drought-stressed area (photo: A. Vilà-Cabrera. Parque Natural de la Sierra Norte de Guadalajara, Spain). (C) Pollarded beech trees (*Fagus sylvatica*) today overgrown and with altered phenotype because of the abandonment of the traditional management practice (photo: J. Astigarraga. Oñati, Gipuzkoa, Spain). (D) Secondary beech (*Fagus sylvatica*) forest established following the abandonment of an agricultural field (photo: J. Astigarraga, Oñati, Gipuzkoa, Spain). (E) *Pinus radiata* plantation surrounding a native stand of sessile oak (*Quercus petraea*; photo: J. Astigarraga. Oñati, Gipuzkoa, Spain). (F) Abandoned plantation of *Eucalyptus nitens* with regenerating native oaks (photo: J. Astigarraga. Oñati, Gipuzkoa, Spain).

Glossary

- **Anthropogenic legacy:** legacy that persist after the abandonment of forest exploitation and that is a distinctive characteristic of human-modified forests
- **Density-dependent processes:** ecological processes (e.g., tree mortality) that occur when population growth is regulated by population density
- **Climate-related impacts on forests:** abrupt or progressive climate-related shifts in forest dynamics and functioning, including forest die-off events, megafires, and forest degradation
- **Forest exploitation:** human-driven exploitation of forest ecosystems for extractive uses, including complete tree cover loss due to land-use changes, partial tree cover loss due to forest management practices, and tree cover increase due to tree planting (reforestation and afforestation).
- **Great acceleration:** continuous and exponential growth rate of human activities since mid-20th century that are accompanied by substantial changes in ecosystems
- **Human-modified forests:** forest ecosystems with long-lasting human impacts that emerge after the abandonment of forest exploitation
- **Legacy:** persistent effects of past conditions and disturbances on current ecosystem dynamics and functioning
- **Resilience:** the ability of forest ecosystems to cope with- and adapt to climate change stressors

4.2. Processes underlying detrimental effects of anthropogenic legacies in forest ecosystems

To identify processes leading to anthropogenic legacy effects that can exacerbate climate-related impacts on forests, we surveyed scientific studies that considered the effects of past forest exploitation on current forest ecosystem responses to climate change. Across studies, we identified processes driven by past forest exploitation that, following its abandonment, shape the current forest distribution, structure, and composition. Hypotheses regarding drivers of detrimental effects of anthropogenic legacies are framed considering the outcomes of their interaction with climatic stressors (Table 4.1).

Table 4.1. Hypotheses regarding drivers of detrimental anthropogenic legacies. Each specific hypothesis is framed considering the interaction outcomes between climatic stressors and contemporary process resulting from past forest exploitation and its subsequent abandonment leading to altered forest properties in terms of forest distribution, structure, or composition.

Altered pattern	Contemporary process	Cause	Hypothesis on drivers of detrimental legacy-effects	Refs
Distribution	Species range re-expansion	Land-cover change	Secondary forests and therefore species range re-expansions occur towards stressful climatic conditions relative to species climatic niches	[14,26–30]
		Abandonment of selective management	Sub-canopy species re-expand under an unfavourable climatic context relative to species climatic niches	[29,31]
		Abandoned plantation	Forest plantations decline and are highly impacted at the edge or out of the species natural range	[22,32–35]
Structure	Shifts in stand-level size distribution and age, and/or tree phenotypes	Land-use change	Climatic stressors exacerbate negative density-dependent processes and fire impact in secondary forests	[30,36]
			Soil legacies result in population-level functional shifts towards tree phenotypes with reduced ability to cope with increased climatic stressors	[44,45]
		Abandonment of management practices	Shifts towards tree phenotypes with reduced ability to cope with climatic stressors and that exacerbate fire impact	[10,19,36,38–43]
		Abandoned plantation	Climatic stressors exacerbate negative density-dependent processes and fire impact	[18,22,33,34,37]
Composition	Shifts in functional composition of tree assemblages, species interactions, and genetic properties	Altered distribution, structure, or both	Novel tree functional assemblages with reduced ability to cope with increased climatic stressors	[31,36,46]
			Increased impact on forests as a result of shifts in species interactions involving mutualisms and antagonisms	[44,47–49]
			Altered genetic properties reduce the ability of forests to cope with- and adapt to climate change	[22,55,62–69]

4.2.1. Forest distribution: Tree species re-expansion toward increased climatic stress

Although the emergence of secondary forests contributes to the recovery of ecosystem functionality to some extent [9,25], ongoing re-expansion of tree species distributions is occurring under a changing climate relative to past conditions (Table 4.1). Therefore, secondary forest regrowth may occur in a context of increased imbalance with species climatic niches, constraining their recovery potential and increasing the chance of climate-related impact on forests, especially if forest re-expansion occurs under stressed conditions relative to species climatic tolerances [14,26–30]. Similar responses may occur without involving land-cover changes, for example, following the abandonment of forest management practices that remove species selectively [29,31]. Human-modified forests may emerge by the abandonment of wood exploitation in tree plantations, which can result in a broadening of tree species distributions where planting has occurred beyond the species' natural range. Planted tree populations growing at the limit or outside of the range of species climatic tolerances may become vulnerable to increased environmental stress (Table 4.1) [22,32–35].

4.2.2. Forest structure: Exacerbated negative density-dependence, increased disturbance impact, and trait-mediated reduced population resilience

Altered stand structure and tree phenotypes are characteristic of human-modified forests. Such changes can derive from the establishment of high-density, structurally homogeneous tree plantations, the abandonment of forest management practices, or the regrowth of secondary forests (Fig. 4.1). Alteration of tree size distribution and stand age due to forest exploitation and its subsequent abandonment may result in exacerbated negative **density-dependent processes** and, therefore, increased climate-related impact on forests (Table 4.1) [30,33,34,36,37]. Similar structural shifts may increase the impact of climate-related wildfires on forests [18,19,22,38]. Following the abandonment of forest management practices (e.g., clearcutting, thinning, pruning, pollarding), their imprint may persist over time, becoming a source of intraspecific functional variation (Fig. 4.1). These human-modified forests may hold trees with functional traits that display reduced resilience ability to cope with climate change stressors (Table 4.1) [10,36,38–43]. Such phenotypic constraints may also arise in forests growing on soils with long-lasting legacies of former agriculture and pasture (e.g., altered soil fertility) [44,45].

4.2.3. Community composition: Alterations in the functional composition of tree assemblages, species interactions, and genetic properties mediate reduced community resilience

Alterations in distribution, structure, or both may lead to alteration in community composition in such a way that community resilience can be compromised. Species replacements within a given trophic level, either in terms of occurrence or relative abundance, may result in human-modified forests holding novel communities. If species replacements involve novel tree species assemblages, tree communities may display reduced ability to respond to climate change because of altered interspecific composition of functional traits (Table 4.1) [31,36,46]. Community shifts and loss of resilience to climatic stressors may also occur at the level of beneficial species interactions such as mutualisms [44,47–49]. Species replacements may also lead to increased performance of antagonists under changing climatic conditions, including tree competitors, invasive species, herbivores, and pathogens [39,50–59]. Finally, forest exploitation-derived shifts in forest structure and distribution, including tree planting, may generate forests with altered genetic diversity and structure [60,61] that may decrease their ability to cope with environmental stressors [22,55,62–69].

4.2.4. Limitations in the current state of knowledge of anthropogenic legacies in forest ecosystems

Current studies suggest that human-modified forests often can be more vulnerable to climate change than less altered forests, but anthropogenic legacies are rarely considered in experimental designs in research. This knowledge limitation is probably triggered by the scarcity of reliable data on past forest exploitation, making it difficult to identify and predict detrimental legacy effects. Furthermore, as the effects of anthropogenic legacies and climatic stressors interact, the detrimental outcomes may vary between different ecological and geographic contexts (Table 4.1), making comparisons among systems (e.g., regions, species, legacy types, etc.) difficult. However, risk-based approaches can support the predictive understanding of interaction outcomes between global change stressors [70]. To advance towards forest adaptation strategies and support forest resilience to risks of climate change, we need to better understand where and to what extent human-modified forests increase climate change-related risks.

4.3. A risk-based framework using the concept of anthropogenic legacy

To overcome the limitations in knowledge of potential detrimental effects of anthropogenic legacies due to the lack of experimental designs, data, and contexts, we incorporate three major knowledge needs to build up a risk-based framework (Fig. 4.2, Key Figure). First, we point out the need to characterise forest properties considering human impact and, among them, identify high-impact forest exploitation legacies (Fig. 4.2A). Here current data on forest distribution, structure, and composition can be used as proxies of legacy-driven alteration of forest properties together with available information on past forest exploitation (Box 4.1). Second, we should explicitly incorporate the alterations of anthropogenic legacies into empirical study designs, so that they are considered alongside environmental drivers of contemporary forest dynamics. Therefore, hypotheses on detrimental legacy effects (Table 4.1) can be tested in the context of a particular study system (Fig. 4.2B; Box 4.1). Finally, the potential outcomes of interactions between anthropogenic legacies and climatic stressors can be better quantified and understood using the risk components and the main forest properties that can be altered (i.e., distribution, structure, and composition), as this can improve our ability to identify and anticipate detrimental ecological effects (Fig. 4.2B-C; Box 4.1).

To define the risk components summarised in Fig. 4.2 (Key Figure) we adapt the IPCC framework [17] to forest ecosystems. When forest anthropogenic legacies are linked to the components of risk (exposure, and vulnerability components: sensitivity, and lack of adaptive capacity), responses of forests to climatic stressors can be framed and understood through the interaction between legacy-driven changes in distribution, forest structure and composition. A reduction in forest distribution followed by re-expansion of species ranges after the abandonment of forest exploitation may result in increased climate-related risk exposure (Fig. 4.2C). For example, secondary forests in the Brazilian Amazon are distributed more toward drier and more seasonal climatic conditions than the biome average because past deforestation was concentrated in these areas. Species re-expansions under dry climatic conditions are constraining the potential of forests for carbon sequestration [26]. The alteration in forest structure may result in increased vulnerability to climatic stressors by means of exacerbated sensitivity (Fig. 4.2C). When management practices are abandoned, their legacies can persist over time, for example in the form of increased competition in overcrowded even-aged stands, which may increase climate-related forest impact [10,38,40]. Legacies altering structure, distribution or both can result in increases in risk through exposure and sensitivity (Fig. 4.2C), such as in the case of abandoned tree plantations. For example, in the Carpathians where abandoned pine plantations grow outside their natural distributions, pine species perform worse than the native conifers in response to drought stress [32]. Decreased performance of abandoned or old plantations may reduce the delivery of ecosystem services, especially in drier areas worldwide [35]. Such legacies in distribution and structure can also result in increased megafire risk, as reported in Australian forests where past logging generated extensive areas characterised by densely stocked forests that today influence fire dynamics [19].

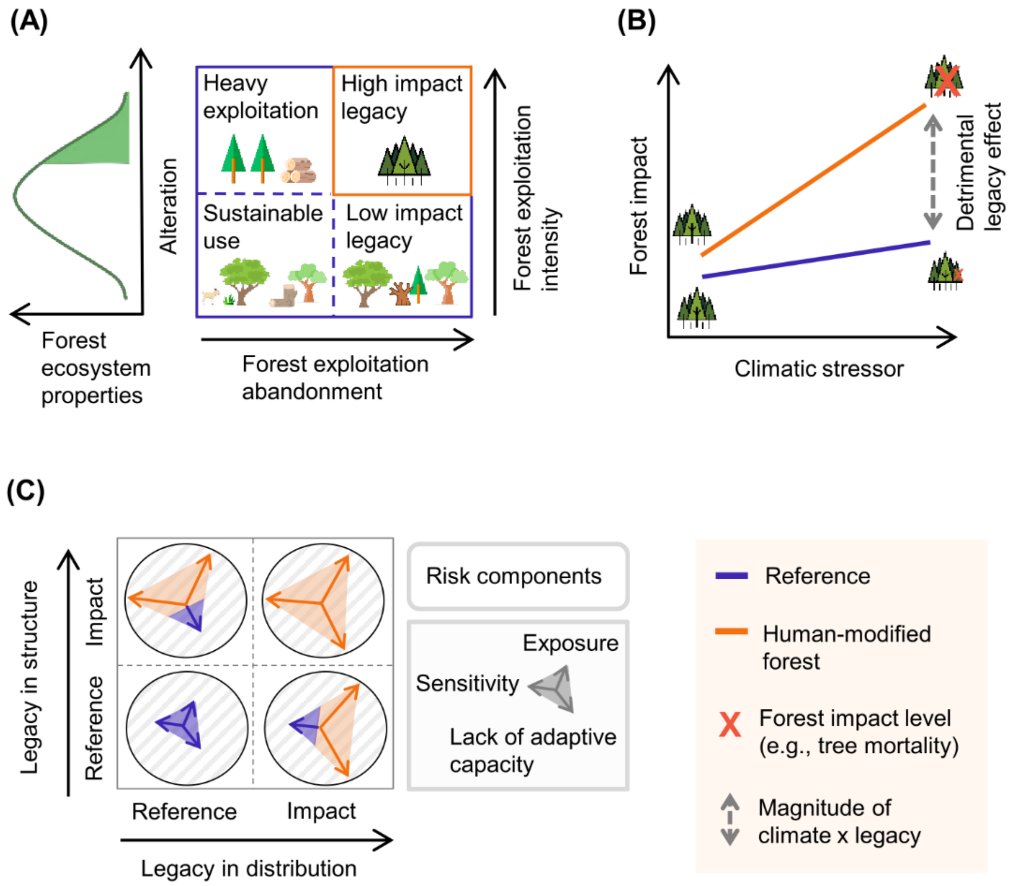

Figure 4.2 (Key Figure). Risk-based framework using the concept of anthropogenic legacy. We adapt the IPCC framework [17] to forest ecosystems considering the risk of forest disruption as the potential response to a climate-related hazard (e.g. increased drought-induced mortality [78]). Risks to forests from climate-related hazards can be exacerbated by anthropogenic legacies of past forest exploitation (Fig. 4.2C) due to the interaction between the exposure (ecological settings that expose forests to hazards, e.g., drought stress at the driest edge of species distributions [16]) and vulnerability (forest intrinsic predisposition to be adversely affected, e.g., where reduced structural and functional forest diversity increases the vulnerability of forest ecosystems to climate change [79]). Vulnerability is defined by two components: *sensitivity* (the degree to which a forest ecosystem is affected, e.g., tree mortality), and lack of *adaptive capacity* (the capacity of forest trees, populations, and communities provided by their functional and/or genetic properties to counteract and/or cope with climatic stressors). (A) Characterisation of human-modified forests and identification of high impact anthropogenic legacies due to high intensity forest exploitation and its subsequent abandonment. (B) Testing the interaction between high-impact anthropogenic legacy and climatic stressors and its potential outcome. The prevalence of detrimental anthropogenic legacies leads to increased climate-related impacts on forests. (C) Linking detrimental anthropogenic legacies (including changes in distribution, structure, and composition) with climate-related risk components supports the predictive understanding of the dynamics of human-modified forests. Note: legacies in composition emerge from shifts in distribution and/or structure.

High vulnerability to climate stressors may occur by the reduction of adaptive capacity. At the population level, the abandonment of forest management (including plantations) may result in the emergence of anthropogenic legacies toward more vulnerable tree phenotypes, such as in the form of high abundance of slow-growing weak trees [39]. Legacy-driven functional shifts may also lead to increased structural and physiological constraints that exacerbate hydraulic failure and fire impact [36,41–43]. For example, past high-intensity management practices might underlie increased drought-induced mortality of larger canopy trees in temperate forests [43]. Anthropogenic legacies affecting the composition of forest communities may also increase risks to forests driven by shifts in their adaptive capacity. For instance, community-level functional shifts towards reduced bark thickness and wood density compromises trait-mediated capacity of forests to withstand fire and drought in tropical and temperate regions [36,46]. Anthropogenic legacies in composition that alter species interactions can also influence the adaptive capacity of forests to climatic stressors. For example, secondary forests may hold distinct and simpler ectomycorrhizal communities because of increased nitrogen and phosphorus availability due to former arable and pasture activities. This alteration may reduce the adaptive capacity of trees to cope with drought stress [44,48,49]. High occurrence of tree stumps or increased stand density and structural homogeneity may alter species interaction networks and favour, for instance, the spread of pathogen and insect outbreaks [51,56,59] that in interaction with climate-related stress may exacerbate negative impacts on forests [39,58]. Anthropogenic legacies altering the genetic properties of forest ecosystems can also lead to decreased adaptive capacity to climate change. For example, widespread tree planting within a species' native range may result in forest dieback if seed material is translocated among lineages with differing climatic niches [67]. In addition, gene flow from planted non-local genotypes into native populations can result in landscape-level genetic homogenisation [64]. Although still highly uncertain, shifts in forest genetic properties have the potential of inducing long-term effects on the adaptive capacity of forest ecosystems [62,68,69].

The proposed risk-based approach can improve our predictive understanding of forest dynamics and climate-related risks to forests, thus supporting adaptation strategies to foster long-term forest resilience in regions highly dominated by human-modified forests. As witnessed in Scots pine (*Pinus sylvestris* L.) in the Iberian Peninsula, anthropogenic legacies in distribution, structure, and composition contribute to large-scale patterns of enhanced climate-driven tree mortality risk (Box 4.1).

Box 4.1. Anthropogenic legacies of past forest exploitation contribute to large-scale tree mortality risk in Iberian Scots pine forests

The Scots pine tree (*Pinus sylvestris* L.) is a widespread species that reaches its driest range edge in the Iberian Peninsula. In this region, the current distribution, structure, and composition of Scots pine forests are affected by widespread abandonment of forest management and large-scale tree planting that occurred over the 20th century [33]. Previous studies have shown how stand-level structural effects influence forest demography [33,75], yet the prevalence of anthropogenic legacies contributing to climate-related Scots pine mortality has not been explicitly assessed. We used large-scale datasets on historical land-use and forest inventory to apply the proposed framework (Fig. 4.2, Key Figure) in Scots pine-dominated forests. We characterised forest inventory plots according to their (i) natural or planted character as an indicator of anthropogenic legacies in distribution and stand composition, and (ii) forest structural characteristics as an indicator of anthropogenic legacies in forest structure (see Supporting Information). Across natural and planted stands, we identified two main forest structural typologies, one associated with high structural diversity and recruitment (‘C1’; Fig. 4.S1-4.S2), and the other one associated with high tree density, basal area, height-to-diameter ratio, and structural homogeneity (‘C2’; Fig. 4.S1-4.S2). Across legacy types (defined as stand character x forest structural typology), planted forests were, as expected, denser and structurally simpler, and displayed greater growth but more limited recruitment than natural forests [76,77] (Fig. 4.S3-4.S4). We hypothesised that anthropogenic legacies in plantations would exacerbate climate-related tree mortality risk exposure and vulnerability. First, we predicted higher tree mortality associated with increased risk exposure in plantations because tree planting can result in a greater chance to encounter environmental pressures relative to the species’ climatic niche. Second, we expected higher tree mortality associated with increased sensitivity in plantations, as legacy-driven shifts in forest structure can exacerbate negative density-dependent processes in response to climatic stressors. And third, we expected higher tree mortality in plantations as these forests may have impoverished genetic diversity and, therefore, display reduced adaptive capacity to climate-related stress [69]. Mortality was overall higher in planted than in natural stands, suggesting that distribution and both structural and compositional legacies can increase, respectively, climate-related risk exposure and vulnerability (Fig. 4.3A and 4.2C). This pattern remained consistent within each forest structural typology (Fig. 4.3A). Notably, mortality risk increased in a climate change scenario that assumed a reduction in water availability and an increase in drought severity, maintaining similar trends among forest structural typologies and higher mortality in plantations (Fig. 4.3A and SI Analyses). In addition, mortality risk was predicted under the same climate change scenario but assuming temporal shifts in stand development, following the observed dominant transition between structural typologies (from ‘C1’ to ‘C2’; Table 4.S1) (Fig. 4.3B, SI Analyses). We found that mortality risk remained high in plantations while it decreased in natural forests, suggesting that the mortality level observed in ‘C1-natural’ was mainly due to natural density-dependent processes. On the contrary, mortality risk remained high in plantations, indicating persistent anthropogenic legacies (Fig. 4.3B). This study case demonstrates that anthropogenic legacies can elevate the risk of climate-related stressors to forests. At the same time, it also highlights that the proposed framework can be a useful approach to (1) improve our predictive understanding of large-scale forest dynamics, and (2) identify hotspots of climate-related risks to forests, providing opportunities to develop and implement mitigation and adaptation strategies during coming decades. *Note: data and code used can be found in Zenodo repository (https://doi.org/10.5281/zenodo.7120609). Data is also available at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/default.aspx.*

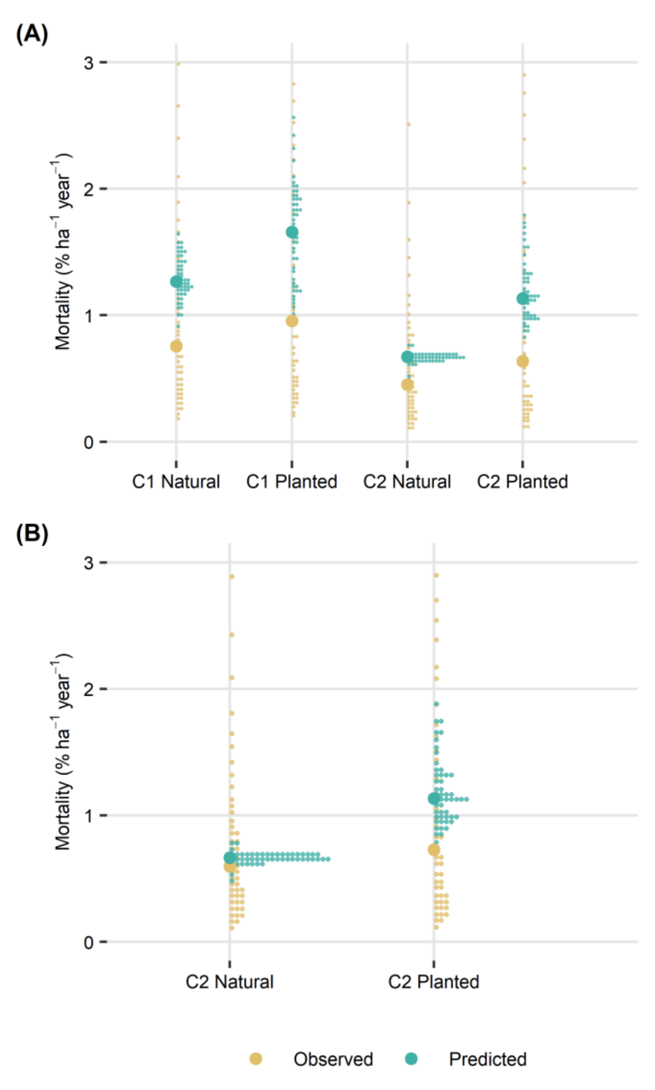

Figure 4.3. Plantations have higher tree mortality risk in Iberian Scots pine forests. (A) Quantile dotplot representing observed tree mortality (yellow) and model-predicted tree mortality (green) in a climate change scenario assuming a 25% reduction of both water availability and SPEI conditions for each legacy type (defined as stand character x forest structural typology). (B) Quantile dotplot representing observed tree mortality (yellow) and model-predicted tree mortality (green) in a climate change scenario such as in *A* across all natural and planted stands, and accounting for stand development, i.e., setting all natural stands as 'C2-natural' and all planted stands as 'C2-planted' (see description of legacy types in the text, and SI). *Note: Mortality was estimated in terms of percentage of dead basal area at the plot level. Large dots represent the median values and small dots represents approximately a 2% (1/50) chance.*

4.4. Concluding remarks

Increased climate change-related risk to forest ecosystems can be intense and extensive in human-modified forests, particularly if anthropogenic legacies of past forest exploitation interact with climatic stressors in such a way that their detrimental ecological effects act synergistically. We recommend that future research explicitly incorporates the impact of past forest exploitation into experimental designs and investigates how forest exposure and vulnerability to climatic stressors is modified by anthropogenic legacies (Fig. 4.2, Key Figure). Such an approach can be of key importance to identify forest regions under critical risks of climate change, and understand and anticipate climate change impacts on forest dynamics, biodiversity, and functioning, providing an opportunity to reduce risks to forests and improve forest resilience [9,21,22,71] (Box 4.1) (see **Outstanding Questions**). To apply the proposed framework and better inform climate-related impacts on forests, we propose using current forest properties as proxies of anthropogenic legacies using available data such as forest inventories and forest historical information (Box 4.1), and emerging high-resolution data as novel remote sensing technologies develop [72]. In addition, understanding how anthropogenic legacies alter forest genetics, functional traits, and species interactions deserve urgent attention as these properties ultimately underpin responses of forest ecosystems to changing climatic conditions. Importantly, although our approach here focusses on anthropogenic legacies that are predominantly detrimental, the proposed framework allows assessment of beneficial effects, highlighting the potential of traditional, sustainable management practices and local knowledge to improve forest ecosystem resilience [62,73]. Finally, while this framework centres on an ecological approach, emerging anthropogenic legacies are inextricably dependent on previous socio-economic contexts [74]. Therefore, a key step towards mitigation and adaptation goals will involve the collaboration of natural and social scientists with local stakeholders and policymakers in decision-making processes from local to global scales. This cooperation will be pivotal for the success of the post-2020 UN Biodiversity Framework and the UN Decade on Ecosystem Restoration.

Highlights

1. How long-lasting effects of past forest exploitation for extractive uses (i.e., anthropogenic legacies) can exacerbate the impacts of climate change on forests is not well understood
2. Anthropogenic legacies that persist in forest ecosystem properties (distribution, structure, and composition) can interact with climatic stressors and lead to detrimental ecological effects
3. Risk-based approaches using the concept of anthropogenic legacy support the identification of highly vulnerable forest ecosystems and the predictive understanding of their potential responses to climate change
4. Current forest ecosystem properties can be used together with available historical data to identify climate change-related increased risk to forests
5. Appropriate adaptation and mitigation strategies that consider the legacy of past forest exploitation will increase forest ecosystem resilience and societal wellbeing in the long-term

Outstanding questions

1. How do anthropogenic legacies of past forest exploitation alter forest properties at different ecological levels (genetic, functional, community) and spatial scales? How do these alterations interact with environmental drivers and influence ecological processes?
2. Can the proposed framework support the identification of beneficial past forest management practices that minimise risk components and improve forest resilience to climate change?
3. Once the risk-based approach to understand the impacts of anthropogenic legacies of past forest exploitation is applied to a specific context, which forest properties need to be prioritised to mitigate and adapt to climate change and how can this be achieved?
4. Can we combine emerging and available data (e.g., remote sensing, forest inventories) to apply the proposed framework and better identify combined impacts of anthropogenic legacies and climatic stressors?
5. How do we build on the proposed risk-based approach to better integrate risks to forest ecosystems with those to societal wellbeing and resilience?

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4.5. References

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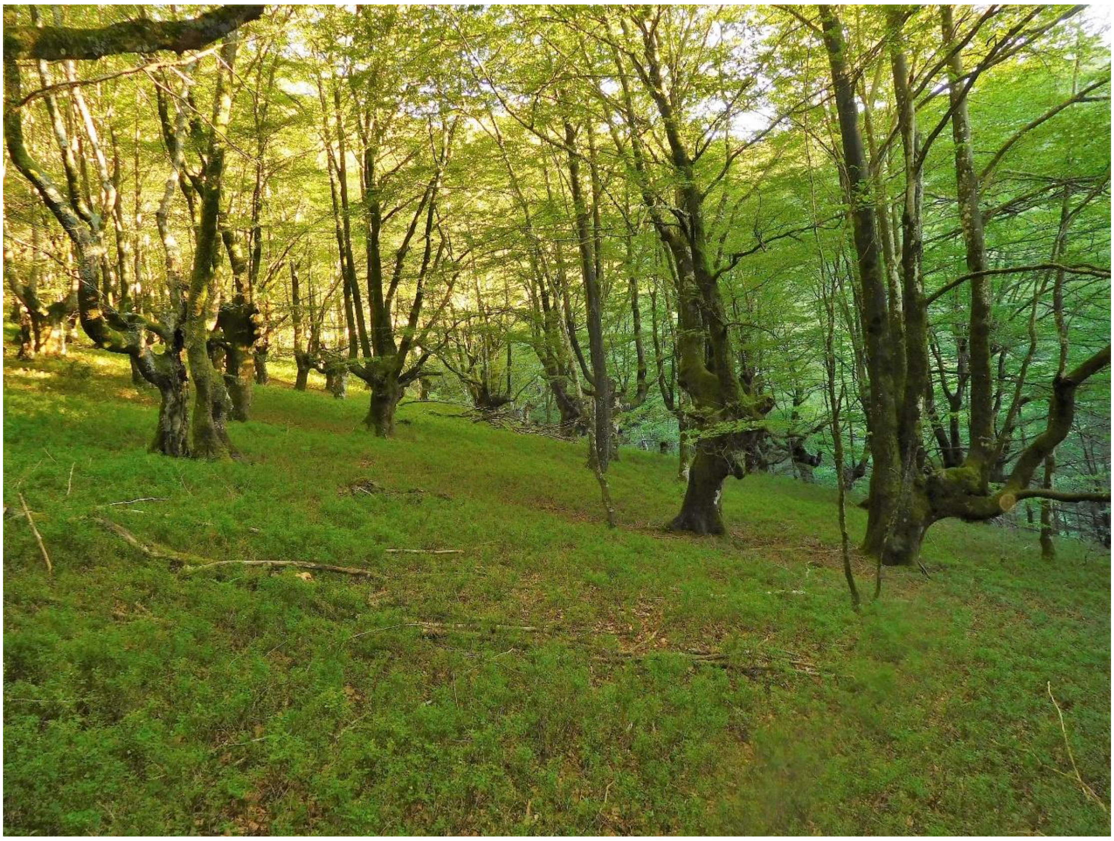
Chapter 5

Land- and forest-use legacies modulate tree growth synchrony in response to climate change through changes in forest structural diversity

Astigarraga, J., Calatayud, J., Ruiz-Benito, P., Madrigal-González, J., Rodríguez-Sánchez, F., Tijerín-Triviño, J., Zavala, M. A., Andivia, E., & Herrero, A. Land- and forest-use legacies modulate tree growth synchrony in response to climate change through changes in forest structural diversity



Abstract

After centuries of deforestation, industrialised countries are experiencing an increase in forest area and biomass since the mid-20th century due to changes in land- and forest-use that alter tree cover completely or partially, respectively. At the same time, the impacts of climate change on forests are aggravating, but how past land- and forest-use (i.e. land- and forest-use legacies) determine forest ecosystems responses to climate change is poorly understood. Here, using network analysis and linear mixed models, we analysed how land- and forest-use legacies modulated tree growth synchrony in response to climate change, studying beech (*Fagus sylvatica* L.) stands with different legacy types at the species rear edge. We observed an increase in tree growth synchrony in response to reduced precipitation and increased heatwaves and late spring frosts over the period 1970-2020. However, land- and forest-use legacies modulated the magnitude of increases in growth synchrony through changes in forest structural diversity. We found that recently-established forests had the greatest tree growth synchrony and that large trees and heterogeneous size distributions decreased growth synchrony. Our results highlight the importance of maintaining large trees and structurally heterogeneous forests to mitigate the negative effects of climate change on tree growth, and thereby, increase forest resilience to future forest climate risks.

Resumen

Tras siglos de deforestación, los países industrializados están experimentando un aumento de la superficie forestal y de la biomasa desde mediados del siglo XX debido a los cambios en el uso del suelo y de los bosques que alteran la cubierta arbórea totalmente o parcialmente, respectivamente. Al mismo tiempo, los impactos del cambio climático en los bosques se están agravando, pero no se sabe muy bien cómo el uso del suelo y forestal pasado (i.e. legados del uso del suelo y forestal) determinan las respuestas de los ecosistemas forestales al cambio climático. Aquí, utilizando análisis de redes y modelos lineales mixtos, analizamos cómo los legados del uso del suelo y del bosque modularon la sincronía en el crecimiento de los árboles en respuesta al cambio climático, estudiando rodales de haya (*Fagus sylvatica* L.) con diferentes tipos de legado en el límite de distribución meridional de la especie. Observamos un aumento de la sincronía en el crecimiento de los árboles en respuesta a la reducción de las precipitaciones y al aumento de las olas de calor y las heladas primaverales tardías en el periodo 1970-2020. Sin embargo, los legados del uso del suelo y forestal modularon la magnitud de los aumentos en la sincronía en el crecimiento a través de los cambios en la diversidad estructural del bosque. Encontramos que los bosques recientemente establecidos tenían la mayor sincronía en el crecimiento de los árboles y que los árboles grandes y las distribuciones de tamaño heterogéneas disminuyen la sincronía en el crecimiento. Nuestros resultados destacan la importancia de mantener los árboles grandes y los bosques estructuralmente heterogéneos para mitigar los efectos negativos del cambio climático en el crecimiento de los árboles y, por lo tanto, aumentar la resiliencia de los bosques ante futuros riesgos climáticos forestales.

5.1. Introduction

Forests cover ~30% of the world's land surface and provide multiple ecosystem components such as climate regulation, wood production and biodiversity conservation (FAO, 2020; IPBES, 2019; van der Plas et al., 2018). Humans are a major driver of global change (Steffen et al., 2007; Vitousek et al., 1997), already altering *c.* 75% of the Earth's ice-free surface (Ellis & Ramankutty, 2008). Forests have also undergone major human-induced changes and today primary forests represent only about 1/4 of the total world forest area (FAO, 2020). Anthropogenic impacts on forests can alter tree cover completely through land-use changes (e.g. deforestation, afforestation or natural regrowth; Song et al. (2018)) or partially through changes in forest-use (e.g. increases in biomass after management abandonment; Jump et al. (2017)). Furthermore, climate change is causing shifts in mean temperature, precipitation and extreme climatic events (IPCC, 2021), having direct impacts on forest dynamics (Allen et al., 2010; McDowell et al., 2020). However, little is known about how anthropogenic imprints modulate forest ecosystems responses to climate change.

After centuries of deforestation, industrialised countries are experiencing an increase in forest area, density and biomass since the mid-20th century due to changes in land- and forest-use such as the abandonment of agriculture and traditional forest management (Bürgi & Gimmi, 2007; Garbarino et al., 2022; Infante-Amate et al., 2022; Song et al., 2018). Land-use changes determine forest age and structure, with greater vulnerability to increased aridity of recently- than long-established forests due to their lower wood density and alterations in ectomycorrhizal communities (Alfaro-Sánchez et al., 2019; Correia et al., 2021; Mausolf et al., 2018). Forest-use changes determine forest structure and, therefore, could also influence forest ecosystems responses to climate (Marqués et al., 2022; Perring et al., 2018; Sangüesa-Barreda et al., 2015). For example, the abandonment of forest-use could lead to structural overshoot processes in which increased tree biomass in a mild climate can lead to forest decline (i.e. growth decrease, crown die-back and increased mortality) when the climate is more severe (Jump et al., 2017; Zhang et al., 2021). However, the underlying drivers by which trees may respond differently to climate as a function of past land- and forest-use (i.e. land- and forest-use legacies) are not well understood.

In the current context of climate change, warming, increased aridity and heatwaves are impacting tree species main demographic rates (Astigarraga et al., 2020; Peng et al., 2011; van Mantgem et al., 2009), shaping forest structure (McIntyre et al., 2015; Zhou et al., 2013), composition (Batllori et al., 2020; Esquivel-Muelbert et al., 2019; Ruiz-Benito et al., 2017) and productivity (García-Valdés et al., 2021; Zhang et al., 2018). At the same time, variations in annual precipitation and late spring frosts are also affecting forest ecosystems (Castagneri et al., 2015; Olano et al., 2021; Sangüesa-Barreda et al., 2021; Zohner et al., 2020). Although the scientific consensus that climate change is increasing tree mortality rates is broad, the same is not true for tree growth since warming can have antagonistic effects on tree growth (Allen et al., 2015; McDowell et al., 2020). For example, warming can increase tree growth, primarily through CO_2 fertilisation and removal of low temperature limitations to photosynthesis, but excess warming may reduce tree growth due to reduced water availability and increased carbon respiration costs (Adams et al., 2009; D'Orangeville et al., 2018; Peñuelas et al., 2017a). Tree growth is a demographic rate of paramount importance that integrates many environmental constraints of tree performance, being considered an indicator of tree vitality (Dobbertin, 2005) and that can be used as an early-warning signal of tree mortality (Cailleret et al., 2019).

In the last years, synchrony in tree growth (i.e. coincident increase in tree growth over time between different tree individuals) has received great attention by researchers worldwide (e.g. del Río et al., 2021; Shestakova et al., 2016). Several studies recorded an increasing trend in tree growth synchrony associated with pervasive climatic effects – mainly warming and increased intensity of climate extremes – at local to regional scales (Boden et al., 2014; Latte et al., 2015; Shestakova et al., 2016; Tardif et al., 2003). Increasing growth synchrony is widely recognized as an indicator of forest vulnerability to climate change (Boden et al., 2014; Shestakova et al., 2016), since more synchronous responses might decrease population stability and persistence (Earn et al., 2000; Liebhold et al., 2004). Thus, increased growth synchrony to climatic stressors exacerbates the risk of widespread negative impacts on tree vitality by losing the benefits of individual-level variability in response to climate, reducing forest resistance and resilience (Clark et al., 2012). However, dendrochronological studies often focus on large size dominant and co-dominant individuals, and rarely account for legacies of land- and forest-uses – although attention to anthropogenic legacies has increased in recent years (see e.g. Alfaro-Sánchez et al., 2019; Gazol et al., 2021; Marqués et al., 2022). This could limit the conclusions drawn from the analyses of tree growth synchrony, since different tree sizes and growth forms usually respond differently to climatic stressors (Day & Greenwood, 2011). In this regard, past land- and forest-use can determine current forest structure, having different tree number and size in stands subjected to different legacies (Rozas et al., 2009), which ultimately could show different growth responses and synchrony. Therefore, assessing growth synchrony in various forest structures resulting from different land- and forest-use legacies could help in the evaluation of forest vulnerability to climate change stressors.

In southern Europe, the interactions between humans and nature have created complex socioecological systems that have lasted for millennia, and the current forest structure, distribution and species composition cannot be understood without taking into account human influence (Blondel, 2006; Scarascia-Mugnozza et al., 2000). In the Iberian Peninsula, forests were intensively managed until the 1950s, which led to a decrease in forest area and biomass (Infante-Amate et al., 2022). However, since the middle of the last century, the abandonment of agricultural activities resulted in an increase in forest extension and density (Poyatos et al., 2003; Vilà-Cabrera et al., 2017). At the same time, the substitution of firewood for fossil fuels led to the abandonment of traditional forest-use, decreasing centuries-old management techniques such as coppicing and pollarding (Infante-Amate et al., 2022; Sjölund & Jump, 2013). All these anthropogenic impacts could interact with the increasing effects of climate change, making the fate of Iberian forests uncertain (Peñuelas et al., 2017b).

Here, we analysed how land- and forest-use legacies modulate tree growth synchrony in response to climate change. We hypothesised that (i) there will be an increase in tree growth synchrony regardless of land- and forest-use legacies as we approach the present as precipitation, heatwaves and late spring frosts are becoming an increasingly limiting factor for tree growth; and (ii) land- and forest-use legacies with greater forest structural diversity will show less tree growth synchrony due to greater individual-level variability in response to climate. Specifically, we tested the effect of land- and forest-use legacies that alter mean tree size and tree size heterogeneity on tree growth synchrony in response to climate change. For this aim, we used as study species the European beech tree (*Fagus sylvatica*, L.), a widely-distributed species of great economic and ecological importance that is susceptible to droughts and spring frosts (Archambeau et al., 2020; Cavin & Jump, 2017; Packham et al., 2012). To test these hypotheses, we quantified tree growth synchrony in contrasting land- and forest-use legacies in an area with similar biotic and abiotic conditions, by mixing 12 European beech stands with four different legacies located in the north of the Iberian Peninsula analysing ~240 tree cores. Our results provide evidence of the key role of anthropogenic legacies in determining forest ecosystems responses to climate change by altering forest structural diversity.

5.2. Materials and methods

5.2.1. Study area

The study area is a natural forest dominated by *Fagus sylvatica*, located at the southern limit of the species global distribution (Packham et al., 2012). It is in the north of the Iberian Peninsula at the easternmost part of the Cantabrian Range (42º58’N - 2º24’W; altitude: 750-1000 m a.s.l.; Fig 5.1). The studied forest is mainly composed of detrital sedimentary rocks and presents an oceanic climate (*Cfb*, Kottek et al., 2006), with an average precipitation of 932 mm and an average temperature of 13 ºC (data from *easyclimate* R package (Cruz-Alonso et al., 2021; Moreno & Hasenauer, 2016; Rammer et al., 2018)). Although *F. sylvatica* is the most abundant species, other tree species characteristic of European temperate forests can also be found (e.g. *Quercus robur* L., *Q. petraea* Matt., *Ilex aquifolium* L., *Sorbus aucuparia* L.;).

During the last centuries, the forest was mainly used for charcoal and firewood, and its traces can be seen in the many pollards and coppiced trees that exist today in the area. Since 1950s with the industrial transition, charcoal and firewood were replaced by fossil fuels, leading to an increase in tree density and biomass. Furthermore, agricultural and livestock activities in the region were also reduced or abandoned resulting in an increase in forest area.

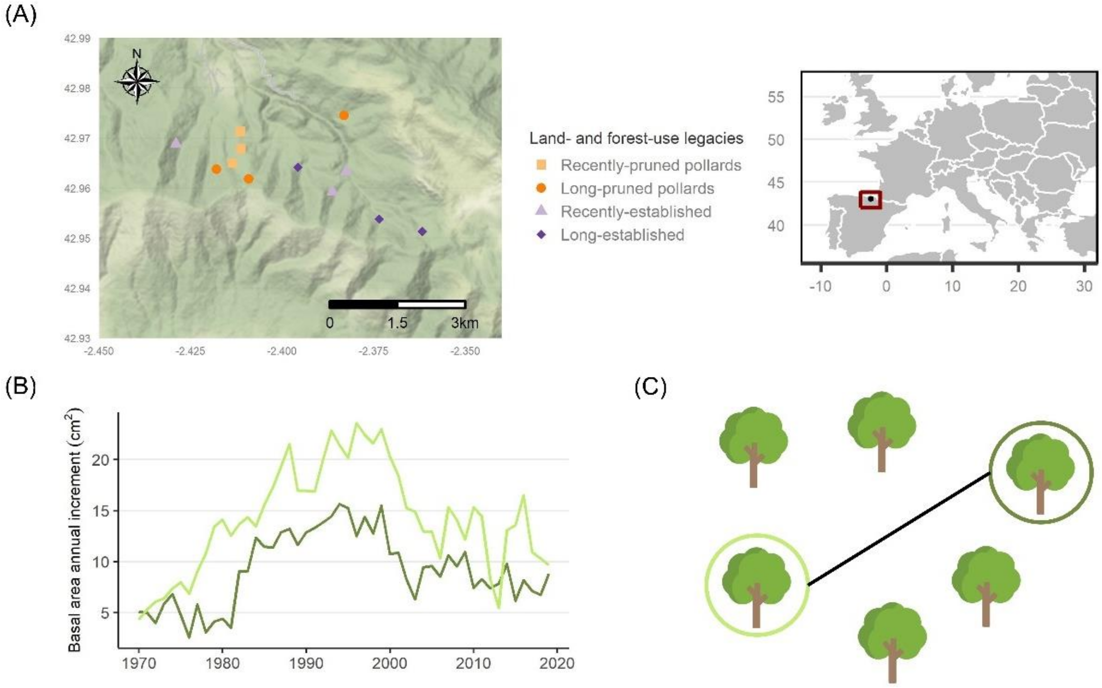


Figure 5.1. Study area and framework representing the calculation of tree growth synchrony. (A) Location map of the study area and position of the 12 sampled stands within it; (B) radial growth of a pair of trees measured as basal area annual increment; and (C) a link was established between a pair of trees (black line connecting the trees) if their growths were significantly correlated over a x-years time window moved from year to year. For each time window we calculated tree growth synchrony as the number of realised links relative to the number of potential links. These calculations were made for each sampled stand.

5.2.2. Characterisation of land- and forest-use legacies

Land- and forest-use legacies were characterised using aerial photographs, forest management plans and interviews to local inhabitants and forest managers. Aerial photographs from 1945/46 (https://www.geo.euskadi.eus/comparador-de-ortofotos/webgeo00-content/es/) allowed the identification of stands that were not occupied by trees prior to 1945/46. Through forest management plans, interviews to local actors and empirical observations, among stands occupied by trees prior to 1945/46, we distinguished high-stands and pollards. Pollarding is a traditional silvicultural technique that favours the production of a dense mass of branches above ground level, out of reach of browsing mammals, often resulting in large trees with a longer lifespan than their naturally growing counterparts (Sjölund & Jump, 2013). Among pollard stands we distinguished recently-pruned pollards (pruned in 2010 and 2014), and long-pruned pollards (not pruned in 2010 & 2014). In the end, we analysed (i) high-stands occupied by trees post to 1945/46 (hereafter, recently-established) and (ii) high-stands occupied by trees prior to 1945/46 (hereafter, long-established), (iii) recently-pruned pollards, and (iv) long-pruned pollards (Fig. 5.S1).

5.2.3. Sampling

In 2020, we extracted two cores per tree in opposite directions using a Pressler increment borer and process using standard dendrochronology techniques (Fritts, 1976). Since each legacy type was replicated three times, 12 different stands were sampled (four legacies × three replicates = 12 stands, Fig. 5.1), collecting samples from 20 individuals in each stand (four legacies × three replicates × 20 individuals = 240 individuals). To control for biotic and abiotic factors that could affect tree growth, all stands were located within *c.* 1300 ha, mixing stands with different land- and forest-use legacies – although recently-pruned pollards were close to each other since the pruning was done only in that area. We georeferenced each sampled tree and measured the diameter at breast height (d.b.h.). Then, we measured ring widths using *trini* R package (Fig. 5.S2; Astigarraga et al., 2022). All cores were visually cross-dated following the procedures described by Yamaguchi (1991).

5.2.4. Climate data

We used daily data on precipitation and minimum and maximum temperatures from *easyclimate* R package (Cruz-Alonso et al., 2021; Moreno & Hasenauer, 2016; Rammer et al., 2018). We calculated total precipitation, number of late spring frosts (i.e. number of days below 0 ºC in meteorological spring – from 1st of March to 31st of May) and number of heatwaves (i.e. number of days above 32 ºC in meteorological summer – from 1st of June to 31st August) annually from 1950 to 2020.

5.2.5. Statistical analyses

5.2.5.1. Tree growth synchrony

We used a network approach to evaluate time variations in tree growth synchrony. We built networks where nodes were trees and a link between a pair of trees was established if their growths were significantly correlated over time ($P < 0.05$, based on Spearman rank correlations, Fig. 5.1). If trees of a stand were growing synchronically, tree growth networks would be densely connected, indicating that several trees showed similar growth patterns over time. Thus, network density or connectivity provides a direct measure of tree growth synchrony. We calculated network connectivity as the number of realised links relative to the number of potential links, $C = \frac{N}{0.5 \times n \times (n-1)}$, where N denotes the number of observed links and n the number of nodes. To evaluate growth synchrony over time we used a 20-years time windows moved from year to year, starting in 1970 to maximise tree samples while having a sufficiently long period to test the effect of climate change. Of the 240 tree cores, we discarded three cores that were younger than 1970 and two other cores due to ring detection problems. For each time window and stand we built a network as described above and calculated its connectivity. Results with different window lengths provided qualitatively and quantitatively similar results (Fig. 5.S3). For each time window, we calculated the mean d.b.h. (i.e. mean tree size), the coefficient of variation of the d.b.h. (i.e. tree size heterogeneity) and the mean of the climatic variables described in *Climate data*.

5.2.5.2. Effect of land- and forest-use legacies and climate change on tree growth synchrony

First, we analysed whether land- and forest use legacies, climate change or both influenced tree growth synchrony from 1970 to 2020. For this aim, we fitted three linear mixed effects models assuming a normal distribution of errors using stand identity as random effect. The first model included only climatic variables (i.e. total precipitation, number of heatwaves and number of late spring frosts) as additive fixed effects. The second model included only legacy type as a fixed effect, and the third model included both climatic and legacy type as additive fixed effects.

Next, to test the underlying drivers of land- and forest-use legacies modulating tree growth synchrony in response to climate change, we compared other three linear mixed models also assuming a normal distribution of errors using stand identity as random effect. One model including climatic variables and legacy type as additive fixed effects and a second model including climatic variables and forest structural diversity (i.e. mean tree size and tree size heterogeneity) as additive fixed effects. With these two models we tested whether legacy type or structural diversity was driving tree growth synchrony in response to climate change. We also included a third model considering climatic variables, legacy type and forest structural diversity as additive fixed effects to test whether there were other variables related to legacy type that were driving tree growth synchrony apart from structural diversity. All fixed predictors were standardised before being included in the models, the models were fitted using *glmmTMB* R package (Brooks et al., 2022) and compared in terms of AICc (Burnham & Anderson, 2002) using *bbmle* R package (Bolker & R Development Core Team, 2022). We also calculated the goodness-of-fit using the pseudo-R^2 described in Nakagawa & Schielzeth (2013) and implemented in *MuMIn* R package (Bartoń, 2022). The models' fits were diagnosed using *DHARMa* R package (Hartig, 2022) (Fig. 5.S4). All analyses were performed using R Statistical Software (v4.2.1; R Core Team 2022).

5.3. Results

5.3.1. Land- and forest-use legacies and climate change drive tree growth synchrony

Land- and forest-use legacies and climate change drove tree growth synchrony in the period 1970-2020. Comparing the model containing land- and forest-use legacies and climatic variables (i.e. total precipitation, number of heatwaves and number of late spring frosts) with the model without climatic variables and the model without legacy type, the model containing both climatic variables and legacy type had the lowest AIC (ΔAICc legacy + climate = 0.0, ΔAICc climate = 15.5, ΔAICc legacy = 189.9). Moreover, climatic variables and legacy type explained similar and complementary portions of the tree growth synchrony variance (marginal R^2 legacy + climate = 0.57, marginal R^2 climate = 0.28, marginal R^2 legacy = 0.29). Specifically, our results indicated more synchronous responses in dry years with high frequency of the number of heatwaves and late spring frosts (Fig. 5.2A,C-E and Fig. 5.3).

The magnitude of tree growth synchrony varied depending on legacy type, with the highest synchrony in recently-established stands and the lowest synchrony in recently-pruned pollards (Fig. 5.2). In addition, tree growth synchrony remained higher over time in recently-established stands than in other legacy types when precipitation increased and the number of heatwaves and late spring frosts decreased (see in Fig. 5.2 the decrease in tree growth synchrony *c.* 1990 for all legacy types except for recently-established stands).

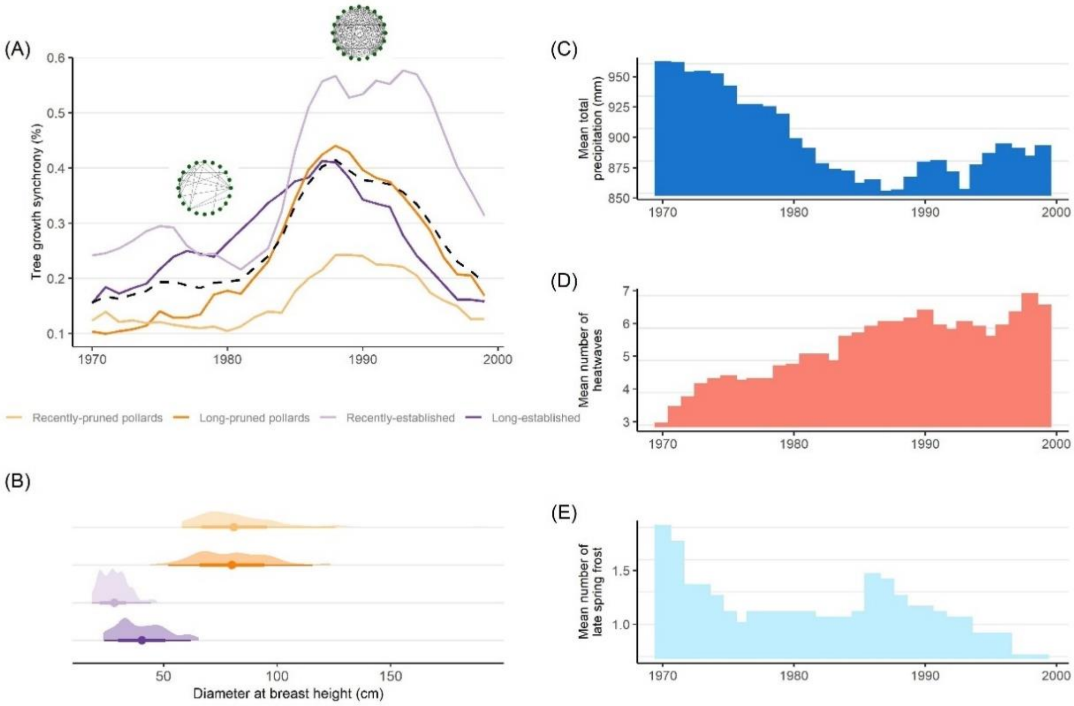


Figure 5.2. Tree growth synchrony as a function of land- and forest- use legacies, structural diversity of each legacy type and climate change trends in the last decades. (A) Tree growth synchrony using 20-years moving windows between 1970-2020 as a function of land- and forest-used legacies. The solid lines represent the mean tree growth synchrony of each legacy type and the dashed line represents the overall mean of tree growth synchrony of all legacy types. Two tree growth synchrony networks are shown, one in a low synchrony period with few links, and one in a high synchrony period with many links. Note that the two networks shown correspond only to one recently-established stand in two time windows and are used as an example to show the calculation and shape of tree growth synchrony networks. (B) Density and interval plot of the diameter at breast height of sampled trees where the point shows the mean tree size, and the 95% interval and density, the distribution of tree size of each legacy type. (C-E) Mean total precipitation, mean number of heatwaves and mean number of late spring frost using 20-years moving windows between 1970-2020.

5.3.2. Forest structural diversity determines tree growth synchrony in response to climate change

We found that the underlying driver determining tree growth synchrony in response to climate change is related to forest structural diversity (i.e. mean tree size and tree size heterogeneity). We observed that lower structural diversity and greater impacts of climate change increased tree growth synchrony (Fig. 5.3). Comparing the model containing legacy type, climatic variables and forest structural diversity with the model without legacy type and the model without forest structural diversity, the model containing legacy type, climatic variables and forest structural diversity, and the model without legacy type had the lowest AIC (*Δ*AICc legacy + climate + structure = 0.0, *Δ*AICc climate + structure = 0.6, *Δ*AICc climate + legacy = 18.9). Since the difference *Δ*AICc was lower than 2 units, we selected the simpler model (i.e. climate + structure, marginal R^2 = 0.53 and conditional R^2 = 0.74). Thus, our results showed more synchronous responses in dry years, with greater number of heatwaves and late spring frosts, and in stands with low tree size heterogeneity and mean tree size (Fig. 5.3).

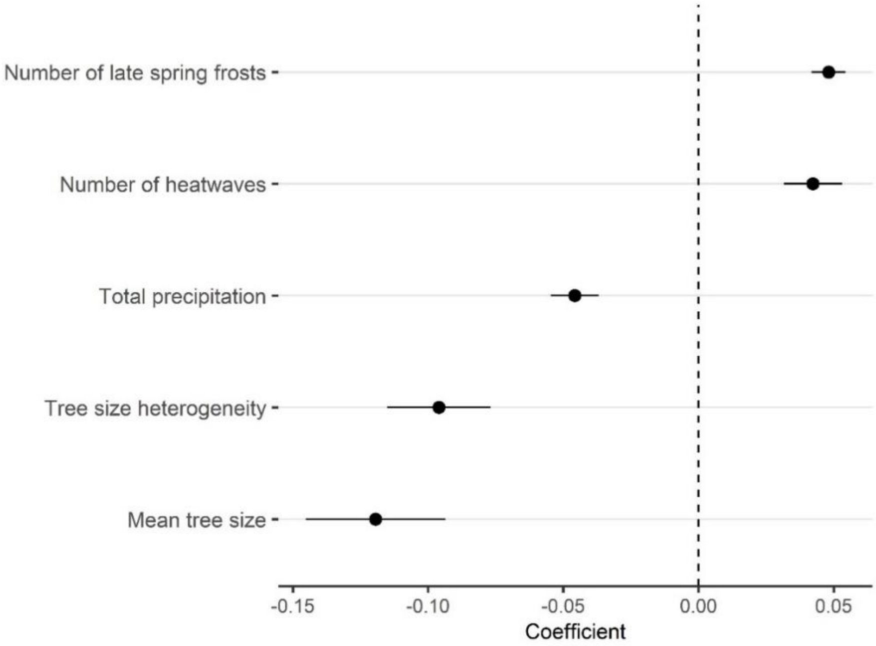


Figure 5.3. Drivers of tree growth synchrony. Estimated coefficients ± 1 standard error for the regression of tree growth synchrony on number of late spring frosts, number of heatwaves, total precipitation, tree size heterogeneity and mean tree size.

5.4. Discussion

Our results showed an increase in tree growth synchrony in response to increasing climate change impacts in a widely distributed temperate tree species. Reduced total precipitation and increased temperature-related extreme events drove the observed increase in tree growth synchrony. However, land- and forest-use legacies modulated the magnitude of increases in synchrony through changes in forest structural diversity (i.e. mean tree size and tree size heterogeneity). Our results, showing that recently-established forests had the greatest tree growth synchrony and that large trees and heterogeneous size distributions decreased growth synchrony, have important implications for forest management since heterogeneous structures could be favoured to adapt forests to novel climatic conditions.

Increases in tree growth synchrony were recorded for the period 1970-2020 in all sampled stands, regardless of land- and forest-use legacies, due to reductions in precipitation and increases in the number of heatwaves and late spring frosts. This result confirms our first hypothesis and is consistent with previous studies that recorded increases in tree growth synchrony in response to increased climatic constraints for different species and forest types around the world (Boden et al., 2014; Latte et al., 2015; Shestakova et al., 2016; Tardif et al., 2003). Although climatic drivers of growth synchrony can vary depending on regional climate (Shestakova et al., 2016), the observed role of dry conditions and heatwaves agrees with the results obtained in populations of *F. sylvatica* in north-western Europe (Latte et al., 2015). Also, the effect of the number of late frosts in synchrony is in line with the detrimental influence of late frosts in the performance of *F. sylvatica* southern populations (Sangüesa-Barreda et al., 2021). Increased growth synchrony is related to increased population vulnerability to climate change (Boden et al., 2014), which in the case of dominant species such as *F. sylvatica*, could jeopardise the stability and persistence of the entire ecosystem. Thus, our results confirm the observations pointing to increased vulnerability to climate change of temperate forests, especially those located at the southern distribution limits (Lindner et al., 2010; Millar & Stephenson, 2015).

The results obtained also support our second hypothesis, as land- and forest-use legacies with greater forest structural diversity showed less tree growth synchrony in response to climate change. Different drivers have been proposed to unravel why trees may respond differently to climate depending on past land- and forest-use, ranging from alterations in biomass (i.e. structural overshoot Jump et al., 2017), in wood density (Alfaro-Sánchez et al., 2019) or in ectomycorrhizal communities (Correia et al., 2021; Mausolf et al., 2018). In this regard, our results suggest the key role of forest structural diversity in how anthropogenic legacies modulate forest vulnerabilities to climate change. The negative effect of tree size heterogeneity on tree growth synchrony indicates that structurally more heterogeneous forests may increase forest resilience by increasing individual-level growth variability in response to climate (Clark et al., 2012). In fact, different tree sizes may show different responses to climate (Day & Greenwood, 2011), spreading the risk of being negatively affected across different tree sizes.

The effect of mean tree size in growth indicates the importance of ontogeny in assessing the impacts of climate change on forests (Heiland et al., 2022). Small trees – usually associated with young individuals – responded more synchronously to climate change than large trees, highlighting the importance of maintaining old-growth forests to mitigate the negative effects of climate change on tree growth synchrony, which is a very relevant result in Europe, where old-growth forests are very scarce (Sabatini et al., 2018). Larger trees can be more independent of the environment than smaller trees because of their larger carbohydrate reserves, more developed root system and greater connection to mycorrhizal networks. This could enhance tree growth resistance and resilience to climatic disturbances compared to younger and smaller trees. In addition, pollarded trees often occur at low densities, which can prevent strong inter-individual competition for resources that worsens the effects of climate change (Linares et al., 2010; Vilà-Cabrera et al., 2011). Although our results showed that forest structural diversity explained a large part tree growth synchrony variance, other variables may also affect growth synchrony (Alfaro-Sánchez et al., 2019; Correia et al., 2021; Jump et al., 2017; Mausolf et al., 2018), suggesting that more than one driver is likely to act synergistically in modulating the impact of climate change on tree growth.

Our results have direct implications for forest adaptation to climate change. We found that recently-established stands had the highest tree growth synchrony. In addition, tree growth synchrony remained higher in recently-established stands over time than in other legacy types when precipitation began to increase and the number of heatwaves and late spring frosts started to decrease. These results suggest that, although recently-established forests are fundamental for carbon sink in the Iberian Peninsula (Vilà-Cabrera et al., 2017), they are vulnerable to climate change due to their more homogeneous structure leading to high tree growth synchrony. The high vulnerability of recently-established forests poses a risk to the carbon sink dynamics in Europe, which is mainly dominated by regrowing forests (Pugh et al., 2019) and where the first signs of carbon saturation are already visible (Nabuurs et al., 2013). Based on our results, recently-established forests could be handled by applying uneven-aged management options to increase forest structural diversity and decrease tree growth synchrony (Lafond et al., 2014). In addition, pollards (both recently- and long-pruned) showed lower synchrony than recently-established forests. Pruning reintroduction in old pollards often improves tree stability and vigour (Sjölund & Jump, 2013), and is likely to be responsible for the lower growth synchrony observed in recently-pruned pollards compared to long-pruned pollards. Recovering tree pollarding and associated wood pastures could bring additional benefits beyond reducing tree growth synchrony, such as, reduced inter-individual tree competition, high biodiversity characteristic of these ecosystems and compatibility of livestock activities and forest-use (Bergmeier et al., 2010; Tucker & Evans, 1997). Our results therefore highlight the most climate-vulnerable forests based on past land- and forest-use, but also show key indications for management actions to adapt forests to the increasing impacts of climate change.

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Chapter 6

General discussion

This thesis assesses the effect of climate and forest-use legacies driving forest dynamics at different spatio-temporal scales. We have quantified how large-scale demographic responses of tree species are changing both in space and time in response to climate (Ch.2 and Ch.3). Although past disturbances strongly alter the way in which Northern Hemisphere forests are influenced by climate, tree species are responding to climate change increasing in abundance towards cold and wet regions of their climate range, and decreasing towards warm and arid regions (Ch.2). In addition, the interaction between increased climate change and tree competition is aggravating over time, indicating non-stationary (i.e. non-time stable) relationships between climate, forest structure and demography (Ch.3). However, the effect of forest structure was considerably higher than the effect of climate on forest dynamics (Ch.2 and Ch.3) and the direct and indirect effects of climate change on forest demography had opposite directions (Ch.3), suggesting that reducing tree competition could ameliorate the negative climate change effects on forest demography.

To better understand the interactive effect of climate change and forest structure on forest dynamics, we analysed how forest-use legacies modulate forest dynamics in response to climate change (Ch.4 and Ch.5). We found that forest-use legacies that persist in the structure, distribution and composition of forests can interact with climatic stressors increasing the probability of climate-induced forest decline (Ch.4), and affect the magnitude of tree growth synchrony (Ch.5). Finally, we proposed a risk-based framework that scientists, managers, and policymakers can apply to anticipate stand- and large-scale forest risk by identifying forest-use legacies and quantifying the impact of their interaction with climate-related stress on forest responses (Ch.4). Thus, the thesis provides insights into spatio-temporal patterns and drivers of forest dynamics by analysing: (1) the effect of climate on recent spatio-temporal dynamics of Northern Hemisphere forests; (2) the impact of forest-use legacies modulating the influence of climate on forest dynamics; and (3) potential forest trajectories based on current trends in forest dynamics. These results, discussed below, will improve our knowledge about the future climate risk of forests and assist in policies and management strategies to adapt forests to the increasing impacts of climate change.

6.1. Recent spatio-temporal dynamics of Northern Hemisphere forests: the interactive effect of climate and forest structure

In this PhD thesis the best available information across space and time are used to better understand forest demographic responses to climate. Spatially, analysing multiple terrestrial and marine species around the globe, the general pattern is that species are moving towards northern and colder latitudes (Lenoir et al., 2020). To answer this question by focussing on trees, previous studies have analysed the variation of demographic rates along geographical gradients (Purves, 2009; Zhu et al., 2012). More recently, largely because of the inconclusive results observed along geographical gradients and a better understanding of the main variables affecting species demography (Jump & Peñuelas, 2005), the scientific community has turned its attention to analysing how species demography varies across climatic space but contrasting results have been obtained depending on the species analysed (Fei et al., 2017; Rabasa et al., 2013; Wason & Dovciak, 2017; Zhu et al., 2014). The results in Ch.2 support the general trend of increasing tree species abundances towards cold and wet regions of their distribution across Northern Hemisphere forests. However, we observed that this pattern is not ubiquitous, depending on the species analysed and other factors driving species persistence, such as forest succession. This result highlights the multifactorial nature describing the probability of species persistence, showing that local factors (e.g. microrefugia or biotic interactions; Dobrowski, 2011; Paquette & Hargreaves, 2021) can modulate the overall pattern (Pironon et al., 2017; Vilà-Cabrera et al., 2019).

We found an increase in tree mortality in Iberian forests since the 1980s, consistent with the trends observed in Northern Hemisphere forests over time (Peng et al., 2011; Senf et al., 2021; Zhou et al., 2013). At the same time, in Ch.2 and Ch.3 our results showed a trend of increasing forest density and productivity, which agrees with studies suggesting that Northern Hemisphere forests are regrowing forests (Pugh et al., 2019), increasing density and basal area (McIntyre et al., 2015; Rautiainen et al., 2011) and thus, carbon sink capacity (Harris et al., 2021; Pan et al., 2011; Zhu et al., 2016). However, these increases in density and basal area could be transient in nature, as they may lead to increased mortality in the future due to increased competition, warming and droughts (Bradford & Bell, 2017; Young et al., 2017). The increasing negative impacts of tree competition and climate change over time are already observed in Iberian forests, leading to non-time stable and non-linear impacts of climate change and increased competition over time as found in Ch.3.

In Ch.3 we observed that the effect of climate change on tree recruitment and growth changed from positive to negative over time, consistent with studies suggesting that warming can increase forest productivity through CO_2 fertilisation and elimination of photosynthesis limitations due to low temperatures, but excess warming may reduce tree growth due to reduced water availability and increased carbon respiration costs (Adams et al., 2009; D'Orangeville et al., 2018; Peñuelas et al., 2017). These results show the difficulty to predict future forest trajectories, as non-linearities open the possibility of tipping points and novel ecological and climatic conditions previously unknown (Armstrong McKay et al., 2022; Cooper et al., 2020; Hillebrand et al., 2020). In addition, the non-stationarity (i.e. non-time stable) nature of climate-forest relationships challenges the use of space-for-time substitutions and future projections of forest dynamics made under stationary assumptions (Johnson & Miyanishi, 2008; Wilmking et al., 2020).

In Ch.2 we observed that shifts in species abundance might be counteracted by forest structure (e.g. species found in forests in early successional stage may be increasing despite being in the warm and arid region of the species climate range) and in Ch.3 we found that climate change direct and indirect (i.e. modulated by forest structure) can act in opposite directions (e.g. climate change could increase tree mortality, but reduced competition could decrease tree mortality), making the study of the interaction between climate and forest structure fundamental. The fact that Northern Hemisphere forests are undergoing secondary succession following past disturbances (Pugh et al., 2019) and increasing in density and productivity (Harris et al., 2021; McIntyre et al., 2015; Pan et al., 2011; Rautiainen et al., 2011; Zhu et al., 2014), is critical to understanding current forest dynamics under climate change, since alterations in forest succession and structure influence forest demographic responses to climate by modifying tree competition (Bradford & Bell, 2017; Young et al., 2017). Therefore, we noted the importance of the interplay between climate and forest structure driving forest dynamics in Ch.2 and Ch.3, highlighting the key role of these interactive effects for understanding future forest trends (Ruiz-Benito et al., 2017). Notably, in Ch.2 we observed that the effect of forest structure was two times greater than the effect of climate shaping species abundance, consistent with previous studies suggesting that forest dynamics are mainly driven by forest structure (Zhang et al., 2015). This finding is also supported in Ch.5, where we found that tree growth synchrony is largely determined by forest structural diversity. Considering the results obtained throughout the PhD thesis, our findings suggest that tree recruitment, growth and mortality are driven by the interactive effects of climate and forest structure, which makes it crucial to take forest structure into account when analysing future forest climate risk. However, changes in forest structure can be the result of natural or human-induced disturbance regimes, and unravelling their causes remains a priority for adapting forests to an increasingly human-altered world.

6.2. Forest-use legacies underpin forest ecosystem dynamics in a warming world

Despite a growing understanding of how climate influences the demography of tree species, little is known about how anthropogenic impacts modulate climate-forest relationships (Perring et al., 2016). However, in a world where more than 75% of the Earth's ice-free land surface is currently altered by humans (Ellis & Ramankutty, 2008), a better understanding on how human imprints influence forest responses to climate is critical. This remains a major challenge, as forest ecosystem responses in many cases are not immediate to anthropogenic and climatic impacts, resulting in delayed forest responses (i.e. legacy effects; Anderegg et al., 2015; Marqués et al., 2022). Thus, long-term records of both climate and forest-use data need to be integrated to understand current forest dynamics (Ruiz-Benito et al., 2020), but these databases are very scarce (see e.g. Madrigal-González et al., 2015). To overcome these limitations in Ch.4 we proposed a framework to identify forest-use legacies based on existing current data on forest structure, distribution, and composition that can be used as proxies of legacy-driven alteration of forest properties together with available information on past forest-use. Then we applied this framework to identify forest-use legacies in Scots pine (*Pinus sylvestris* L.) stands in Iberian forests allowing us to distinguish forest inventory plots according to their (i) natural or planted character as an indicator of forest-use legacies in distribution and stand composition, and (ii) forest structural characteristics as an indicator of forest-use legacies in forest structure. This framework might allow future studies to identify forest-use legacy effects. Yet, once legacy effects are detected we need to incorporate them into empirical study designs, so that they are considered alongside environmental drivers of contemporary forest dynamics.

In recent years, there has been increasing interest in better understanding how forest-use or anthropogenic legacies modulate tree responses to climate change (see e.g. Jump et al., 2017; Marqués et al., 2022). To date, most evidence suggests that past human-induced disturbances need to be considered when analysing forest dynamics, as forest responses to climate vary greatly depending on past anthropogenic imprints (Alfaro-Sánchez et al., 2019; Mausolf et al., 2018; Perring et al., 2018). This finding is supported by the literature review in Ch.4, where we observed strong evidence of how human-driven changes in forest structure, distribution and species composition can exacerbate the probability of forest decline in response to climate change. Furthermore, we found that the interactive effect of changes in climate and forest-use can occur at large spatial scales, as shown by the case of Scots pine in Iberian forests, or on a local scale, as observed in Ch.5 by analysing beech forests at their rear edge. Thus, first we provided a framework for identifying forest-use legacy effects and then we tested this framework both at regional and local scale by quantifying the interaction between climate change and forest-use legacies on tree growth (Ch.5) and mortality (Ch.4). However, open questions remain, such as whether the proposed framework can support the identification of beneficial past forest management practices that minimise risk components and improve forest resilience to climate change, or what are the drivers underlying these climate-human-forest relationships.

So far, different drivers have been proposed to unravel why forests may respond differently to climate depending on past forest-use, ranging from alterations in biomass (i.e. structural overshoot Jump et al., 2017), in wood density (Alfaro-Sánchez et al., 2019) or in ectomycorrhizal communities (Correia et al., 2021; Mausolf et al., 2018). In this sense, in Ch.5 we aimed to better understand the mechanistic relationships between climate change, forest-use legacies and tree growth synchrony. We found that forest-use legacies drove tree growth synchrony in response to climate change through changes in forest structural diversity (i.e. mean tree size and tree size heterogeneity). Specifically, we observed that lower mean tree size and tree size heterogeneity increased tree growth synchrony. Alterations in forest structural diversity could also be one of the underlying drivers explaining the divergent species demographic responses to climate observed so far at large spatial scales (Fei et al., 2017; Rabasa et al., 2013; Wason & Dovciak, 2017; Zhu et al., 2014). This finding suggests that more than one driver is likely to act synergistically driving climate-human-forest relationships that future studies should investigate further, as the interactive impacts of climate change and human disturbances will largely determine the future of Northern Hemisphere forests.

6.3. Potential trajectories of Northern Hemisphere forests based on current trends in forest dynamics

Tree recruitment, growth and mortality rates are increasing in Northern Hemisphere forests (see e.g. for increases in tree recruitment and growth Harris et al. (2021), Pan et al. (2011) and Zhu et al. (2016), and for increases in mortality Peng et al. (2011); Senf et al. (2021) and Zhou et al. (2013)). This result is in line with the greater recruitment than mortality observed in Ch.2 and the greater recruitment and growth than mortality observed in Ch.3. Based on these past trends and the expected increasing impacts of climate change (IPCC, 2021), tree mortality is highly likely to increase (McDowell et al., 2020). However, tree recruitment and growth trajectories are not as clear-cut due the antagonistic effects that the drivers of global change might have on tree recruitment and growth (e.g. increases in forest productivity through the elimination of photosynthesis limitations due to low temperatures vs. increased carbon respiration costs (Adams et al., 2009; Peñuelas et al., 2017)). Thus, while mortality rates are highly likely to increase, recruitment and growth trajectories remain uncertain.

These shifts in forest dynamics will lead to changes in the structure, distribution and species composition of Northern Hemisphere forests in the 21st century. However, to completely understand how current demographic trends can determine forest trajectories, along with tree recruitment and mortality, future research should incorporate other vital rates that are critical in the life cycle of trees (e.g. fecundity and seedling establishment) to obtain a complete picture of the spatio-temporal variation of climate change impacts on forest dynamics.

In both Ch.2 and Ch.3 we observed an increase in tree density, but in Ch.4 and Ch.5 we highlighted that forest structure cannot be understood without considering forest-use legacies. Thus, in a historically intensively managed forest such as those in the Northern Hemisphere (McGrath et al., 2015), tree density is likely to continue to increase, both due to the effects of climate change increasing the number of small trees, and due to the abandonment of traditional forest-use (McIntyre et al., 2015; Seijo et al., 2018). In addition, shifts in species distribution are occurring with a general pattern of poleward species movements (Lenoir et al., 2020; Sharma et al., 2022). However, this trend is altered by multiple natural and anthropogenic disturbances, such as biotic interactions (Paquette & Hargreaves, 2021), land-use changes (Guo et al., 2018) or shifts in forest succession as observed in Ch.2. Moreover, species movements might be responding to legacies of past climate or forest-use (Goring & Williams, 2017; Peñuelas et al., 2007; Sánchez de Dios et al., 2021), highlighting the importance of including past climatological and ecological legacies to understand current forest dynamics as shown in Ch.4 and Ch.5. At the same time, compositional shifts towards more arid- and warm-affiliated species and traits are expected to occur under future scenarios of increased warming and droughts (Batllori et al., 2020; Esquivel-Muelbert et al., 2019; Ruiz-Benito et al., 2017; Trugman et al., 2020). In this sense, our results in Ch.2 suggested that warm-affiliated species with broad minimum temperature niche width will increase in abundance following the thermophilization hypotheses (Gottfried et al., 2012). Interestingly, there may be feedbacks between changes in forest structure, distribution and composition, and forest dynamics. For example, large trees' mortality due to climate change could increase small trees' density, but at the same time, this increase in tree density could increase tree mortality in the future due to increased competition leading to self-thinning (McDowell et al., 2020).

Shifts in forest structure, distribution and species composition will have direct consequences on the ecosystem contributions that forests provide to society (Anderegg et al., 2013; Brodribb et al., 2020). As seen in Ch.5, recently-established forests might be more vulnerable to climate change than long-established forests threatening their persistence, and the above-ground productivity of Iberian forests could continue to decline following current trends (Ch.3), reducing their carbon sink capacity. However, from Ch.2 to Ch.5 our results indicated that changes in forest structure, distribution and species composition are highly dependent on human-driven disturbances opening an opportunity to ameliorate the negative effects of climate change on forest dynamics through forest management. For example, as found in Ch.5 greater forest structural diversity might decrease tree growth synchrony, increasing forest resistance and resilience to climate change. In this sense, the risk-based framework provided in Ch.4 might help managers and policymakers to anticipate large-scale forest mortality events in response to climatic stressors by analysing current forest structure, distribution and composition. Forest ecosystems will continue to change in response to climate change and therefore, remains essential to continue investigating forest dynamics at multiple spatio-temporal scales: from large inventory networks and remote sensing to detect patterns and key drivers of changes in forest dynamics, to intensive monitoring to understand the mechanistic relationship between drivers and forest responses, to research under control conditions to elucidate the underlying species physiological responses to climate. All of this will be needed to model future forest trajectories under climate change.

6.4. References

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Chapter 7

General conclusions

General conclusions

1. Even if past disturbances strongly alter the way in which Northern Hemisphere forests are influenced by climate, tree species are responding to climate change, increasing in abundance towards cold and wet regions of their climate range, and decreasing towards warm and arid regions.
2. Northern Hemisphere forests are increasing in density and productivity and, therefore, the carbon stored aboveground is increasing. However, these increases in density and productivity could be transient in nature, as tree mortality is increasing as a consequence of increased competition leading to self-thinning and because of the increasing impacts of climate change.
3. The interaction between increased tree competition and climate change is aggravating over time indicating non-stationary (i.e. non-time stable) relationships between climate, forest structure and demography.
4. The effect of forest structure is considerably greater than the effect of climate on forest dynamics and the direct and indirect (i.e. modulated by forest structure) effects of climate change on forest demography might have opposite directions, suggesting that reducing tree competition could ameliorate the negative effects of climate change on forest demography.
5. Forest-use legacies that persist in the structure, distribution and composition of forests can interact with climatic stressors increasing the probability of climate-induced forest decline at regional (the case of *Pinus sylvestris* in Iberian forests) and local scales (the case of *Fagus sylvatica* at its rear edge).
6. A risk-based framework to identify forest-use legacies in forest ecosystems and quantify the impact of their interaction with climate-related stress on forest responses can provide scientists, managers, and policymakers with an approach to anticipate stand- and large-scale forest riskm, and promote ecosystem stability and resilience in regions dominated by human-modified forests.
7. Alterations in forest structural diversity could be one of the underlying drivers explaining the divergent demographic responses of species to climate observed so far at large spatial scales.
8. Following past trends, tree mortality rates are highly likely to increase in the future, while recruitment and growth trajectories remain uncertain. These shifts in forest dynamics will lead to changes in the structure, distribution and species composition of Northern Hemisphere forests in the 21st century.
9. Tree density is likely to continue increasing, species distribution shifting poleward and arid- and warm-affiliated species increasing their dominance in the coming decades due to climate change. However, this trend might be greatly altered by forest-use legacies.
10. Shifts in forest structure, distribution and species composition will have direct consequences on the ecosystem contributions that forests provide to society which makes essential further research on forest dynamics at multiple spatio-temporal scales.

Conclusiones generales

1. A pesar de que las perturbaciones pasadas alteran fuertemente la manera en que los bosques del hemisferio norte están influenciados por el clima, las especies arbóreas están respondiendo al cambio climático, aumentando su abundancia hacia las regiones frías y húmedas de su rango climático, y disminuyendo hacia las regiones cálidas y áridas.
2. Los bosques del hemisferio norte están aumentando en densidad y productividad y, por tanto, el carbono aéreo almacenado está aumentando. Sin embargo, estos aumentos en densidad y productividad podrían ser de carácter transitorio, ya que la mortalidad de los árboles está aumentando como consecuencia del aumento de la competencia que conduce al autoaclareo y por los crecientes impactos del cambio climático.
3. La interacción entre el aumento de la competencia de los árboles y el cambio climático se está agravando con el tiempo, lo que indica relaciones no estacionarias (i.e. no estables en el tiempo) entre el clima, la estructura forestal y la demografía.
4. El efecto de la estructura forestal es considerablemente mayor que el efecto del clima en la dinámica forestal y los efectos directos e indirectos (i.e. modulados por la estructura del bosque) del cambio climático en la demografía forestal podrían tener direcciones opuestas, lo que sugiere que la reducción de la competencia de los árboles podría reducir los efectos negativos del cambio climático en la demografía forestal.
5. Los legados del uso forestal que persisten en la estructura, distribución y composición de los bosques pueden interactuar con los estresores climáticos aumentando la probabilidad de un declive forestal inducido por el clima a escala regional (el caso de *Pinus sylvestris* en los bosques ibéricos) y local (el caso de *Fagus sylvatica* en el límite meridional de la especie).
6. Un marco basado en el riesgo para identificar los legados del uso forestal en los ecosistemas forestales y cuantificar el impacto de su interacción con el estrés climático en las respuestas de los bosques, puede proporcionar a los científicos, gestores y responsables políticos una metodología para anticiparse al riesgo forestal a gran escala, y promover la estabilidad y resiliencia de los ecosistemas en las regiones dominadas por los bosques modificados por los humanos.
7. Las alteraciones de la diversidad estructural de los bosques podrían ser uno de los factores subyacentes que explican las divergentes respuestas demográficas de las especies al clima observadas hasta ahora a grandes escalas espaciales.
8. Siguiendo las tendencias pasadas, es muy probable que las tasas de mortalidad de los árboles aumenten en el futuro, mientras que las trayectorias de reclutamiento y crecimiento siguen siendo inciertas. Estos cambios en la dinámica forestal darán lugar a modificaciones en la estructura, distribución y composición de especies de los bosques del hemisferio norte en el siglo XXI.

9. Es probable que la densidad de los árboles siga aumentando, que la distribución de las especies se desplace hacia los polos y que las especies afines a las zonas áridas y cálidas aumenten su predominio en las próximas décadas debido al cambio climático. Sin embargo, esta tendencia podría verse muy alterada por los legados del uso de los bosques.
10. Los cambios en la estructura, la distribución y la composición de las especies de los bosques tendrán consecuencias directas en las contribuciones de los ecosistemas a la sociedad, lo que hace esencial seguir investigando la dinámica de los bosques a múltiples escalas espacio-temporales.

Supporting information of Chapter 2: Recent dynamics of Northern Hemisphere tree species along climatic and successional gradients

Appendix 2.S1. National forest inventories

Table 2.S1. Plot shape, mean plot area in hectares, minimum census date, maximum census date, mean census interval, number of species and number of plots in each of the national forest inventories analysed.

Plot shape	Mean plot area (ha)	Minimum census date	Maximum census date	Mean census interval	N. species	N. plots
Belgium						
variable radius & concentric circles	0.10	1994	2019	12	10	1404
Czech Republic						
concentric circles	0.05	2008	2015	5	11	545
Finland						
variable radius	0.03	1985	1995	9	5	1863
Netherlands						
concentric circles	0.04	2001	2019	7	11	1142
Poland						
concentric circles	0.03	2005	2014	4	12	20124
Spain						
variable radius	0.20	1986	2008	11	17	39965
Sweden						
concentric circles	0.03	2003	2017	4	9	11706
US						
circular	0.07	1998	2018	6	55	50958

Appendix 2.S2. Forest succession

A good measurement of forest succession is basal area, as basal area increases during forest succession (Westoby, 1984). However, the maximum stand basal area (i.e. that expected to be observed in late successional stages) depends on climate and soil conditions. Thus, we calculated forest succession based on the basal area of each plot with respect to the maximum basal area found in plots with similar climatic and soil characteristics.

First, we created clusters of similar abiotic and soil characteristics along Europe and the U.S. considering key factors driving basal area increment: annual mean temperature, annual precipitation (ln scale) and nitrogen availability availability (Berendse & Aerts, 1987; Ruiz-Benito et al., 2014; Vayreda et al., 2012). Annual mean temperature and annual precipitation at 1 km^2 were obtained from WorldClim 2 (Fick & Hijmans, 2017) and nitrogen availability in 0-30 cm at 250 m from SoilGrids v2 (Poggio et al., 2021).

To reduce abiotic variability within clusters, we selected the number of clusters when the median cluster size, the minimum cluster size and within the sum of squares started to draw an exponential curve (i.e. from 40 to 30 for both Europe and the U.S., see Fig. 2.S2.1 and 2.S2.2). We also found that the coefficient of variation of cluster precipitation (ln scale), mean temperature and nitrogen availability followed a similar pattern (Fig. 2.S2.1 and 2.S2.2). Furthermore, we observed that the coefficient of variation of basal area remained relatively high regardless of the number of clusters, suggesting a high variability of forest successional stage within the cluster. Once the number of clusters was set to 40, we validated it using the silhouette method (Fig. 2.S2.3 and 2.S2.4).

For each of the forest inventory plots we obtained a forest succession value ranging from 0 to 1 by dividing the basal area of each plot to the maximum basal area of the cluster (i.e. 95th percentile of the basal area of the cluster to which this plot belonged).

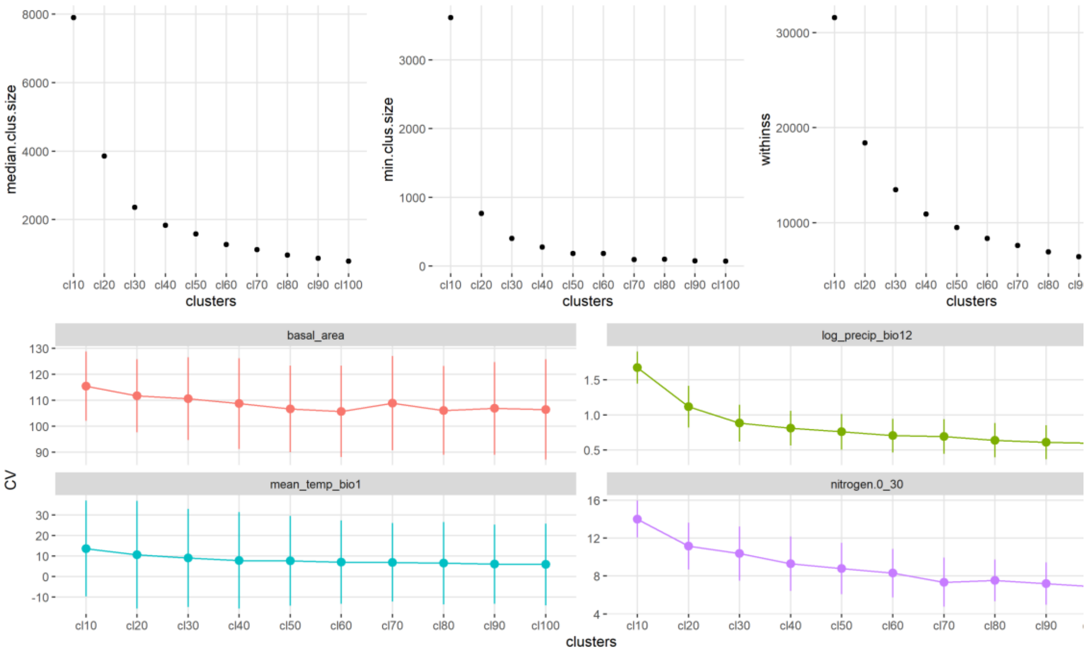


Figure 2.S2.1. Metrics for determining the appropriate number of clusters (n = 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 clusters) for characterising forest development based on the kmeans method in Europe. Top panel: median cluster size, minimum cluster size and within sum of squares vs. the number of clusters. Bottom panel: the coefficient of variation of cluster basal area, precipitation (ln scale), mean temperature and nitrogen availability vs. the number of clusters.

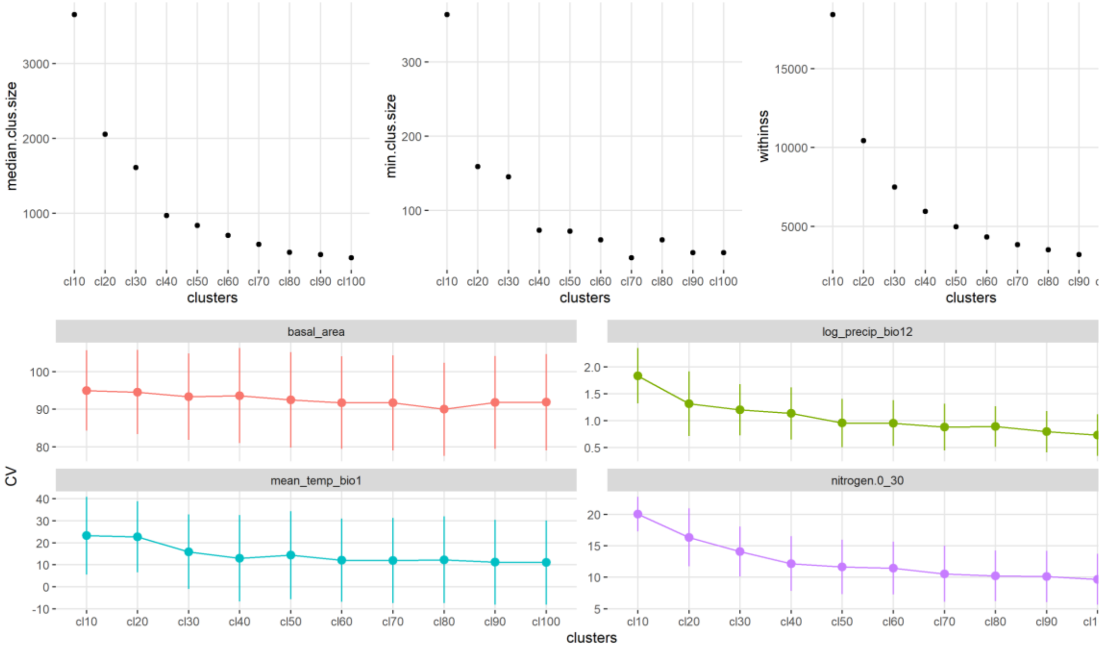


Figure 2.S2.2. Metrics for determining the appropriate number of clusters (n = 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 clusters) for characterising forest development based on the kmeans method in the U.S. Top panel: median cluster size, minimum cluster size and within sum of squares vs. the number of clusters. Bottom panel: the coefficient of variation of cluster basal area, precipitation (ln scale), mean temperature and nitrogen availability vs. the number of clusters.

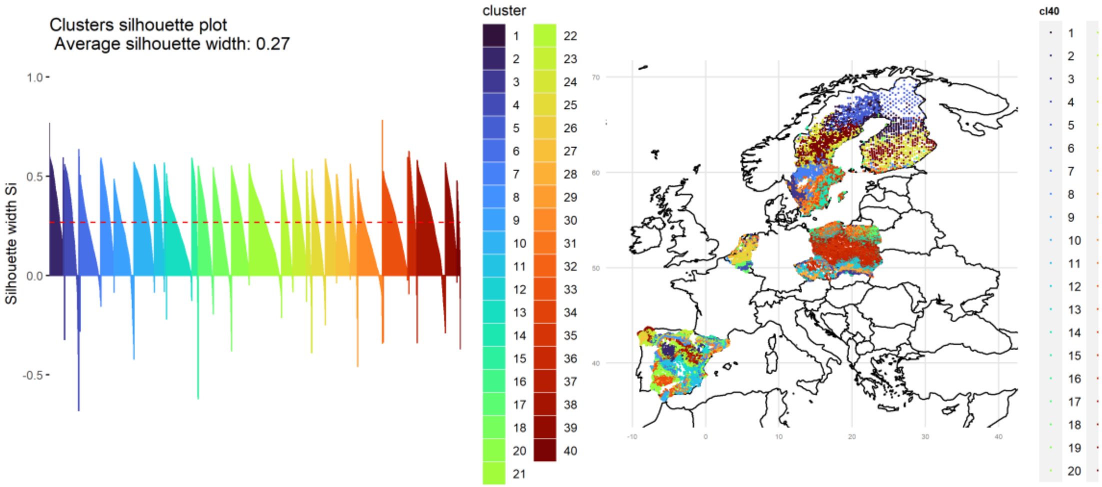


Figure 2.S2.3. Cluster validation in Europe based on clusters silhouette plot using 40 clusters.

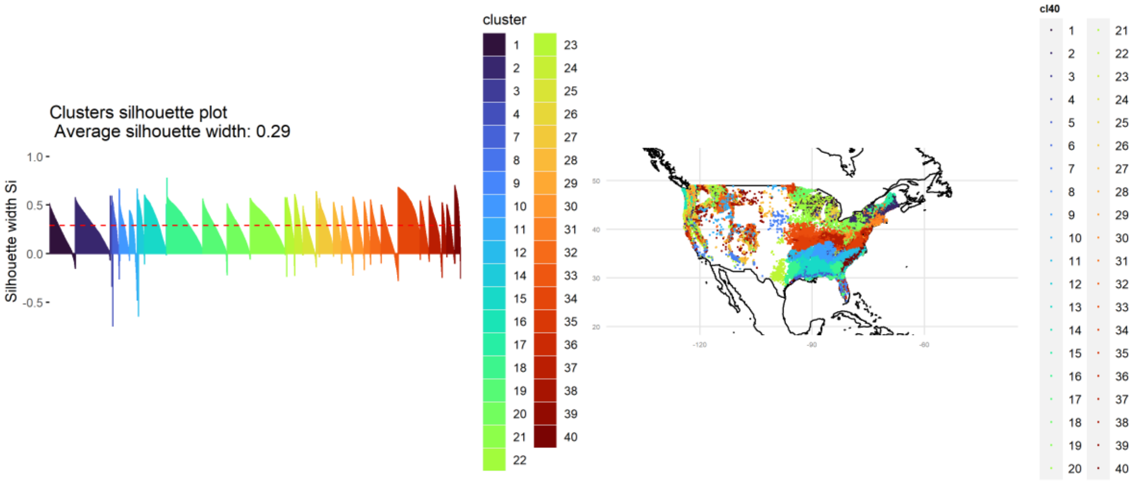


Figure 2.S2.4. Cluster validation in the U.S. based on clusters silhouette plot using 40 clusters.

Appendix 2.S3. Further modelling details

Generalised additive models (GAM)

Exploratory analyses, *gam* model evaluation and predictions of the number of stems in the second census model when regressed on the interaction of aridity, minimum temperature and forest succession of each plot, the interaction of the natural logarithm of the number of stems in the first census and census interval, the country in which each plot was measured, and including an offset of the natural logarithm of stand area. Note that below is an example for *Fagus sylvatica* but when the paper is submitted, all species model fits will be published in a public repository.

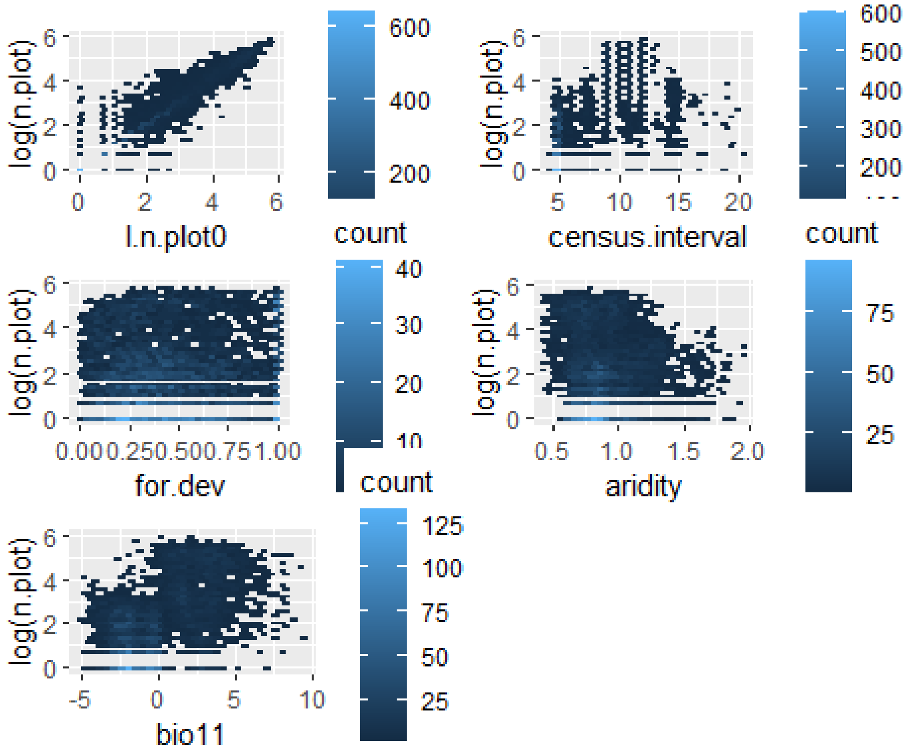
Fagus sylvatica

```
data_model <- readRDS(file = here("02-data", "models", "data_model.rds"))

data_model <- data_model |>
  mutate(
    l.n.plot0 = log(n.plot0),
    l.plot.area = log(plot.area),
    country = as.factor(country)
  )

class(data_model$country)

## [1] "factor"

sp <- data_model |>
  filter(species.cor == "Fagus sylvatica")
```

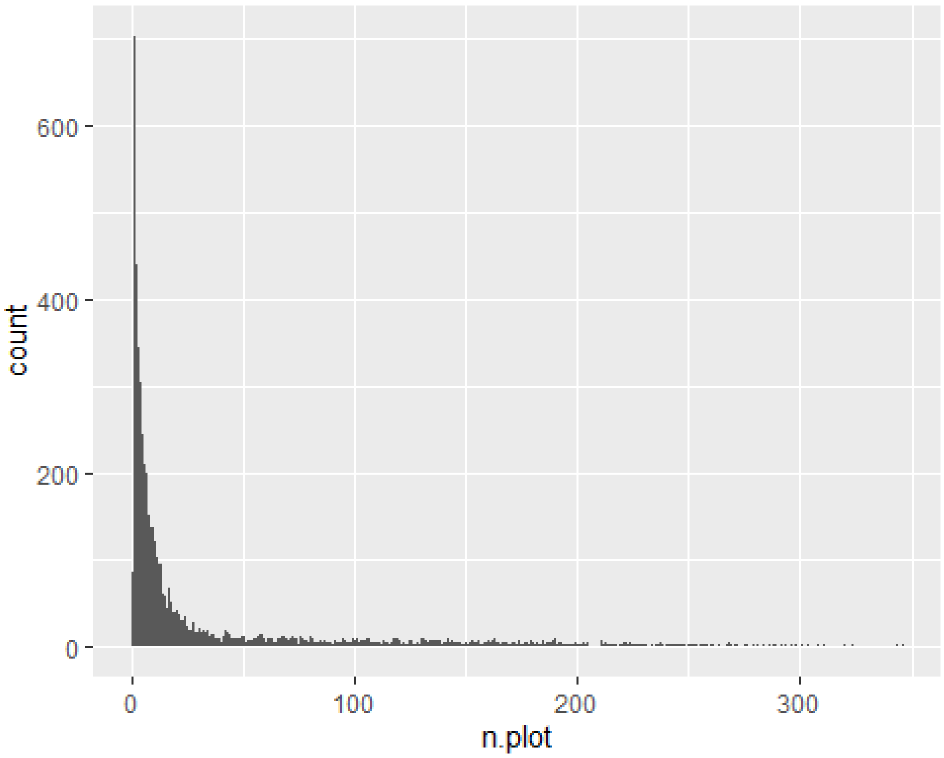
EDA

Univariate plots

```
plot_eda(sp)
```



```
# response variable distribution (after rpois)
ggplot(sp, aes(n.plot)) +
  geom_histogram(binwidth = 1) +
  coord_cartesian(xlim = c(0, max(sp$n.plot)))
```



Data summary for all species together

```
summary(data_model$n.plot)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    0.00    1.00    4.00   15.01   12.00  568.00
```

```
summary(data_model$n.plot0)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    1.00    2.00    4.00   13.87   12.00  484.00
```

```
summary(log(data_model$n.plot0))
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##  0.0000  0.6931  1.3863  1.5764  2.4849  6.1821
```

```
summary(data_model$census.interval)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##   4.000   4.978   5.337   6.982   9.834  21.622
```

```
summary(data_model$for.dev)
```

```
##      Min.   1st Qu.    Median      Mean   3rd Qu.      Max.
## 0.0002914 0.2587241 0.4483680 0.4553103 0.6306841 1.0000000
```

```
summary(data_model$bio11)
```

```
##     Min.  1st Qu.   Median     Mean  3rd Qu.     Max.
## -15.2333  -4.2500   0.6333   0.1973   5.1833  19.1500
```

```
summary(data_model$aridity)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##  0.1529  0.7075  0.8524  0.8433  0.9995  4.1413
```

```
summary(log(data_model$plot.area))
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##  -4.962  -2.700  -2.700  -2.673  -2.700  -1.609
```

Data summary for Fagus sylvatica

```
summary(sp$n.plot)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    0.00    3.00    8.00   33.06   28.00  346.00
```

```
summary(sp$n.plot0)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##    1.00    3.00    8.00   29.89   25.00  346.00
```

```
summary(log(sp$n.plot0))
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##   0.000   1.099   2.079   2.192   3.219   5.846
```

```
summary(sp$census.interval)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##   4.310   4.975   5.095   7.444  10.466  20.452
```

```
summary(sp$for.dev)
```

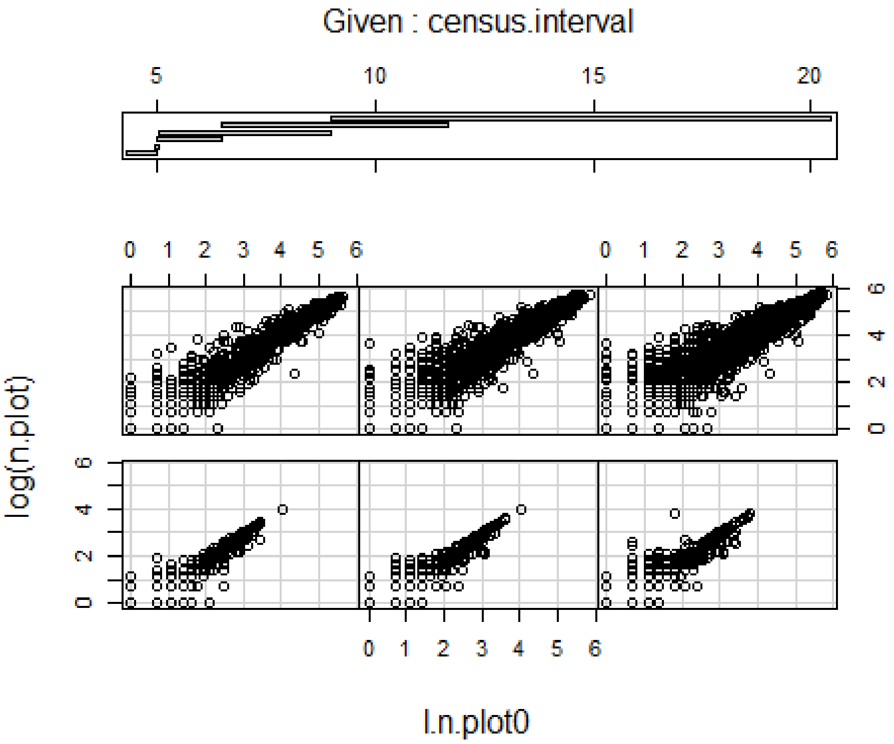
```
##     Min.  1st Qu.   Median     Mean  3rd Qu.     Max.
## 0.001139 0.256508 0.436059 0.477931 0.677566 1.000000
```

```
summary(sp$bio11)
```

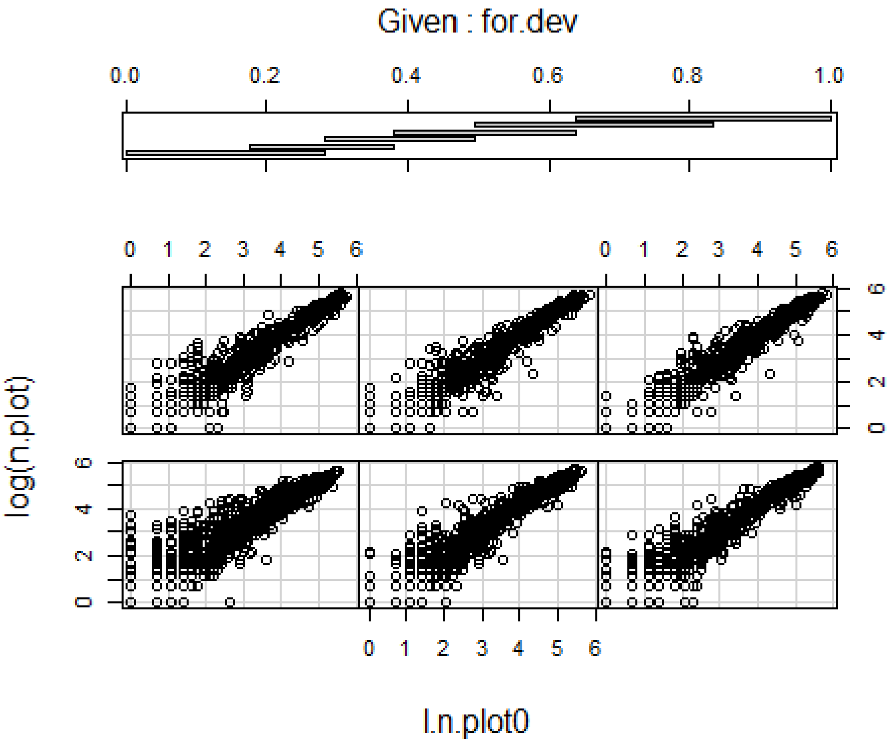
```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
## -4.9000 -1.9000 -0.2167  0.3242  2.5167  9.3833

summary(sp$aridity)

##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##  0.4192  0.7340  0.8659  0.9154  1.0471  1.9465

summary(log(sp$plot.area))

##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##  -4.854  -3.219  -3.219  -2.716  -1.609  -1.609
```

Coplots

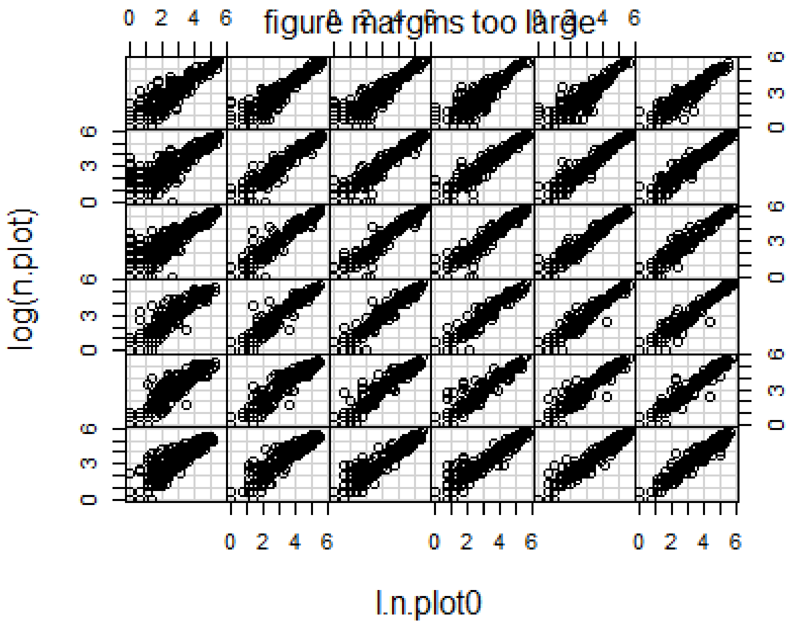
```
x11()
coplot_n0_ci(sp)
```



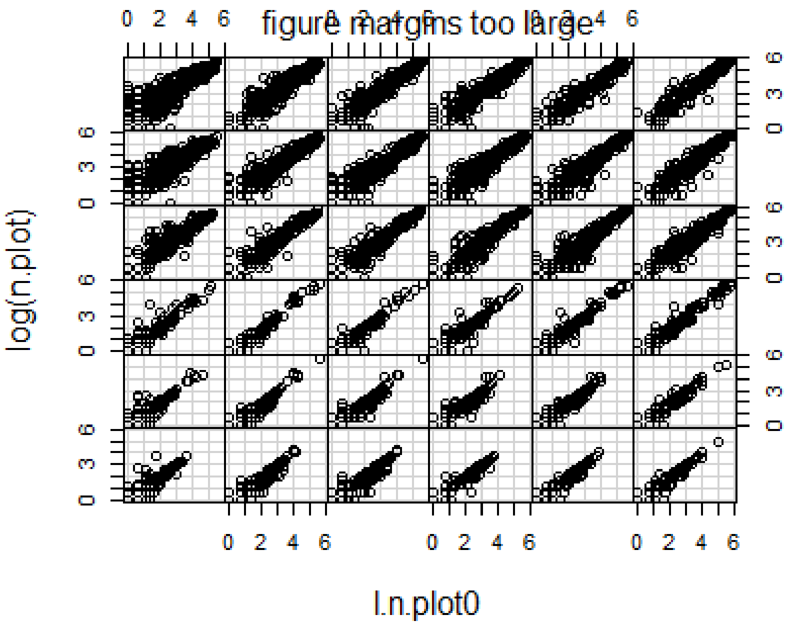
```
coplot_n0_fd(sp)
```



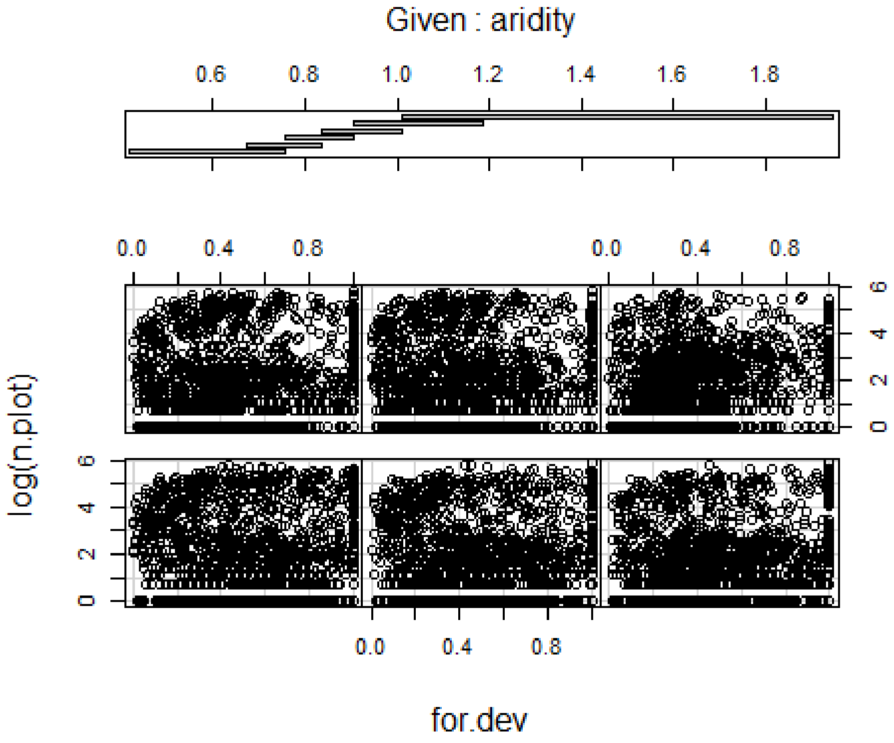
```
coplot_n0_fd_arid(sp)
```



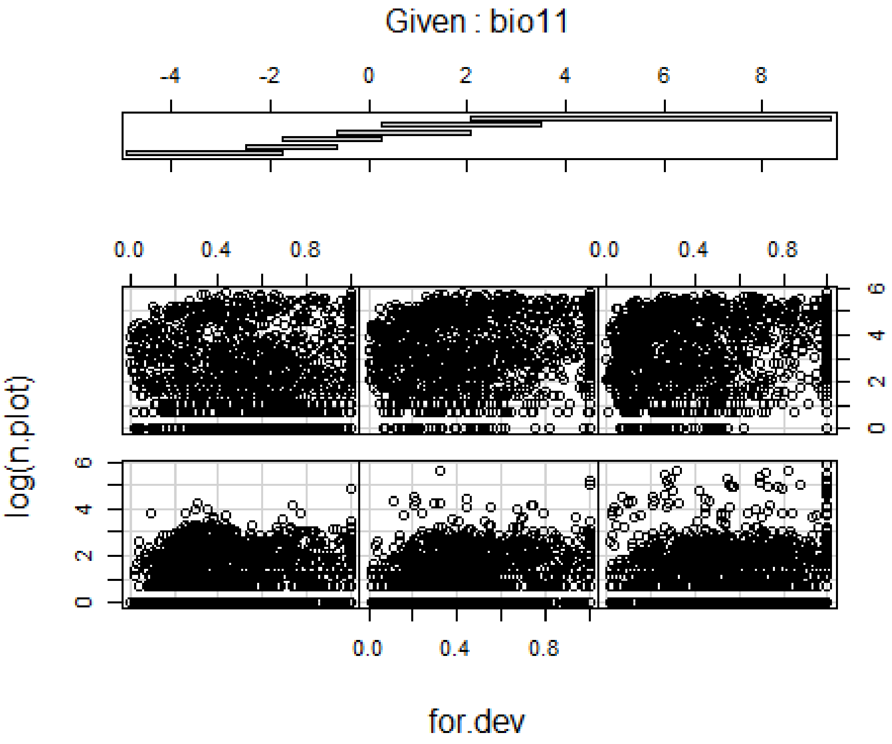
```
coplot_n0_fd_bio11(sp)
```



```
coplot_fd_arid(sp)
```

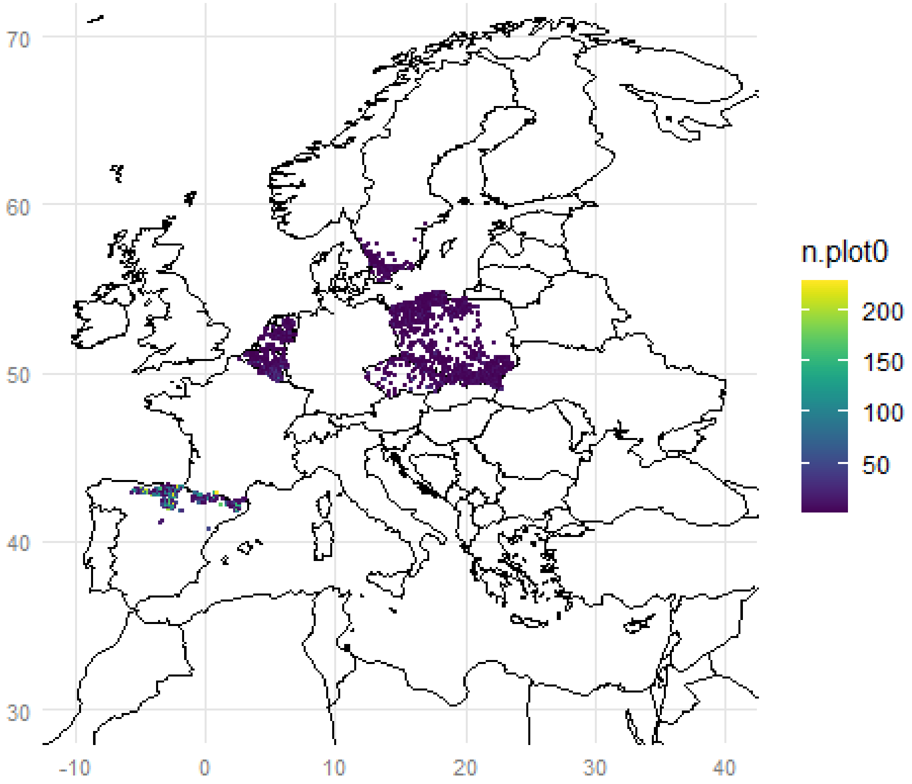


```
coplot_fd_bio11(sp)
```

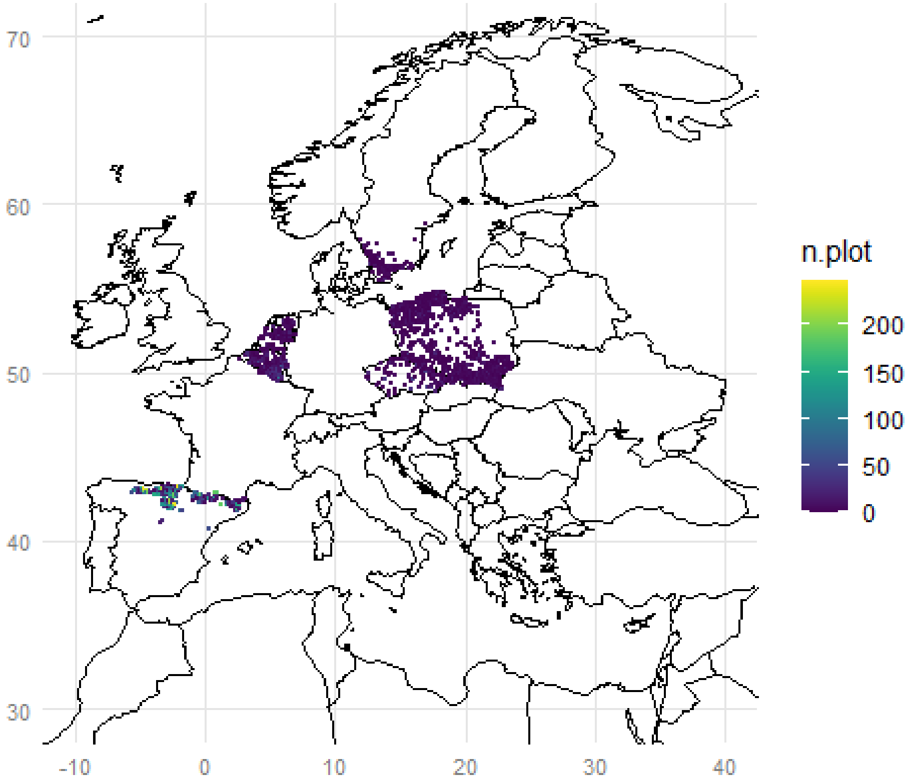


Maps of covariates

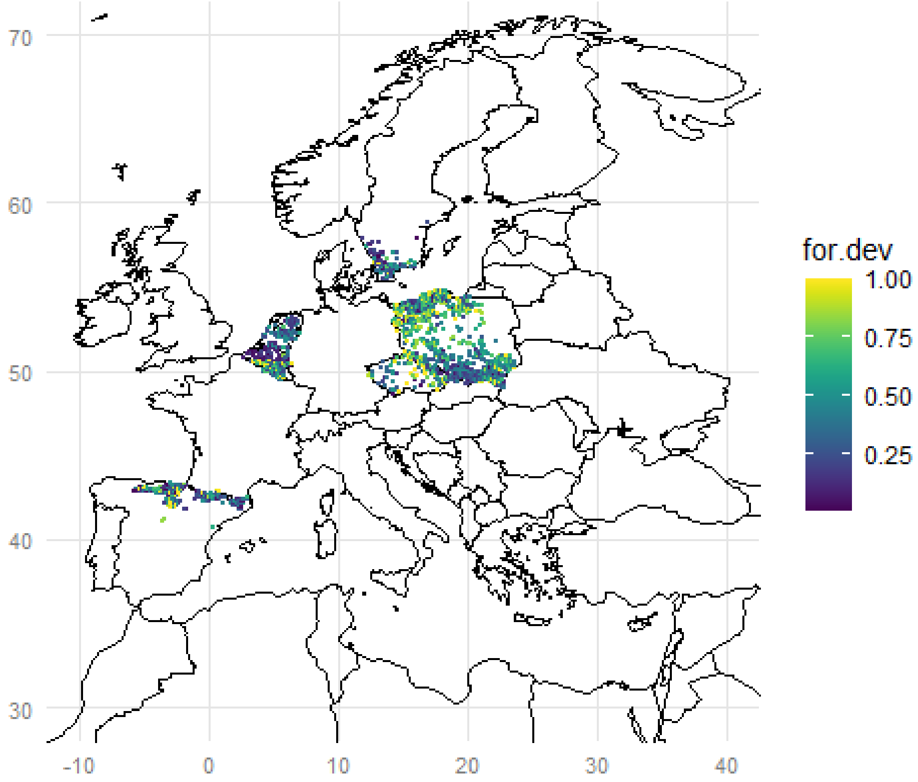
```
# quantile filtering for data vis
sp_n.plot0_q <- sp |>
  filter(n.plot0 < quantile(n.plot0, .99))

map_vars(dat = sp_n.plot0_q, var = "n.plot0") +
  coord_fixed(
    xlim = c(-10, 40), ylim = c(30, 70), ratio = 1.3
    )
```



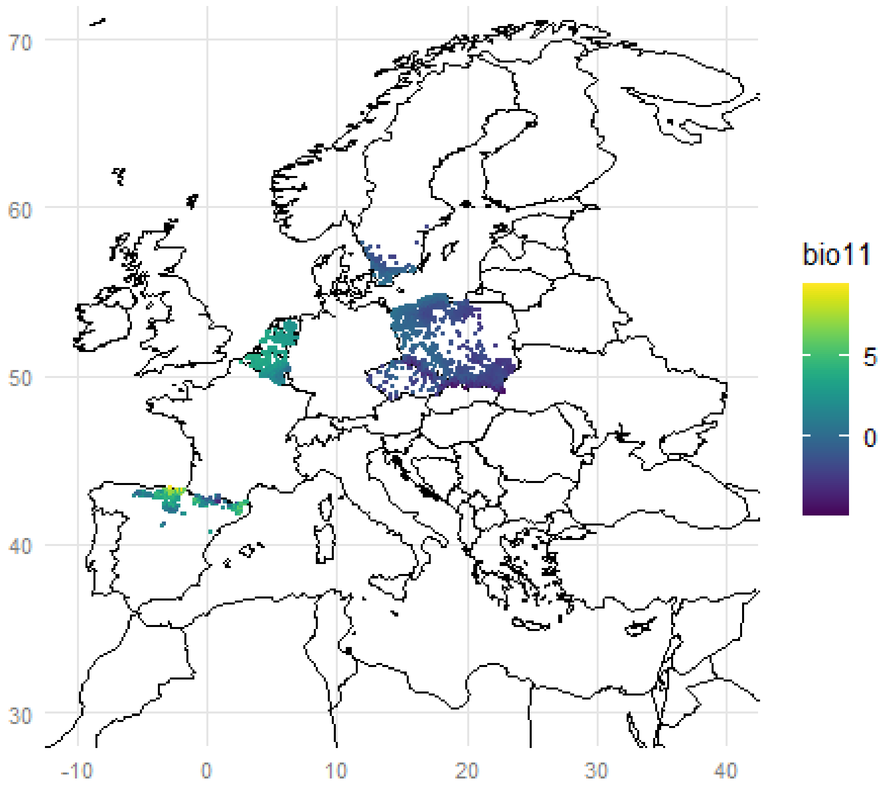
```
sp_n.plot_q <- sp |>
  filter(n.plot < quantile(n.plot, .99))

map_vars(dat = sp_n.plot_q, var = "n.plot") +
  coord_fixed(
    xlim = c(-10, 40), ylim = c(30, 70), ratio = 1.3
    )
```



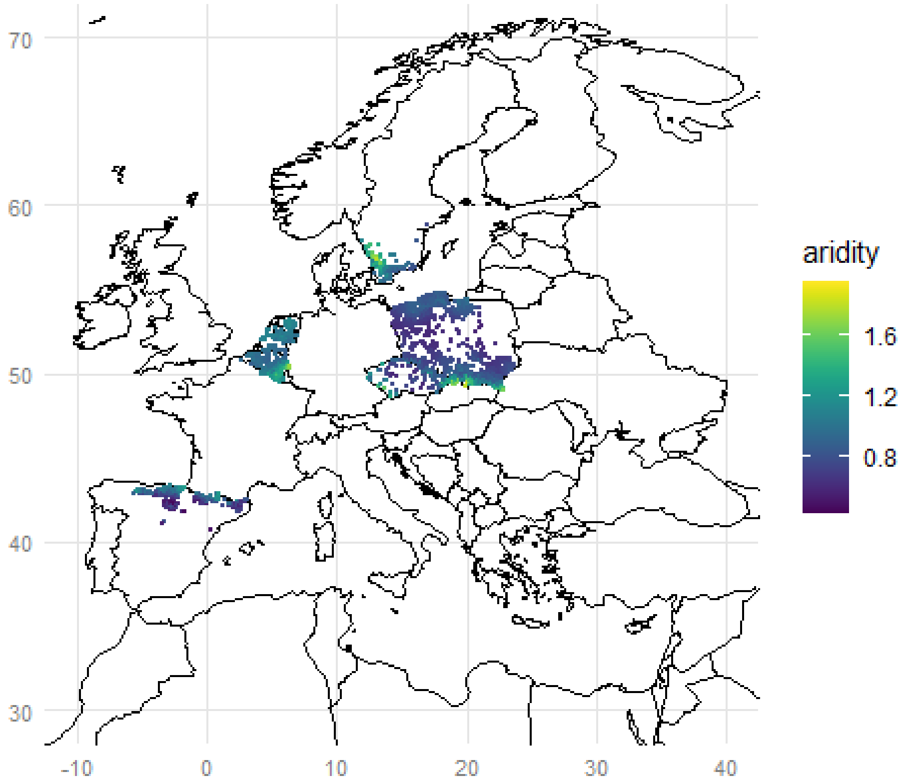
```
# other covariates
vector_vars <- c("for.dev", "bio11",
       "aridity")

map(vector_vars, ~map_vars(dat = sp,
         var = .x) +
  coord_fixed(
    xlim = c(-10, 40), ylim = c(30, 70), ratio = 1.3
    ))

## [[1]]
```



```
##
## [[2]]
```



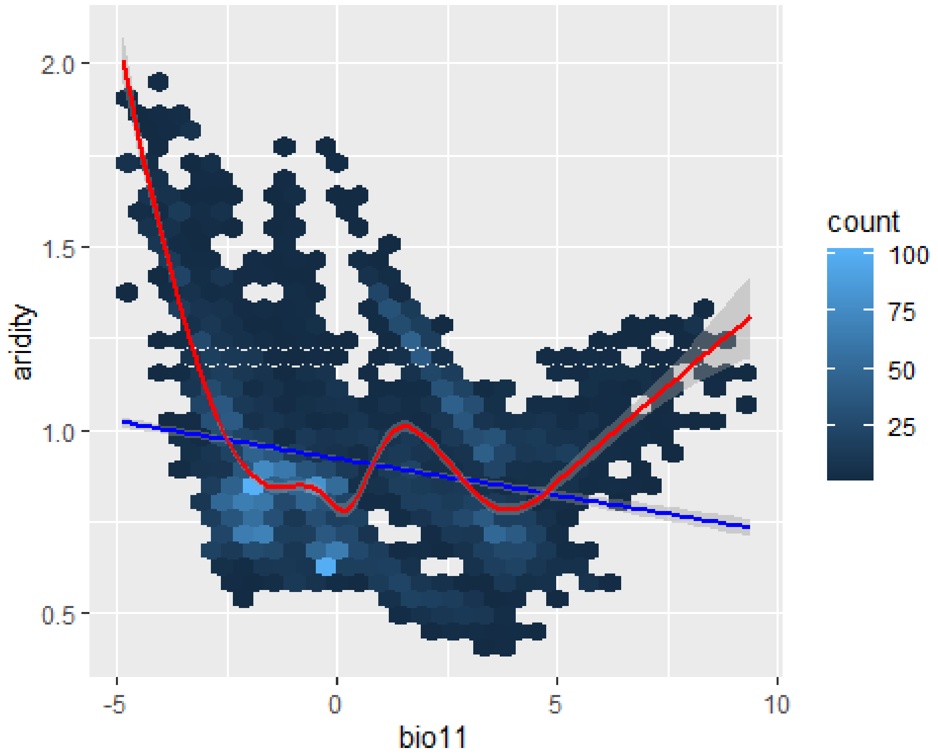
```
##
## [[3]]
```



Climate data covariation

```
ggplot(sp, aes(x = bio11,
               y = aridity)) +
  geom_hex() +
```

```
  geom_smooth(method = "lm", col = "blue") +
  geom_smooth(col = "red")
```

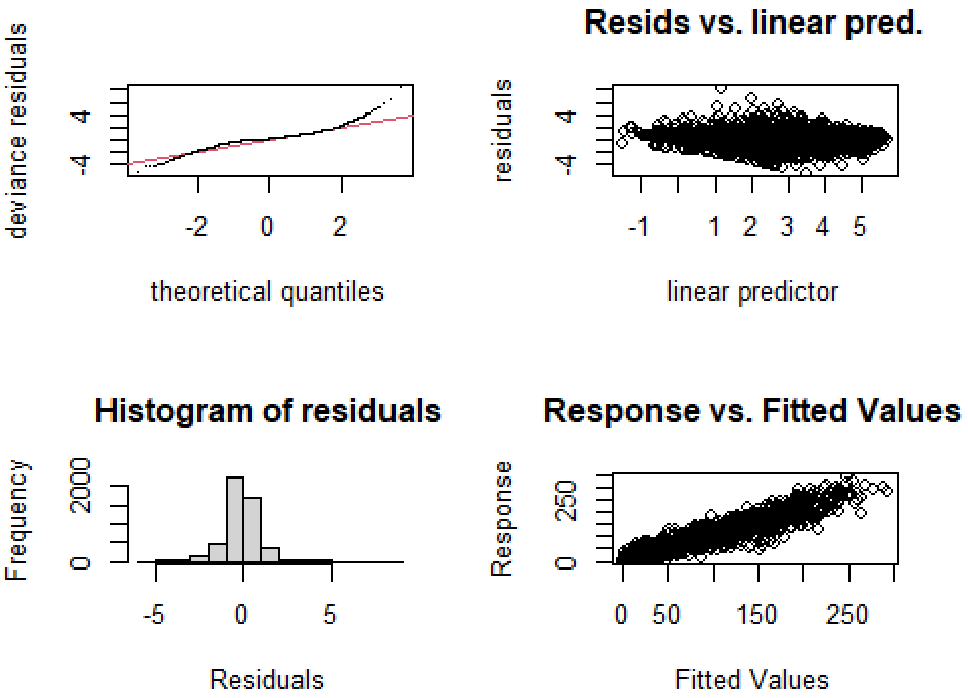


```
cor(sp$bio11, sp$aridity)

## [1] -0.2159113
```

GAM fitting & diagnostics

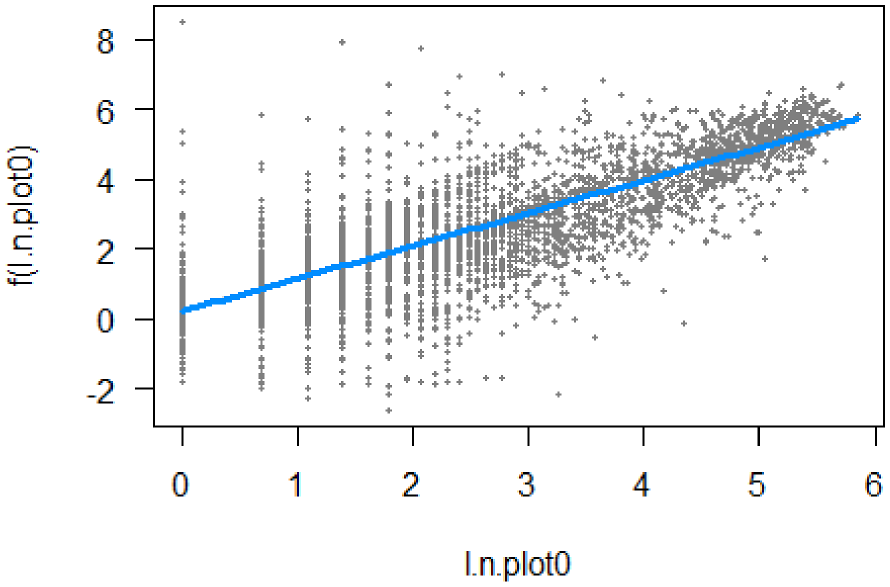
```
if(length(unique(sp$country)) > 1){
  m <- gam(n.plot ~ l.n.plot0 * census.interval +
         country +
         offset(l.plot.area) +
         te(bio11, aridity, for.dev, bs = "cr"),
       family = "nb",
       data = sp,
       method = "REML")
  }else{
    m <- gam(n.plot ~ l.n.plot0 * census.interval +
           offset(l.plot.area) +
           te(bio11, aridity, for.dev, bs = "cr"),
         family = "nb",
         data = sp,
         method = "REML")
}

summary(m)

##
## Family: Negative Binomial(10.49)
## Link function: log
##
## Formula:
## n.plot ~ l.n.plot0 * census.interval + country + offset(l.plot.area) +
##     te(bio11, aridity, for.dev, bs = "cr")
##
## Parametric coefficients:
```

```
##                            Estimate Std. Error z value Pr(>|z|)
## (Intercept)                2.357229   0.085644  27.523  < 2e-16 ***
## l.n.plot0                  1.023689   0.020579  49.745  < 2e-16 ***
## census.interval            0.056348   0.007484   7.529 5.12e-14 ***
## countryCzech Republic      0.568754   0.067736   8.397  < 2e-16 ***
## countryNetherlands         0.328343   0.054633   6.010 1.85e-09 ***
## countryPoland              0.778259   0.051865  15.005  < 2e-16 ***
## countrySpain              -0.522941   0.032688 -15.998  < 2e-16 ***
## countrySweden              0.803166   0.067406  11.915  < 2e-16 ***
## l.n.plot0:census.interval -0.016336   0.002113  -7.732 1.06e-14 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                             edf Ref.df Chi.sq p-value
## te(bio11,aridity,for.dev) 27.66  35.47  505.5  <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.937   Deviance explained = 85.8%
## -REML =  15036  Scale est. = 1         n = 5069

x11()
gam.check(m)
```



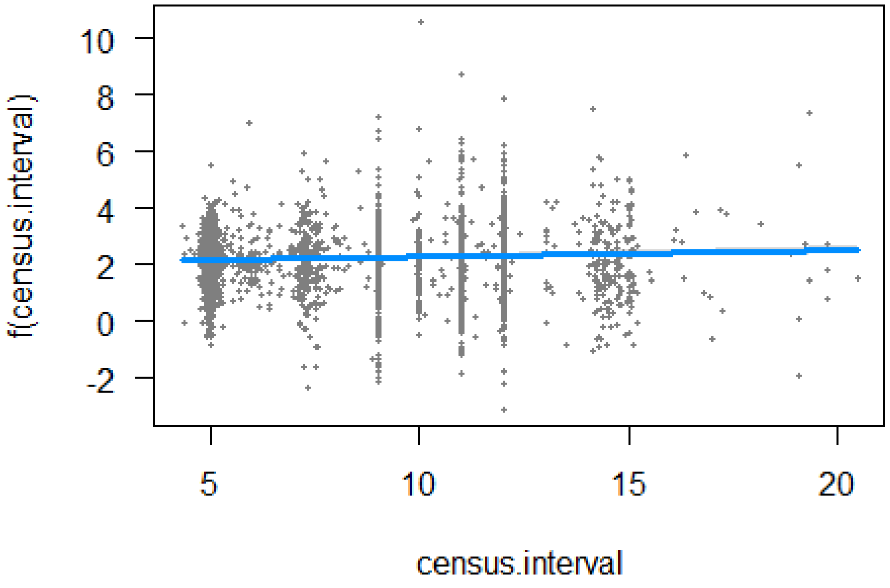
```
##
## Method: REML   Optimizer: outer newton
## full convergence after 7 iterations.
## Gradient range [-0.01347234,0.0007148671]
## (score 15036.39 & scale 1).
## Hessian positive definite, eigenvalue range [0.150194,755.4588].
## Model rank =  133 / 133
##
## Basis dimension (k) checking results. Low p-value (k-index<1) may
## indicate that k is too low, especially if edf is close to k'.
##
##                               k'   edf k-index p-value
## te(bio11,aridity,for.dev) 124.0  27.7    0.97    0.06 .
```

```
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

performance::r2(m)

## $R2
## Adjusted R2
##   0.9372131

## visreg
visreg(m)

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.

## Conditions used in construction of plot
## census.interval: 5.094573
## country: Poland
## l.plot.area: -3.218876
## bio11: -0.2166667
## aridity: 0.8659
## for.dev: 0.4360585

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.
```

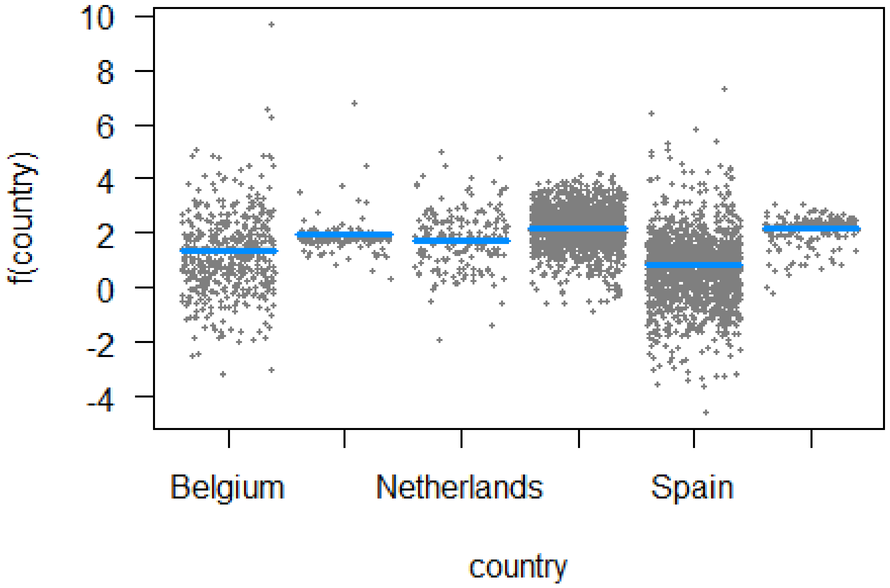


```
## Conditions used in construction of plot
## l.n.plot0: 2.079442
## country: Poland
## l.plot.area: -3.218876
## bio11: -0.2166667
```

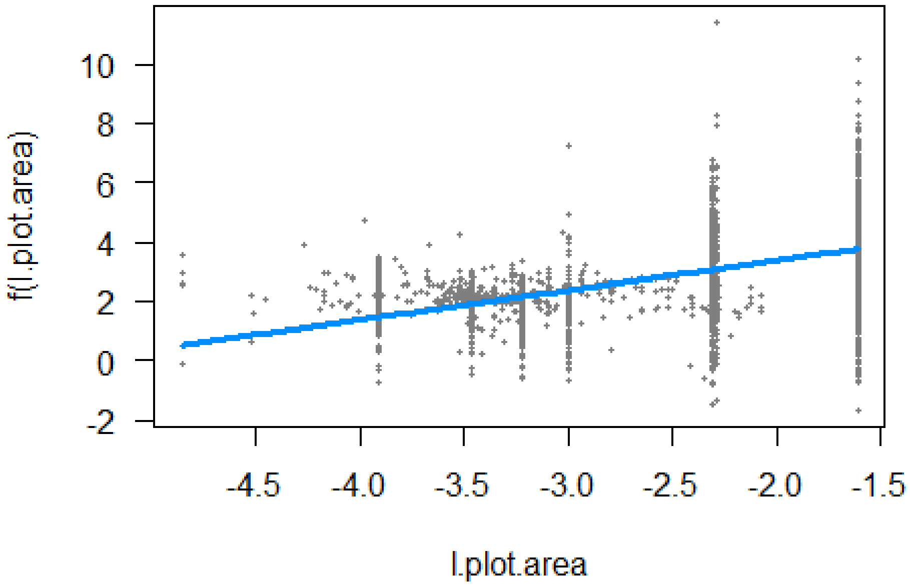
```
## aridity: 0.8659
## for.dev: 0.4360585

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.
```



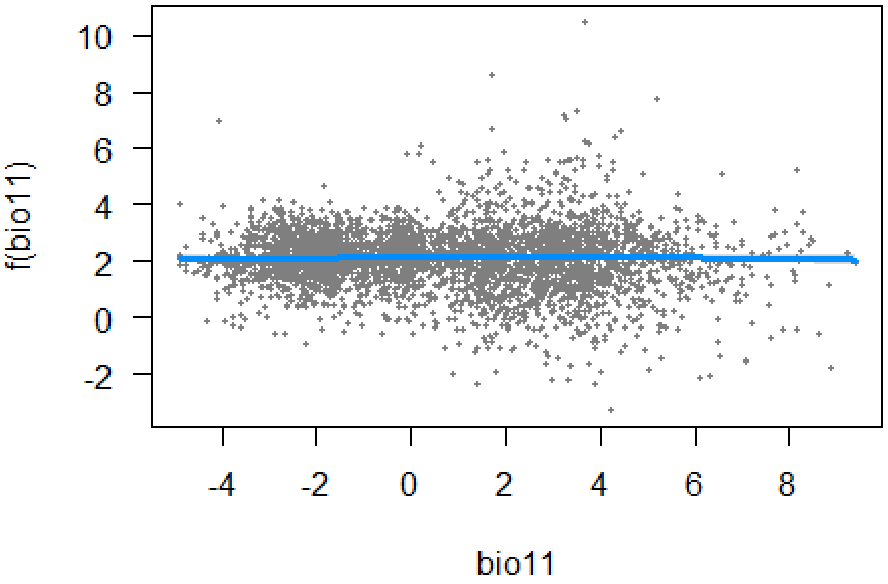
```
## Conditions used in construction of plot
## l.n.plot0: 2.079442
## census.interval: 5.094573
## l.plot.area: -3.218876
## bio11: -0.2166667
## aridity: 0.8659
## for.dev: 0.4360585

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.
```



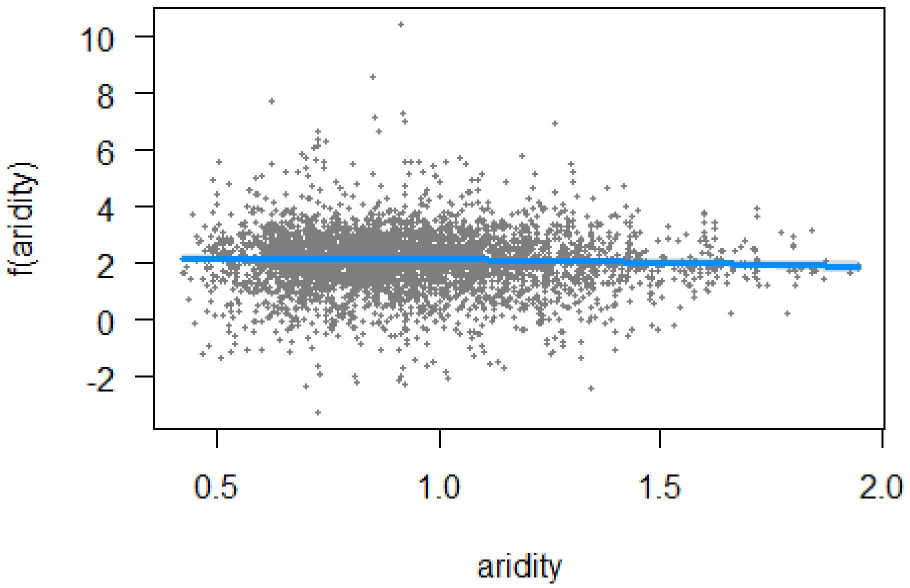
```
## Conditions used in construction of plot
## l.n.plot0: 2.079442
## census.interval: 5.094573
## country: Poland
## bio11: -0.2166667
## aridity: 0.8659
## for.dev: 0.4360585

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.
```



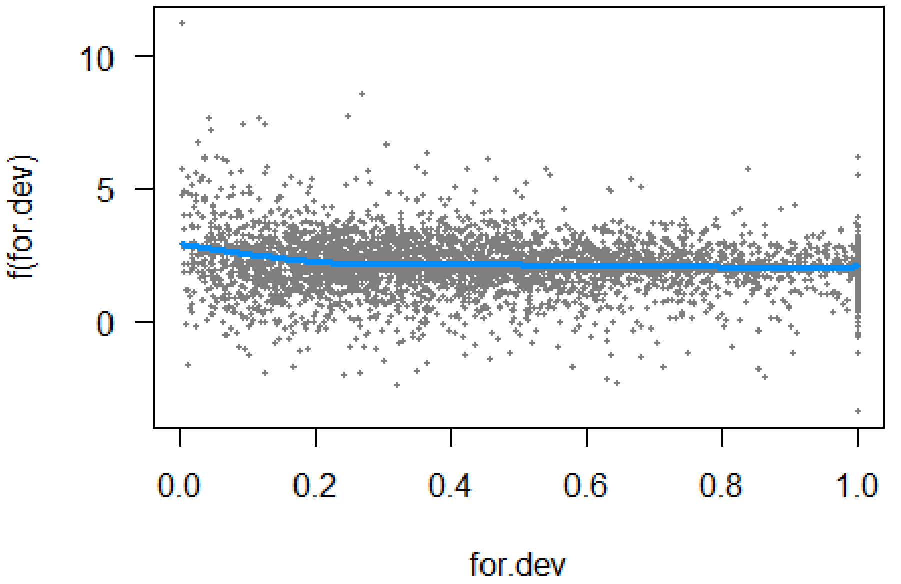
```
## Conditions used in construction of plot
## l.n.plot0: 2.079442
## census.interval: 5.094573
## country: Poland
## l.plot.area: -3.218876
## aridity: 0.8659
## for.dev: 0.4360585

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.
```



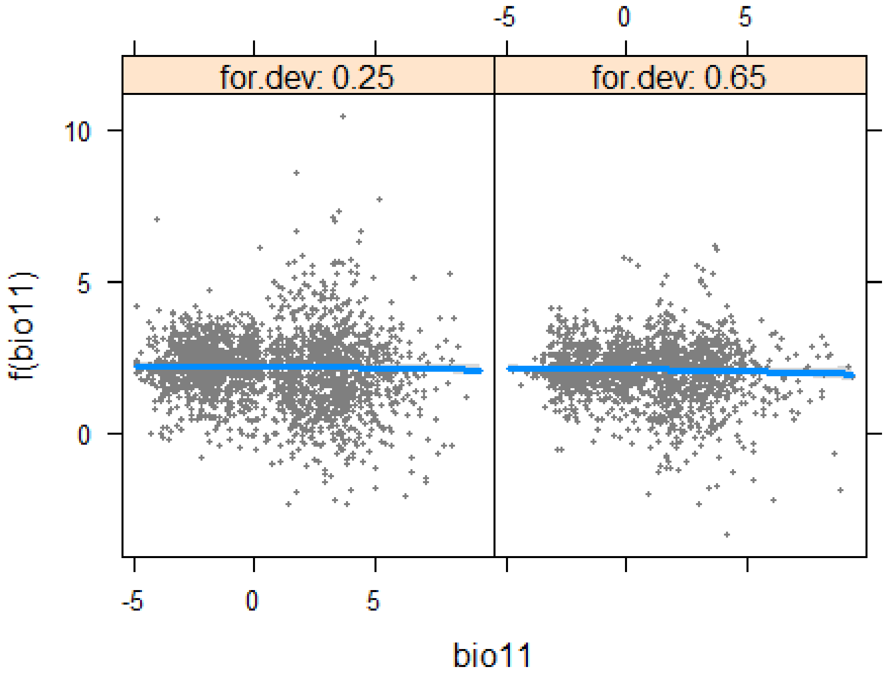
```
## Conditions used in construction of plot
## l.n.plot0: 2.079442
## census.interval: 5.094573
## country: Poland
## l.plot.area: -3.218876
## bio11: -0.2166667
## for.dev: 0.4360585

## Warning:   Note that you are attempting to plot a 'main effect' in a model that
contains an
##   interaction.  This is potentially misleading; you may wish to consider using t
he 'by'
##   argument.
```



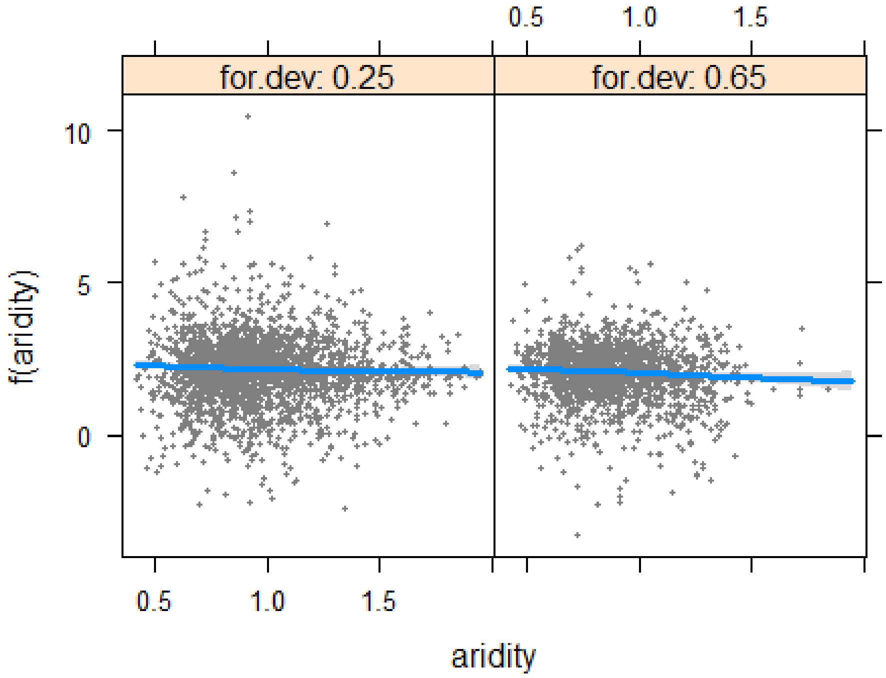
```
## Conditions used in construction of plot
## l.n.plot0: 2.079442
## census.interval: 5.094573
## country: Poland
## l.plot.area: -3.218876
## bio11: -0.2166667
## aridity: 0.8659
```



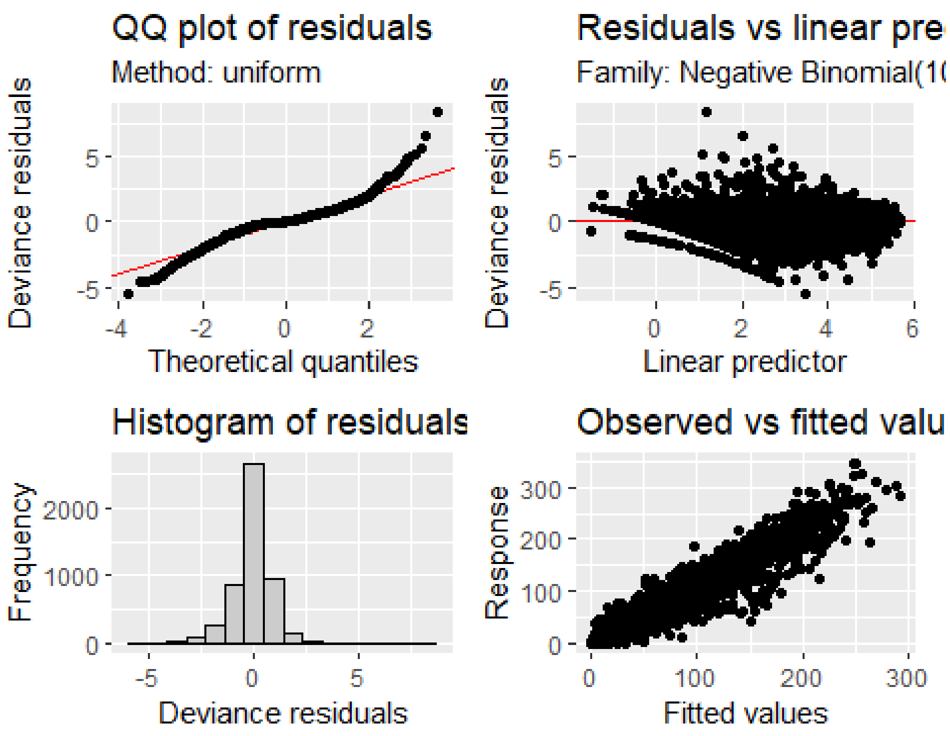
```
visreg(m, xvar = "bio11", by = "for.dev", breaks = c(0.25, 0.65))
```



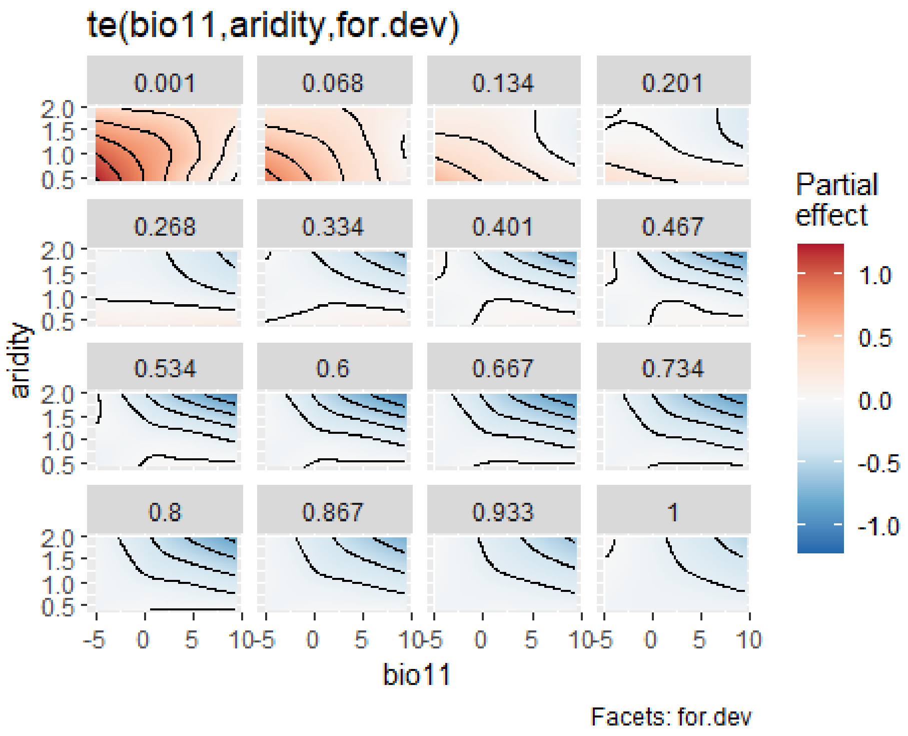
```
visreg(m, xvar = "aridity", by = "for.dev", breaks = c(0.25, 0.65))
```



```
## gratia
gratia::appraise(m)
```

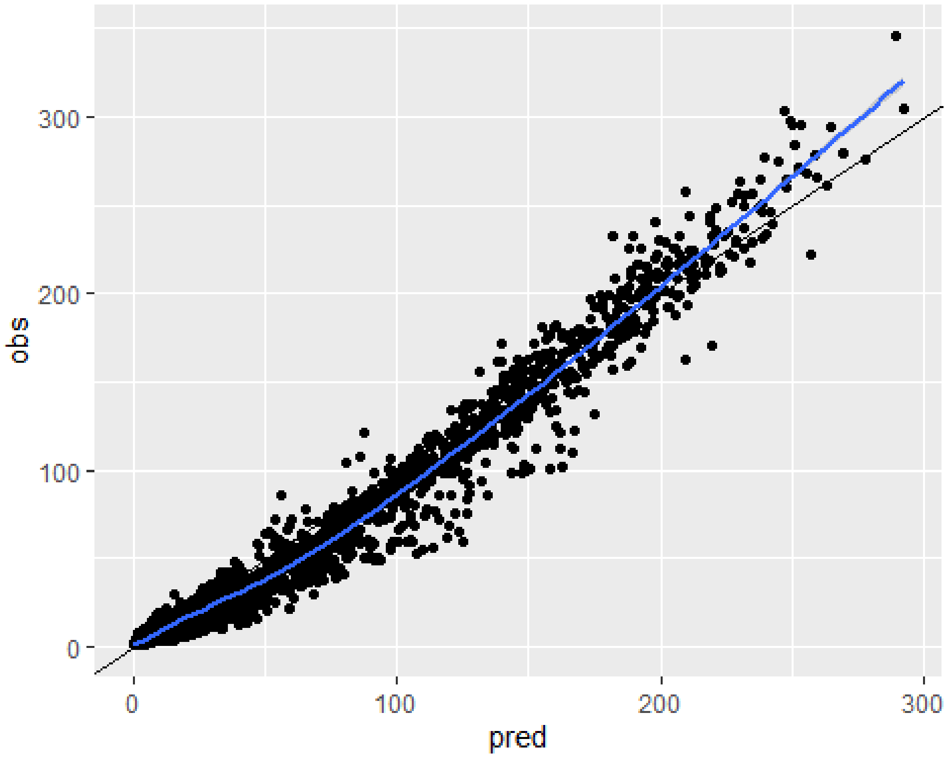


```
draw(m)
```

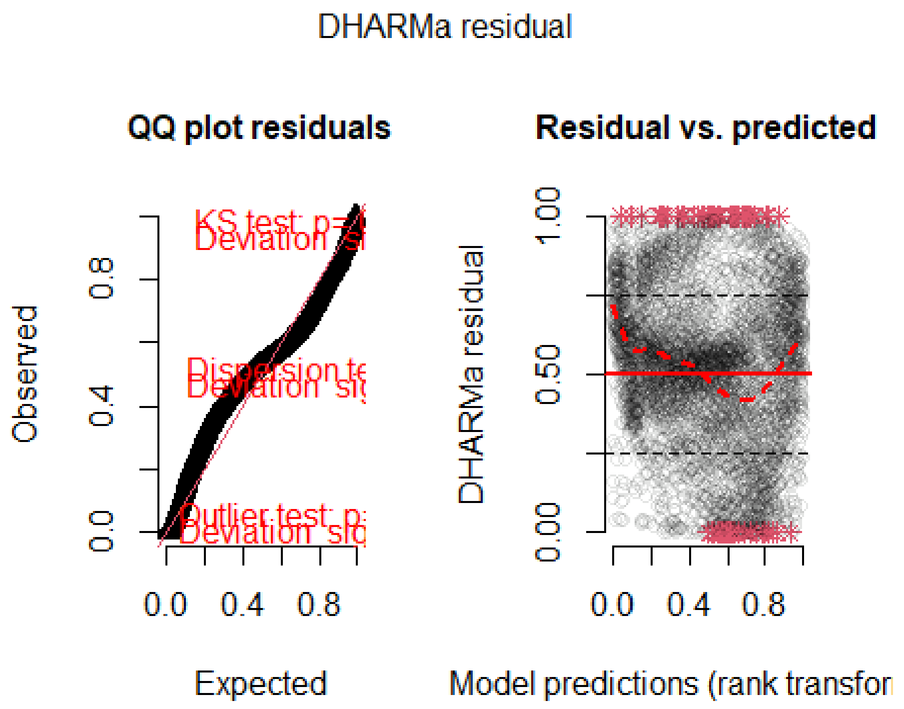


```
## Calibration plot
pred <- predict(m, newdata = sp, type = "response")
ggplot(data.frame(obs = sp$n.plot0, pred = pred)) +
  geom_point(aes(pred, obs)) +
  geom_abline(intercept = 0, slope = 1) +
  geom_smooth(aes(pred, obs))
```

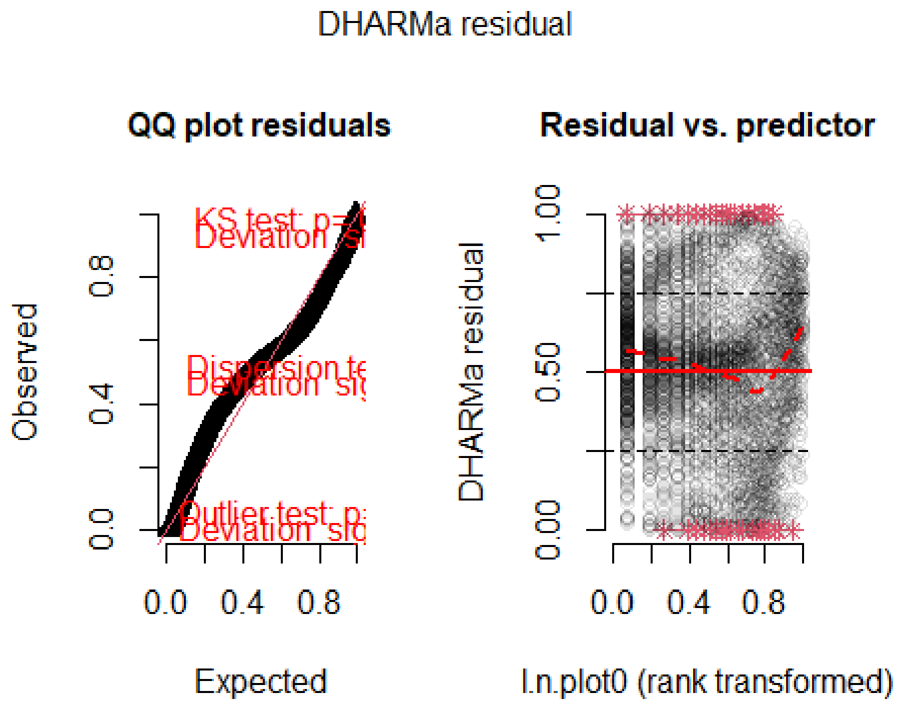
```
## `geom_smooth()` using method = 'gam' and formula 'y ~ s(x, bs = "cs")'
```



```
## DHARMa
res <- simulateResiduals(m, integerResponse = TRUE)

## Registered S3 method overwritten by 'GGally':
##   method from
##   +.gg   ggplot2

## Registered S3 methods overwritten by 'mgcViz':
##   method       from
##   +.gg         GGally
##   simulate.gam gratia

x11()
plot(res)

## DHARMa:testOutliers with type = binomial may have inflated Type I error rates fo
r integer-valued distributions. To get a more exact result, it is recommended to re
-run testOutliers with type = 'bootstrap'. See ?testOutliers for details
```

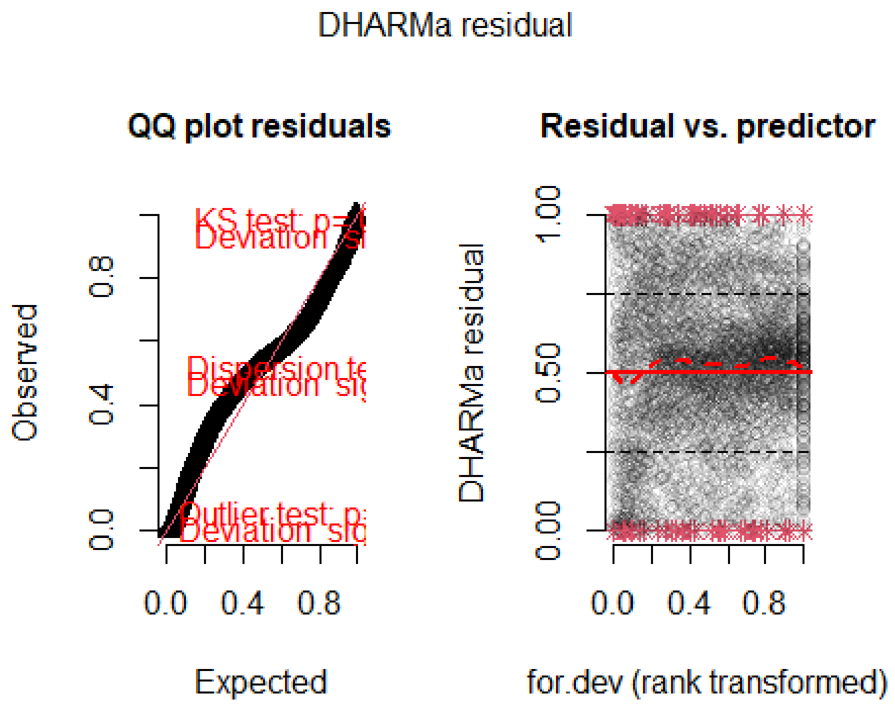


```
plot(res, form = sp$l.n.plot0)

## DHARMa:testOutliers with type = binomial may have inflated Type I error rates fo
r integer-valued distributions. To get a more exact result, it is recommended to re
-run testOutliers with type = 'bootstrap'. See ?testOutliers for details
```

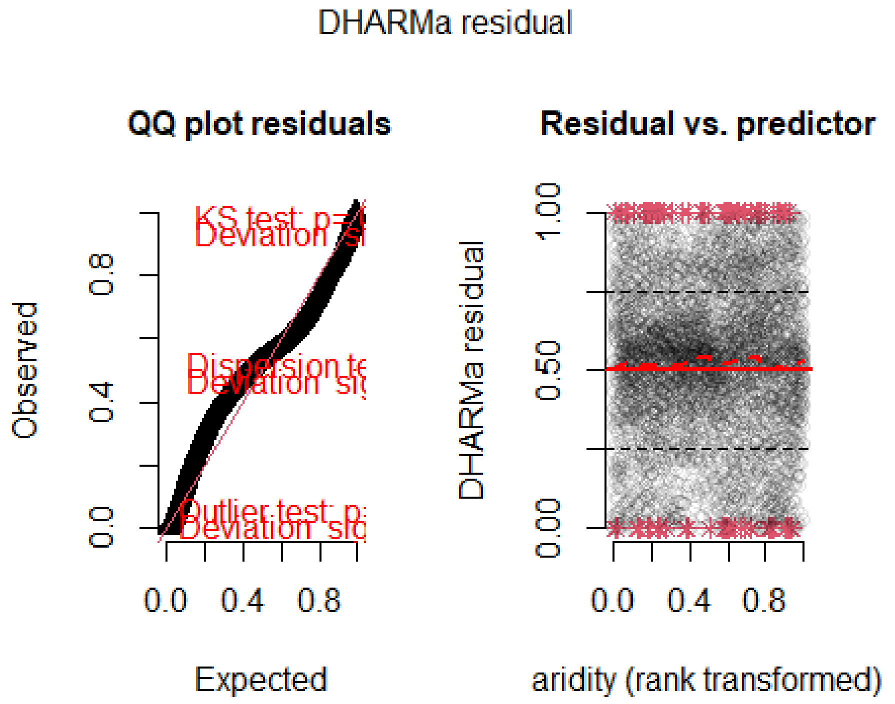


```
plot(res, form = sp$for.dev)
```

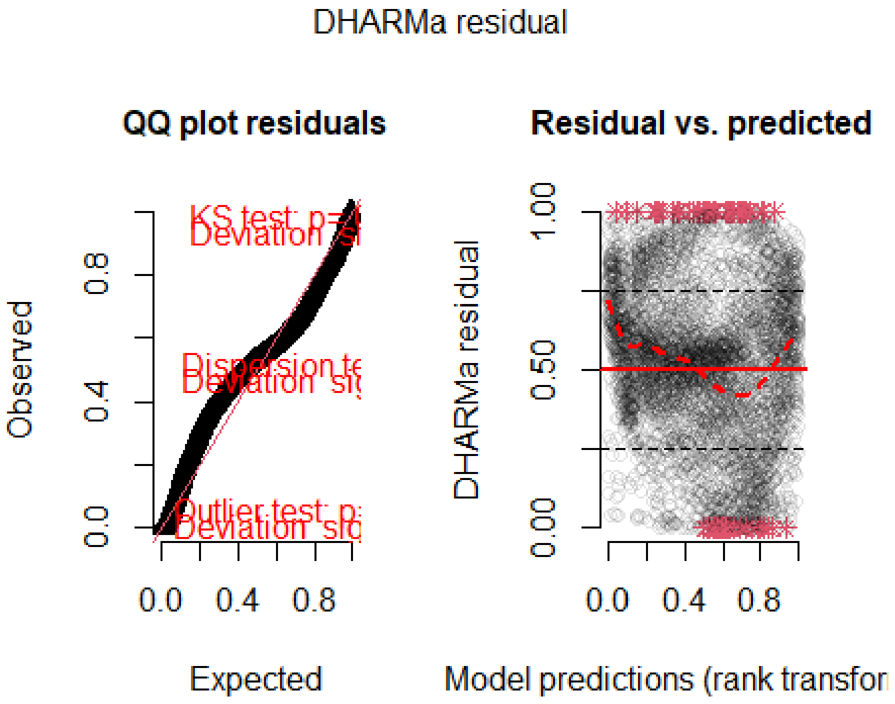
```
## DHARMa:testOutliers with type = binomial may have inflated Type I error rates fo
r integer-valued distributions. To get a more exact result, it is recommended to re
-run testOutliers with type = 'bootstrap'. See ?testOutliers for details
```



```
plot(res, form = sp$aridity)

## DHARMa:testOutliers with type = binomial may have inflated Type I error rates fo
r integer-valued distributions. To get a more exact result, it is recommended to re
-run testOutliers with type = 'bootstrap'. See ?testOutliers for details
```



```
plot(res, form = sp$tmin)

## DHARMa:testOutliers with type = binomial may have inflated Type I error rates fo
r integer-valued distributions. To get a more exact result, it is recommended to re
-run testOutliers with type = 'bootstrap'. See ?testOutliers for details

## Warning: Unknown or uninitialised column: `tmin`.
```



Predictions

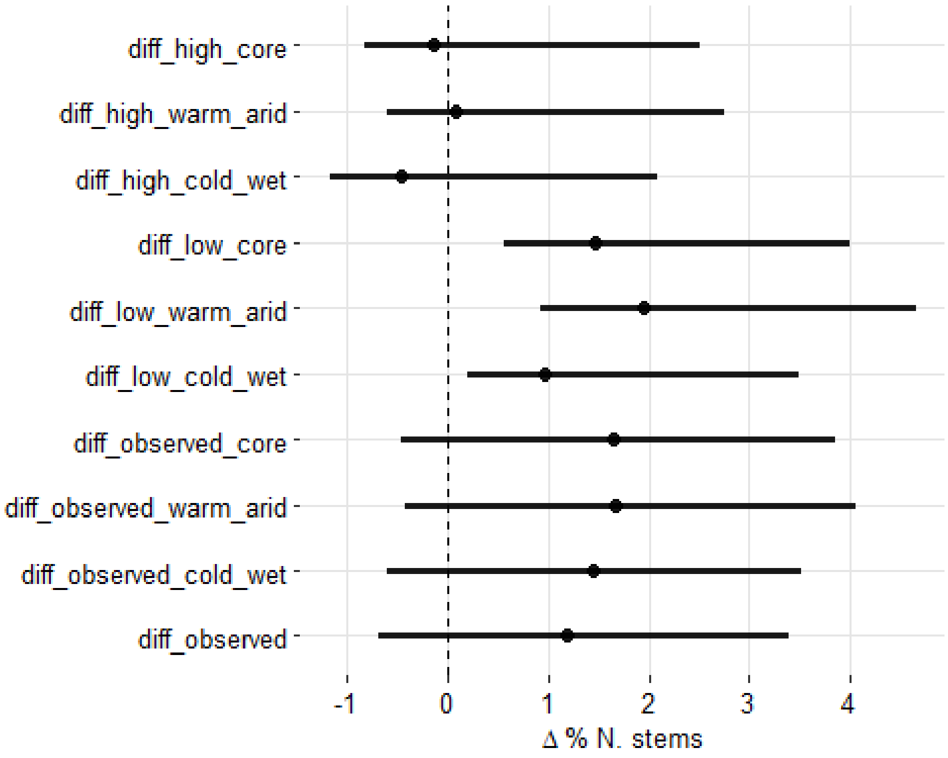
```
fd_observed <- sp

bio11_q <- quantile(sp$bio11, c(0.25, 0.5, 0.75))
aridity_q <- quantile(sp$aridity, c(0.25, 0.5, 0.75))

# observed
## cold & wet edge
fd_observed_cold_wet <- sp |>
  mutate(
    bio11 = bio11_q[[1]],
    aridity = aridity_q[[3]]
  )

## warm & arid edge
fd_observed_warm_arid <- sp |>
  mutate(
    bio11 = bio11_q[[3]],
    aridity = aridity_q[[1]]
  )

## core
fd_observed_core <- sp |>
  mutate(
    bio11 = bio11_q[[2]],
    aridity = aridity_q[[2]]
  )
```

```
# young
## cold & wet edge
fd_low_cold_wet <- sp |>
  mutate(
    for.dev = 0.25,
    bio11 = bio11_q[[1]],
    aridity = aridity_q[[3]]
  )

## warm & arid edge
fd_low_warm_arid <- sp |>
  mutate(
    for.dev = 0.25,
    bio11 = bio11_q[[3]],
    aridity = aridity_q[[1]]
  )

## core
fd_low_core <- sp |>
  mutate(
    for.dev = 0.25,
    bio11 = bio11_q[[2]],
    aridity = aridity_q[[2]]
  )

# mature
## cold & wet edge
fd_high_cold_wet <- sp |>
  mutate(
    for.dev = 0.65,
    bio11 = bio11_q[[1]],
    aridity = aridity_q[[3]]
  )

## warm & arid edge
fd_high_warm_arid <- sp |>
  mutate(
    for.dev = 0.65,
    bio11 = bio11_q[[3]],
    aridity = aridity_q[[1]]
  )

## core
fd_high_core <- sp |>
  mutate(
    for.dev = 0.65,
    bio11 = bio11_q[[2]],
    aridity = aridity_q[[2]]
  )

newdata_list <- list(
  fd_observed,
  fd_observed_cold_wet,
  fd_observed_warm_arid,
  fd_observed_core,
  fd_low_cold_wet,
  fd_low_warm_arid,
  fd_low_core,
  fd_high_cold_wet,
  fd_high_warm_arid,
  fd_high_core
)

# make the predictions for each dataset
predictions <- map(newdata_list, ~predict(
```

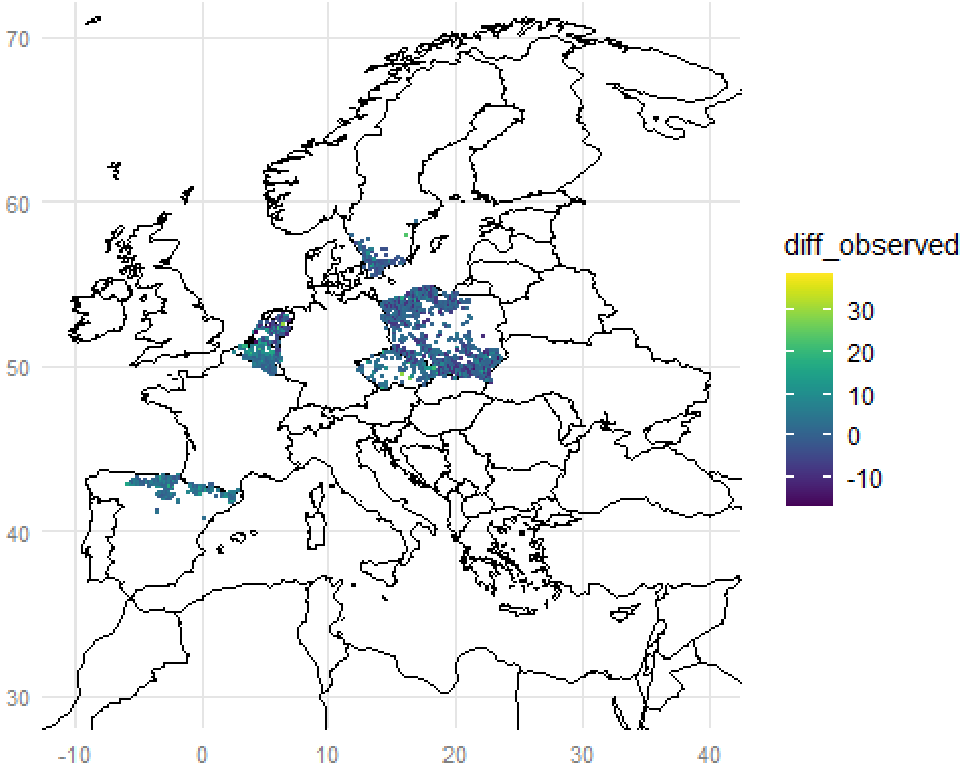
```
  object = m, newdata = ., se.fit = TRUE, type = "response"
  ))

arg2_dat_pred <- list(dat = newdata_list, pred = predictions)

# add predictions to the corresponding dataset
add_predictions <- function(dat, pred){
  dat |>
    mutate(
      predFE = pred$fit
    )
}

newdata_list_predictions <- arg2_dat_pred %>%
  pmap(add_predictions)

names(newdata_list_predictions) <- c(
  "fd_observed",
  "fd_observed_cold_wet",
  "fd_observed_warm_arid",
  "fd_observed_core",
  "fd_low_cold_wet",
  "fd_low_warm_arid",
  "fd_low_core",
  "fd_high_cold_wet",
  "fd_high_warm_arid",
  "fd_high_core"
)

# select the variables of interest from each dataset
predictions_selected <- map(
  newdata_list_predictions,
  ~dplyr::select(.x, tmt.plot.id, latitude,
          longitude, census.interval,
          for.dev, n.plot0,
          n.plot, predFE))

# add prediction name to each dataset
mutate_name <- function(x, names_df){
  predictions_selected[[x]] |>
    dplyr::mutate(
      df = names_df
    )
}

arg2_x_names_df <- list(x = 1:length(predictions_selected), names_df = names(predic
tions_selected))

predictions_selected <- arg2_x_names_df %>%
  pmap_df(mutate_name)

# calculate changes between the prediction of
# n.stems time 1 vs time 0 (%)
calculate_changes <- function(dat, var_name, pred_name){
  predictions_selected |>
    filter(df == dat) |>
    dplyr::select(tmt.plot.id, latitude, longitude,
                  census.interval,
                  n.plot0, n.plot, predFE) |>
    mutate(
      {{var_name}} := (predFE - n.plot0) /
        n.plot0 * 100 / census.interval
    ) |>
    rename({{pred_name}} := predFE)
}
```

```
dat_v <- c(
  "fd_observed",
  "fd_observed_cold_wet",
  "fd_observed_warm_arid",
  "fd_observed_core",
  "fd_low_cold_wet",
  "fd_low_warm_arid",
  "fd_low_core",
  "fd_high_cold_wet",
  "fd_high_warm_arid",
  "fd_high_core"
)

var_name_v <- c(
  "diff_observed",
  "diff_observed_cold_wet",
  "diff_observed_warm_arid",
  "diff_observed_core",
  "diff_low_cold_wet",
  "diff_low_warm_arid",
  "diff_low_core",
  "diff_high_cold_wet",
  "diff_high_warm_arid",
  "diff_high_core"
)

pred_name_v <- c(
  "predFE_observed",
  "predFE_observed_cold_wet",
  "predFE_observed_warm_arid",
  "predFE_observed_core",
  "predFE_low_cold_wet",
  "predFE_low_warm_arid",
  "predFE_low_core",
  "predFE_high_cold_wet",
  "predFE_high_warm_arid",
  "predFE_high_core"
)

arg3_dat_var_pred_v <- list(
  dat = dat_v, var_name = var_name_v,
  pred_name = pred_name_v
  )

predictions_selected_changes <- arg3_dat_var_pred_v %>%
  pmap(calculate_changes)

predictions_all_changes <- predictions_selected_changes |>
  reduce(left_join, by = c("tmt.plot.id",
"latitude", "longitude", "n.plot", "n.plot0",
"census.interval"))

pred_all_changes_l <- predictions_all_changes |>
  pivot_longer(
    cols = c(
      diff_observed,
      diff_observed_cold_wet,
      diff_observed_warm_arid,
      diff_observed_core,
      diff_low_cold_wet,
      diff_low_warm_arid,
      diff_low_core,
      diff_high_cold_wet,
      diff_high_warm_arid,
```

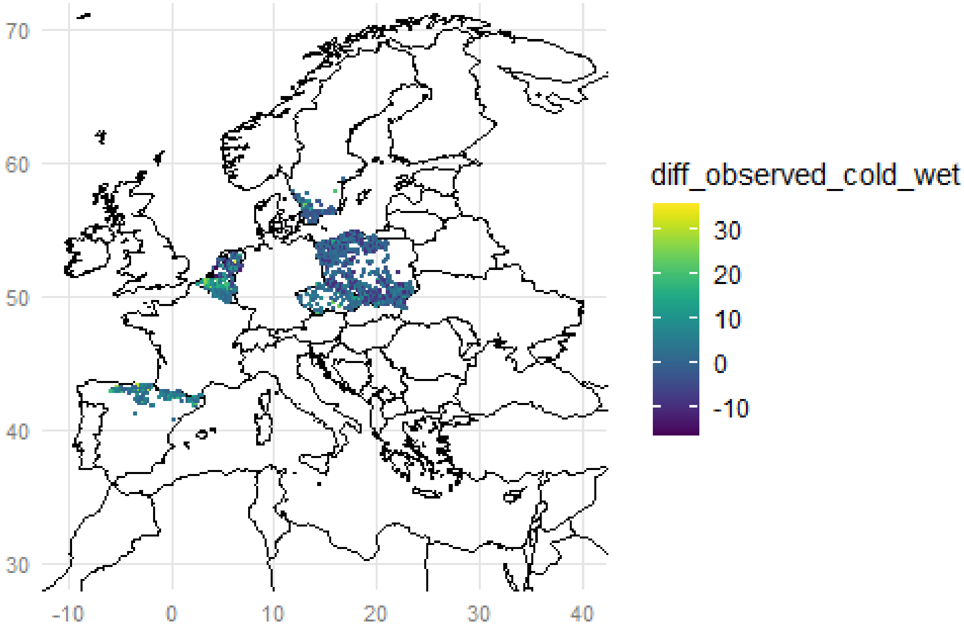
```
      diff_high_core
      ),
    names_to = "name_diff_fd",
    values_to = "val_diff_fd"
    )

pred_changes_l_rel <- pred_all_changes_l |>
  mutate(
    name_diff_fd = fct_relevel(
    name_diff_fd,
    "diff_observed",
    "diff_observed_cold_wet",
    "diff_observed_warm_arid",
    "diff_observed_core",
    "diff_low_cold_wet",
    "diff_low_warm_arid",
    "diff_low_core",
    "diff_high_cold_wet",
    "diff_high_warm_arid",
    "diff_high_core"
    )
  )

ggplot(pred_changes_l_rel, aes
       (x = name_diff_fd, y = val_diff_fd,
         fill = name_diff_fd)) +
   stat_pointinterval(
   # now we are showing the mean
   point_interval = mean_qi, .width = .5,
   position = position_dodge(width = .4), alpha = .9,
   ) +
  # stat_halfeye(scale = 0.5) +
  ylab(expression(paste(Delta~"% N. stems"))) +
  geom_hline(yintercept = 0, linetype = "dashed") +
  coord_flip() +
  theme(
    plot.title = element_text(color = "black", size = 10),
    plot.subtitle = element_text(color = "black", size = 8),
    legend.position = "none",
    panel.grid.major = element_line(colour = "grey90", size = 0.5),
    panel.background = element_blank(),
    axis.title.y = element_blank(),
    axis.title.x = element_text(color = "black", size = 10),
    axis.text.x = element_text(color = "black", size = 10),
    axis.text.y = element_text(color = "black", size = 10),
    strip.text = element_text(color = "black", size = 10)
    )
```



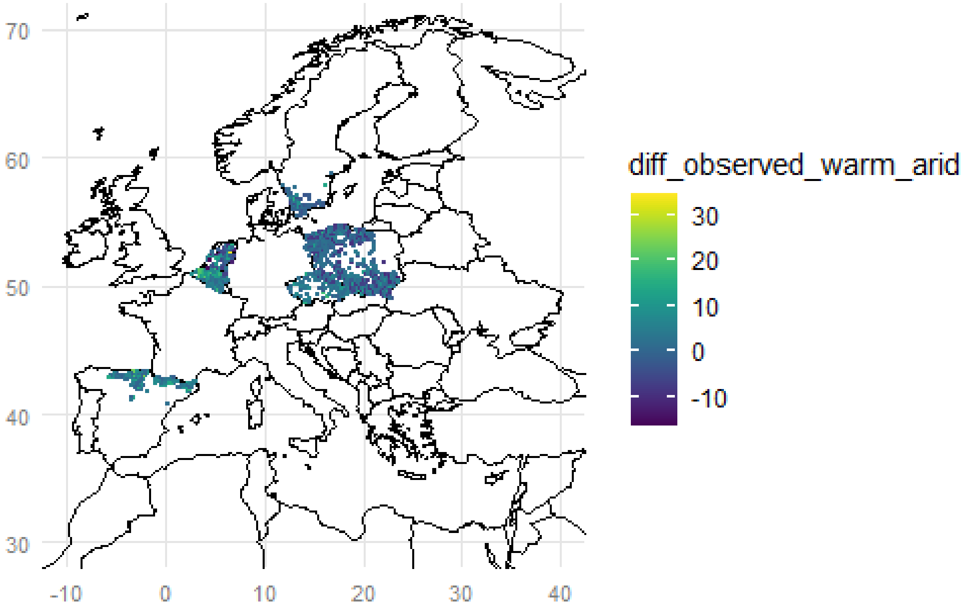
```
# map changes in n.stems
# note that map_vars function is created in 02-f_EDA.R
map_dat_diff <- function(dat_diff){
  map_vars(dat = predictions_all_changes,
           var = dat_diff) +
    coord_fixed(xlim = c(-140, 40), ylim = c(25, 70), ratio = 1.3)
}

# map predictions
map(var_name_v, ~map_dat_diff(.x) + coord_fixed(
      xlim = c(-10, 40), ylim = c(30, 70), ratio = 1.3))

## [[1]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_observed
30
20
10
0
-10

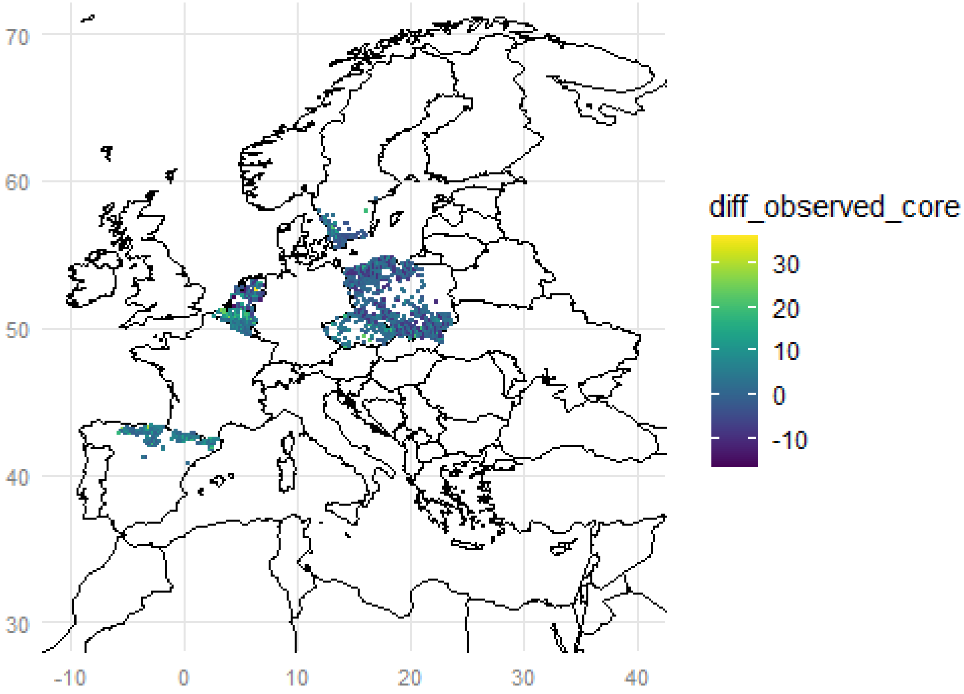
```
##
## [[2]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_observed_cold_wet
30
20
10
0
-10

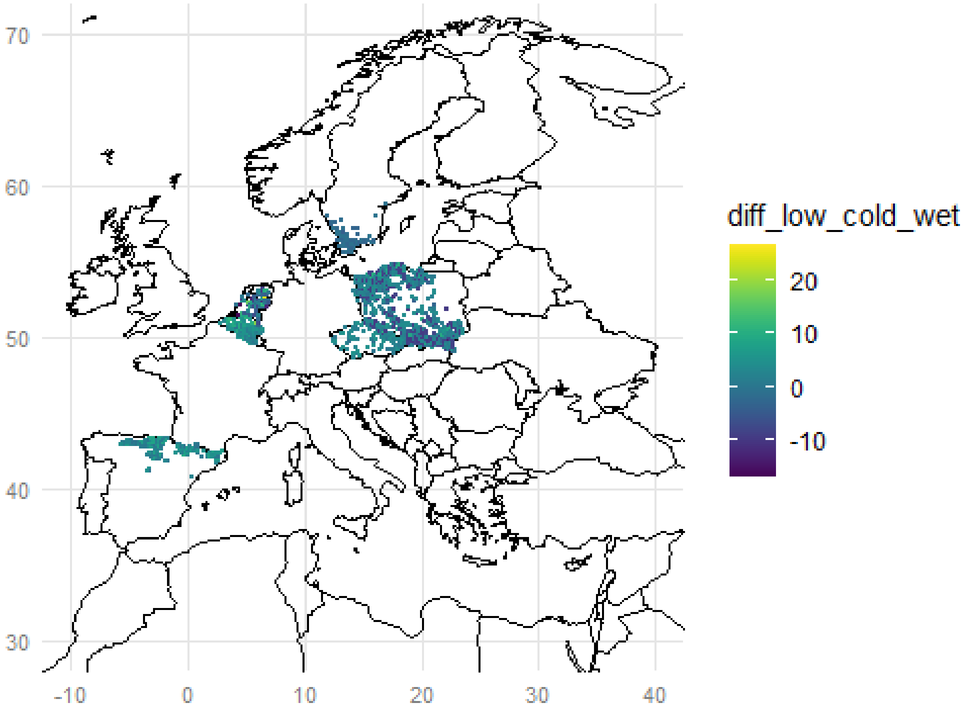
```
##
## [[3]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_observed_warm_arid
30
20
10
0
-10

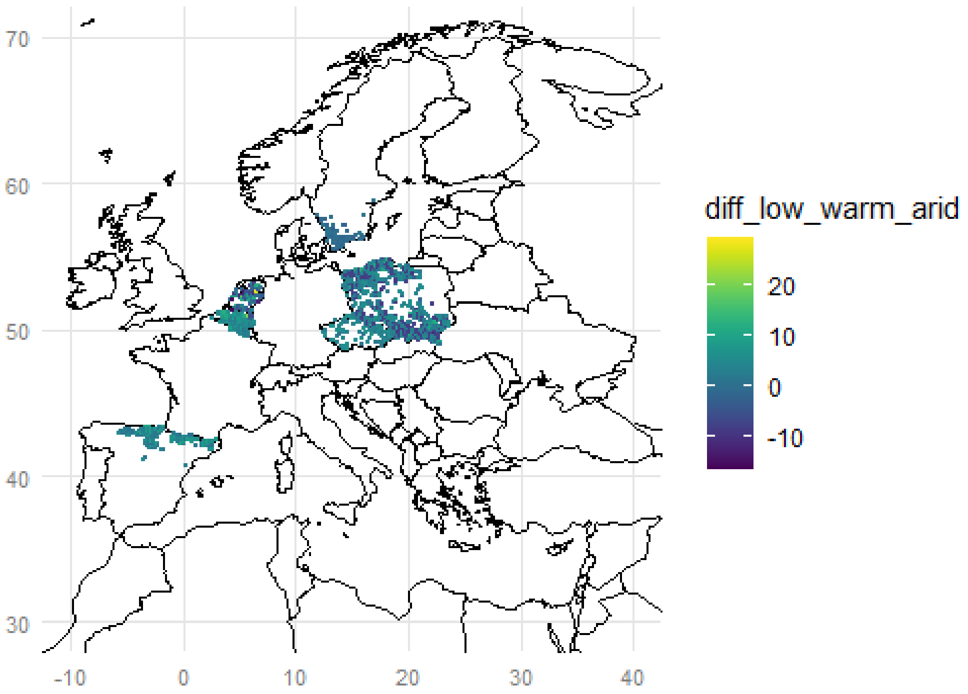
```
##
## [[4]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_observed_core
30
20
10
0
-10

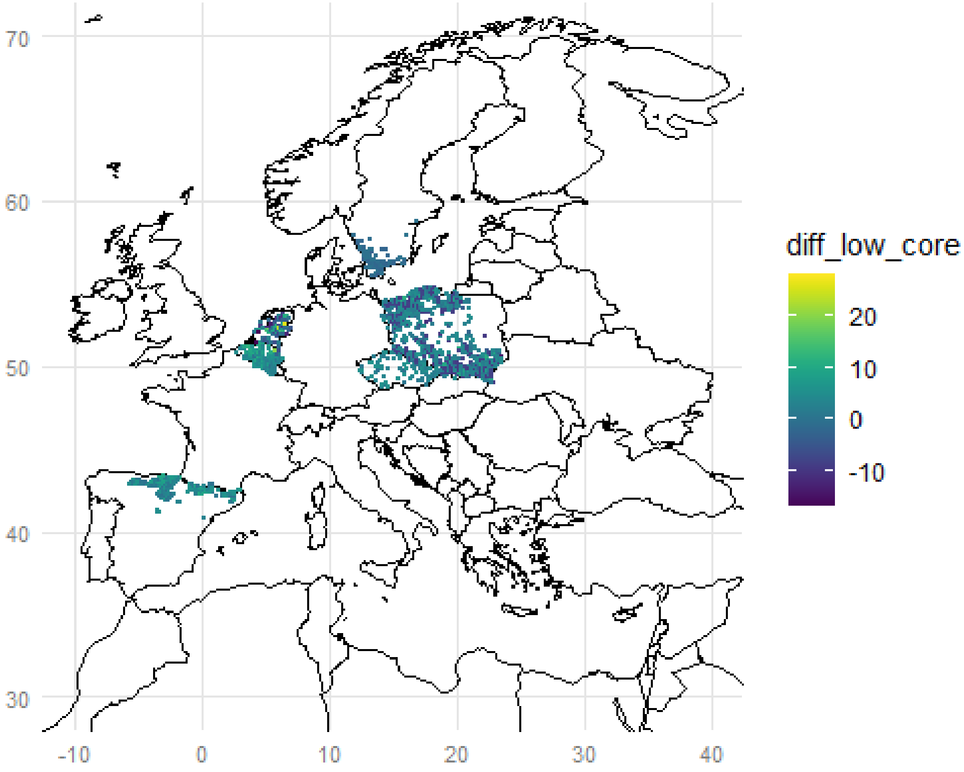
```
##
## [[5]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_low_cold_wet
20
10
0
-10

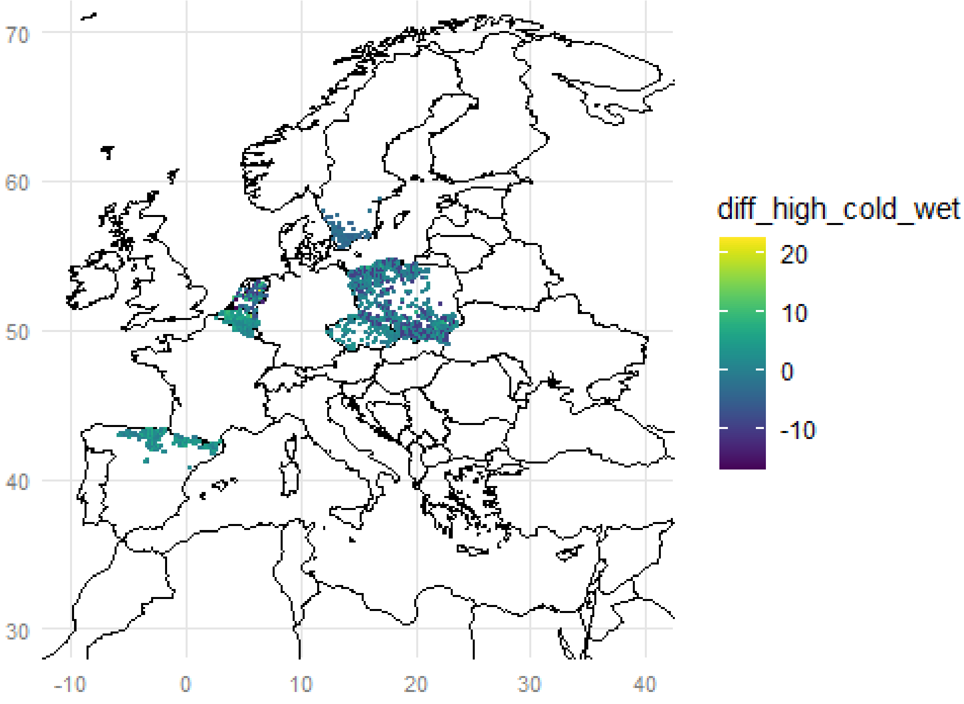
```
##
## [[6]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_low_warm_arid
20
10
0
-10

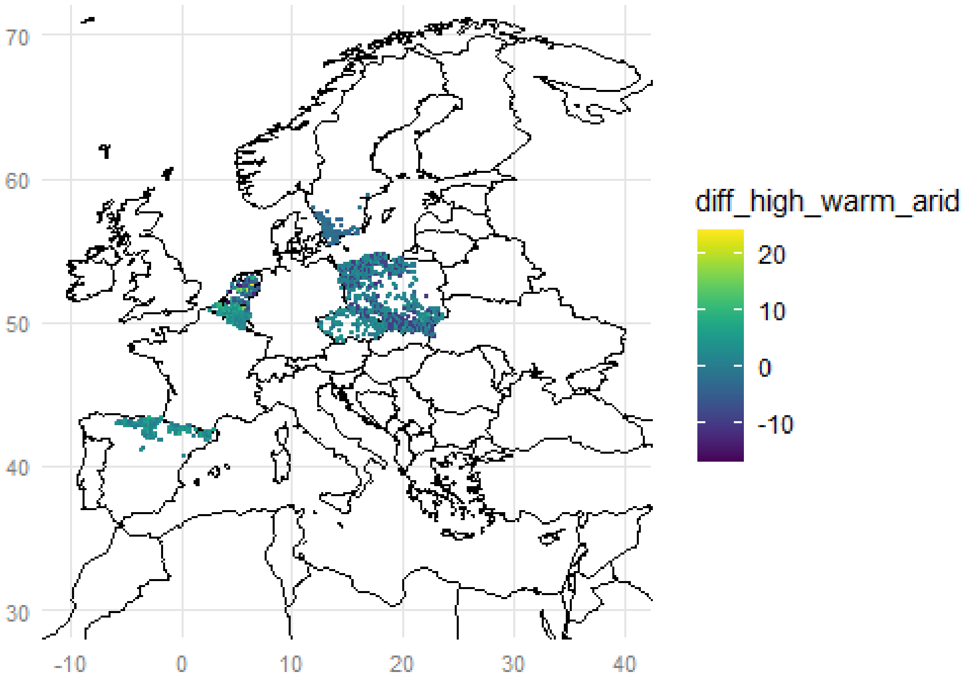
```
##
## [[7]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_low_core
20
10
0
-10

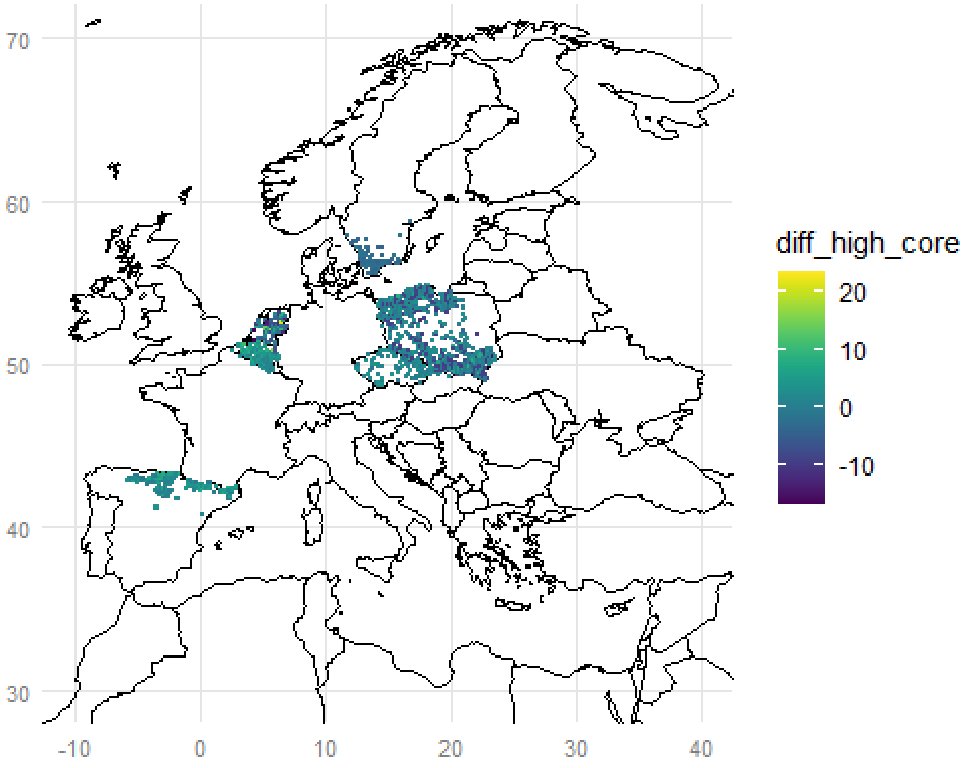
```
##
## [[8]]
```


70
60
50
40
30
-10
0
10
20
30
40
diff_high_cold_wet
20
10
0
-10

```
##
## [[9]]
```

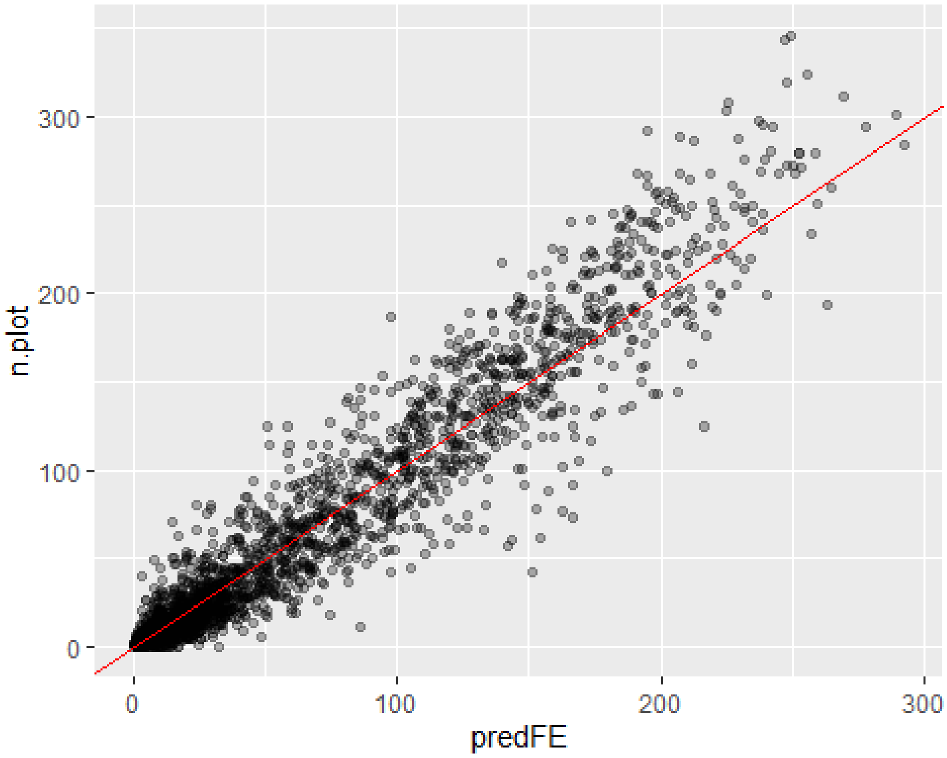


```
##
## [[10]]
```



```
# check whether the predictions make sense
predictions_filtered_test <- predictions_selected |>
  filter(df == "fd_observed") |>
  dplyr::select(tmt.plot.id, n.plot, predFE)

ggplot(predictions_filtered_test, aes(
```

```
  predFE, n.plot
  )) +
  geom_point(alpha = 0.3) +
  geom_abline(slope = 1, intercept = 0, col = "red")
```

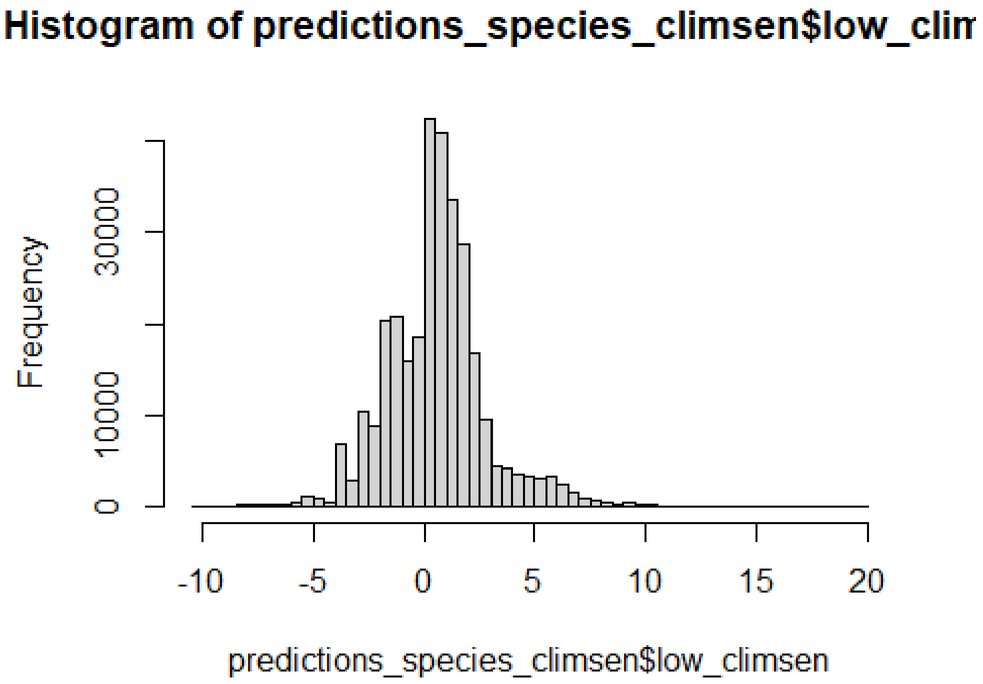


```
saveRDS(predictions_all_changes, file = here("02-data", "models", "predictions", pa
ste(sub(" ", "_", "Fagus sylvatica"), "predictions.rds", sep = "_")))
```

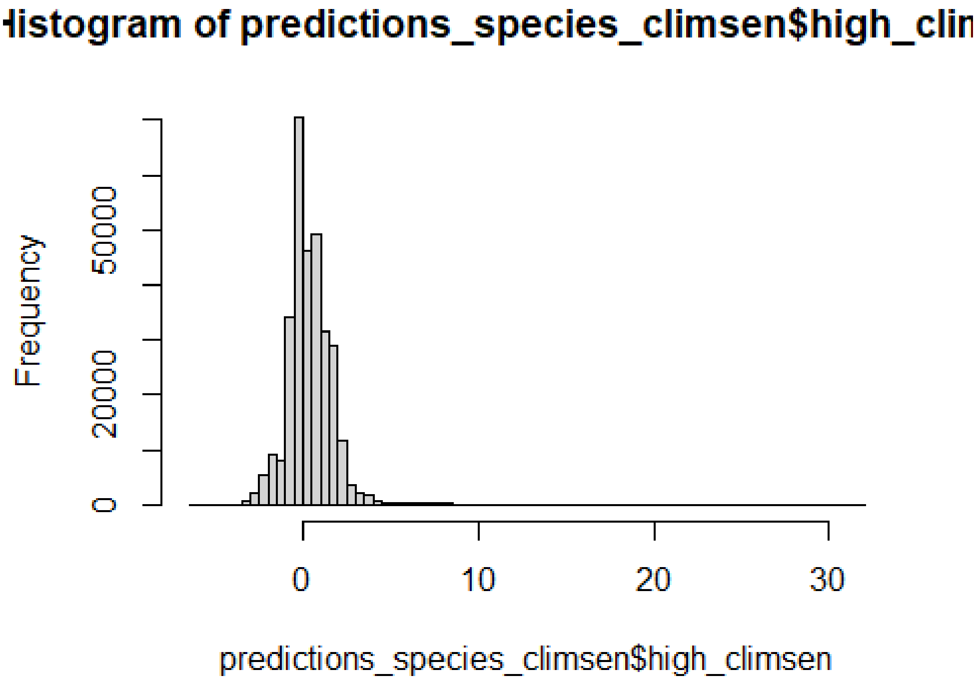
Linear mixed effects models

Model evaluation of species climatic sensitivity (i.e. difference in percentage between cold and wet regions of species climate range, and warm and arid regions) when regressed on species minimum temperature niche position and niche width, aridity niche position and niche width, wood density and seed dry mass as additive fixed effects, and including species identity and plot identity as random effects. Note that we fitted the same model in early and late successional stage forests for climate sensitivities of ± 6% year^{-1} (i.e. data between 1st and 99th quantiles).

```
predictions_species_climsen <- predictions_species |>
  mutate(
    low_climsen = diff_low_cold_wet - diff_low_warm_arid,
    high_climsen = diff_high_cold_wet - diff_high_warm_arid,
    )

# response variable distributions
hist(predictions_species_climsen$low_climsen, breaks = 100)
```

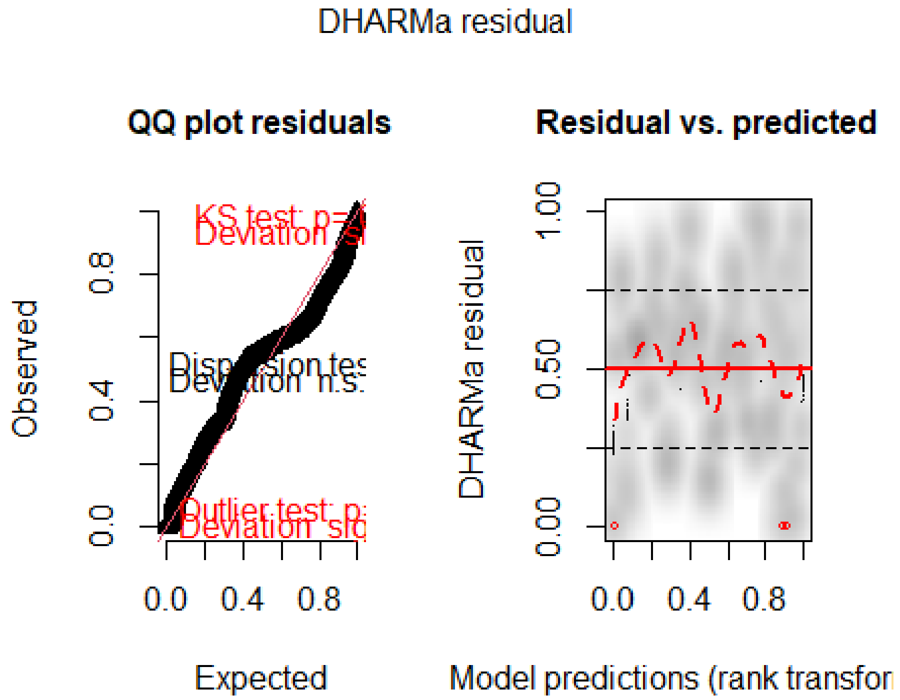


```
hist(predictions_species_climsen$high_climsen, breaks = 100)
```

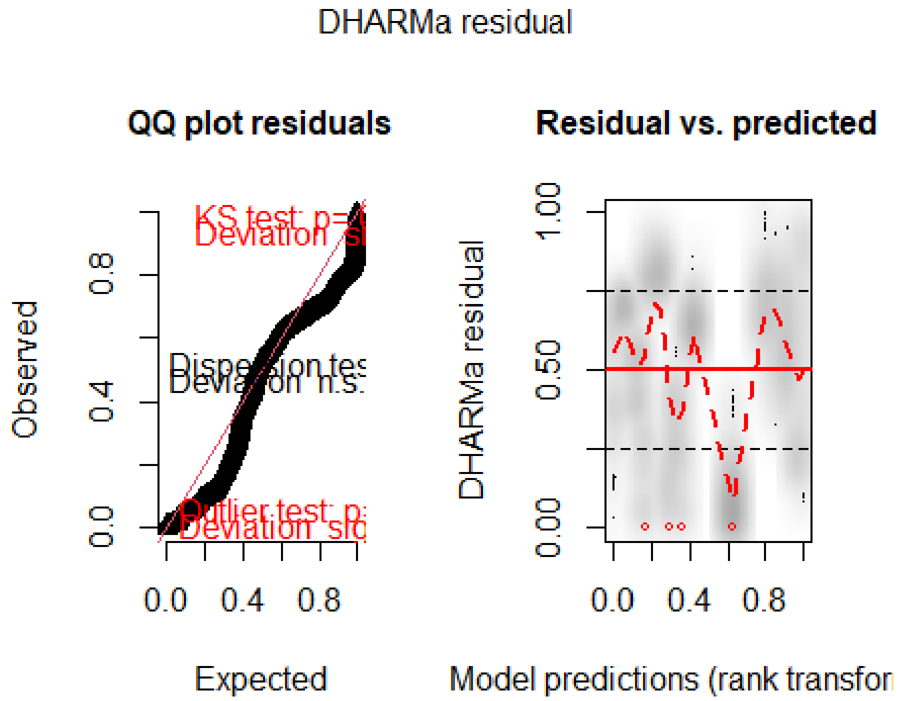


```
# standardisation
predictions_climsen_sd <- predictions_species_climsen |>
  mutate(
    wood.density.mean.sp.nsd = wood.density.mean.sp,
    seed.dry.mass.mean.sp.nsd = seed.dry.mass.mean.sp,
    bio11.mean.sp.nsd = bio11.mean.sp,
    bio11.sd.sp.nsd = bio11.sd.sp,
    aridity.mean.sp.nsd = aridity.mean.sp,
    aridity.sd.sp.nsd = aridity.sd.sp,
    across(c(wood.density.mean.sp, seed.dry.mass.mean.sp,
             bio11.mean.sp, bio11.sd.sp,
             aridity.mean.sp, aridity.sd.sp,
             ),
           ~as.numeric(scale(.x, center = TRUE, scale = TRUE)))
  )

# early ----
predictions_climsen_sd$clade.sp <- factor(
  predictions_climsen_sd$clade.sp, levels = c("Angiosperm", "Gimnosperm")
  )


summary(predictions_climsen_sd$low_climsen)

##     Min.  1st Qu.   Median     Mean  3rd Qu.     Max.
## -10.3171  -0.7686   0.6012   0.5291   1.6160  19.9319

quantile(predictions_climsen_sd$low_climsen, c(0.01, 0.99))

##       1%      99%
## -4.73877  6.93945

predictions_climsen_sd_low <- predictions_climsen_sd |>
  filter(low_climsen > -6 & low_climsen < 6)

summary(predictions_climsen_sd_low$low_climsen)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max. 
## -5.9968 -0.8224  0.5178  0.4050  1.5283  5.9996

fit_mod_low <- function(dat){
  lmer(
    low_climsen ~ (1 | tmt.plot.id) +
      (1 | species.cor) +
      wood.density.mean.sp + seed.dry.mass.mean.sp +
      bio11.mean.sp + bio11.sd.sp +
      aridity.mean.sp + aridity.sd.sp,
      # clade.sp,
    data = dat
    )
}

pred_reg_low <- predictions_climsen_sd_low |>
  group_by(region) |>
  nest() |>
  mutate(
    m_low = map(data, ~fit_mod_low(dat = .x)),
  )

pred_reg_low

## # A tibble: 2 × 3
## # Groups:   region [2]
##   region data                   m_low    
##   <fct>  <list>                 <list>   
## 1 USA    <tibble [189,505 × 17]> <lmerMod>
## 2 Europe <tibble [112,397 × 17]> <lmerMod>

names(pred_reg_low$m_low) <-
  c("USA", "Europe")

simres_m_low_usa <- simulateResiduals(pred_reg_low$m_low[["USA"]])
x11()
par(mfrow = c(2, 2))
plot(simres_m_low_usa)
```

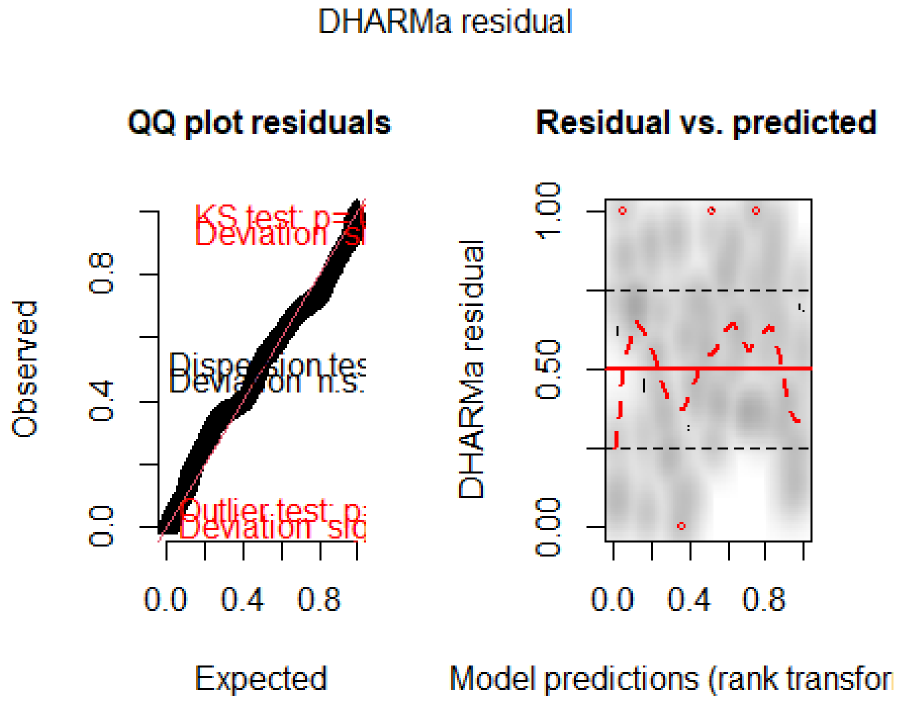


```r
simres_m_low_eu <- simulateResiduals(pred_reg_low$m_low[["Europe"]])
x11()
par(mfrow = c(2, 2))
plot(simres_m_low_eu)
```

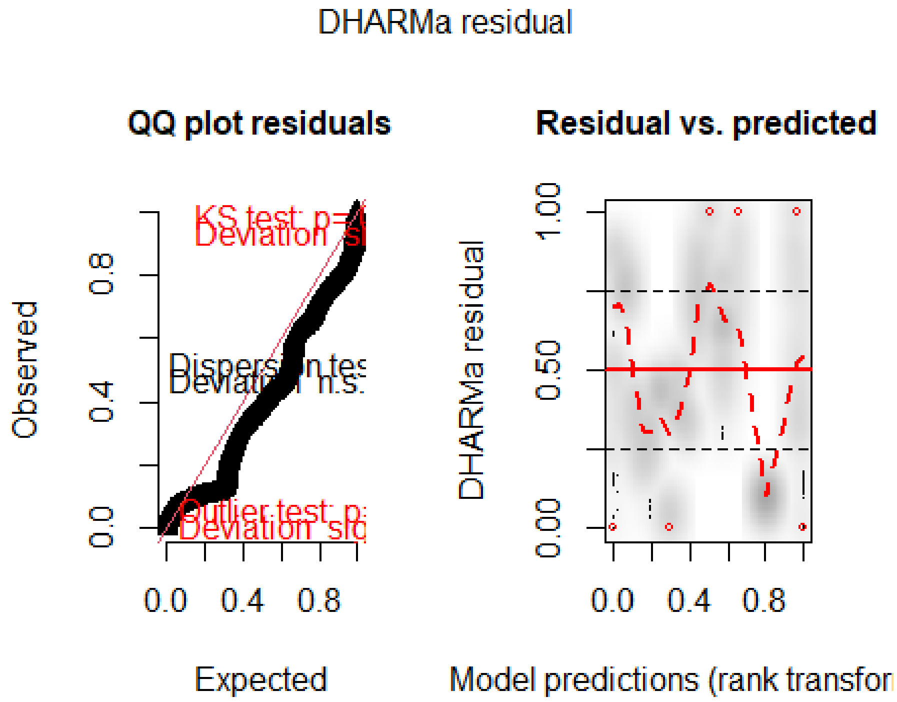


```r
# Late ----
summary(predictions_climsen_sd$high_climsen)
```

```
##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
## -6.4538 -0.3514  0.2831  0.4056  1.1152 31.6943

quantile(predictions_climsen_sd$high_climsen, c(0.01, 0.99))

##        1%       99%
## -2.474136  4.470355

predictions_climsen_sd_high <- predictions_climsen_sd |>
  filter(high_climsen > -6 & high_climsen < 6)

summary(predictions_climsen_sd_high$high_climsen)

##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
## -5.3474 -0.3584  0.2762  0.3488  1.0959  5.9964

fit_mod_high <- function(dat){
  lmer(
    high_climsen ~ (1 | tmt.plot.id) +
      (1 | species.cor) +
      wood.density.mean.sp + seed.dry.mass.mean.sp +
      bio11.mean.sp + bio11.sd.sp +
      aridity.mean.sp + aridity.sd.sp,
      # clade.sp,
    data = dat
    )
}

pred_reg_high <- predictions_climsen_sd_high |>
  group_by(region) |>
  nest() |>
  mutate(
    m_high = map(data, ~fit_mod_high(dat = .x)),
  )

pred_reg_high

## # A tibble: 2 × 3
## # Groups:   region [2]
##   region data                      m_high
##   <fct>  <list>                    <list>
## 1 USA    <tibble [197,077 × 17]> <lmerMod>
## 2 Europe <tibble [110,775 × 17]> <lmerMod>

names(pred_reg_high$m_high) <-
  c("USA", "Europe")

simres_m_high_usa <- simulateResiduals(pred_reg_high$m_high[["USA"]])
x11()
par(mfrow = c(2, 2))
plot(simres_m_high_usa)
```



```
simres_m_high_eu <- simulateResiduals(pred_reg_high$m_high[["Europe"]])
x11()
par(mfrow = c(2, 2))
plot(simres_m_high_eu)
```



Appendix 2.S4. Further analyses

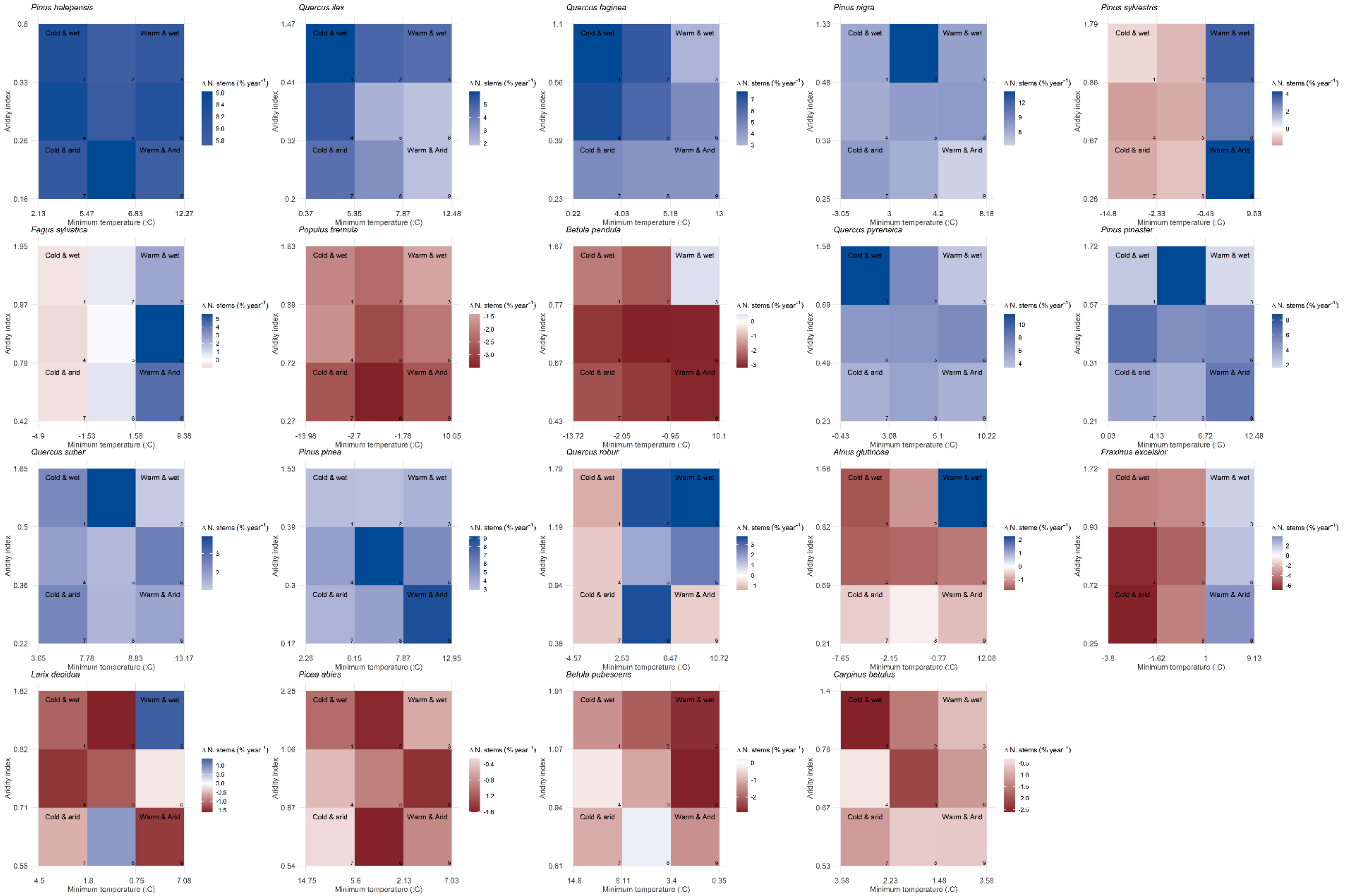


Figure 2.S4.1. Mean changes in species abundance (i.e. annual changes in the number of stems, %) across the climate range of each European species. The climate range is quantified dividing minimum temperature and aridity index into the first, second and third terciles. Note that legends are on different scales. The number in the bottom-right corner in each cell corresponds to each cell id.

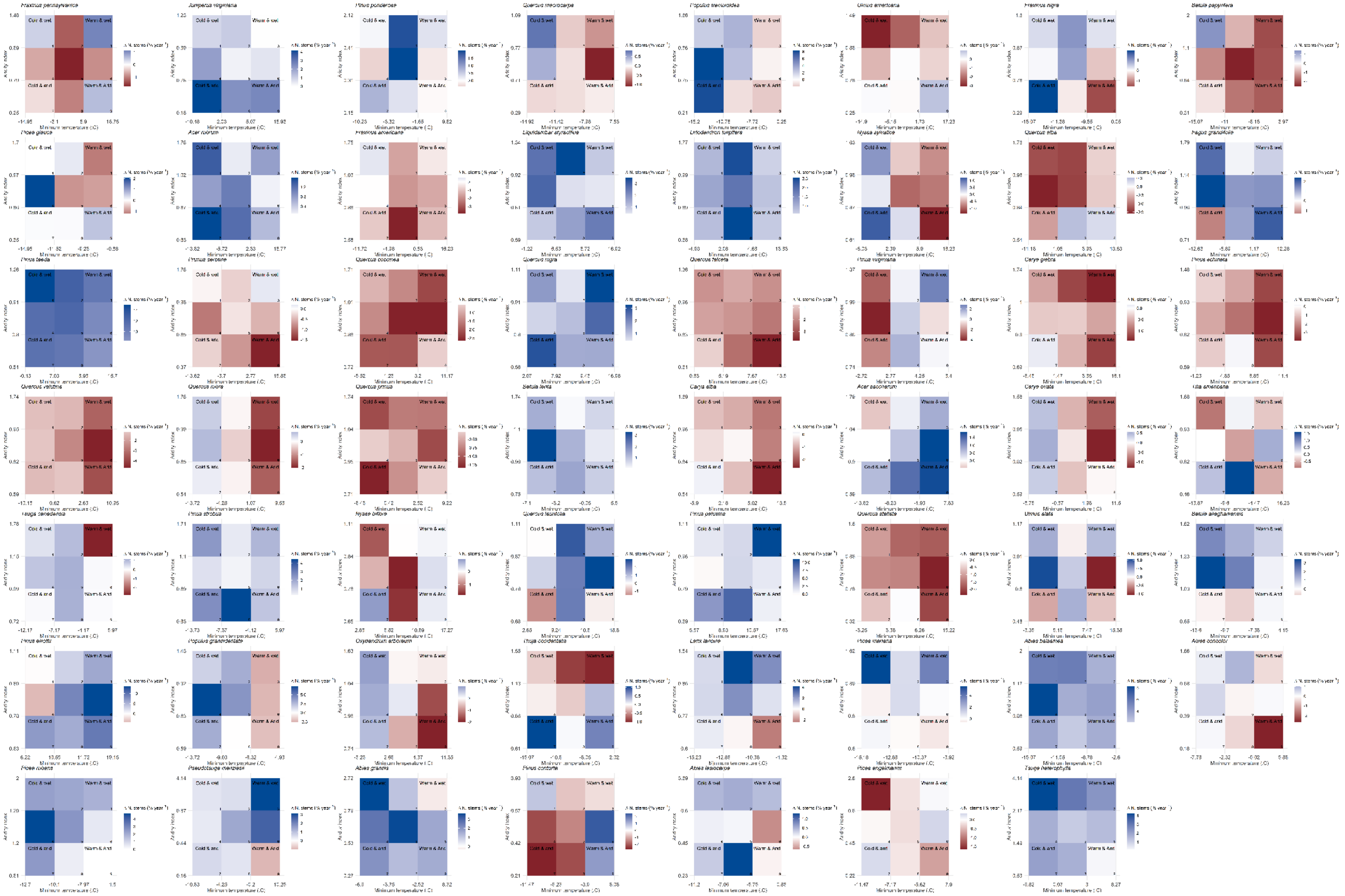


Figure 2.S4.2. Mean changes in species abundance (i.e. annual changes in the number of stems, %) across the climate range of each U.S. species. The climate range is quantified dividing minimum temperature and aridity index into the first, second and third terciles. Note that legends are on different scales. The number in the bottom-right corner in each cell corresponds to each cell id.

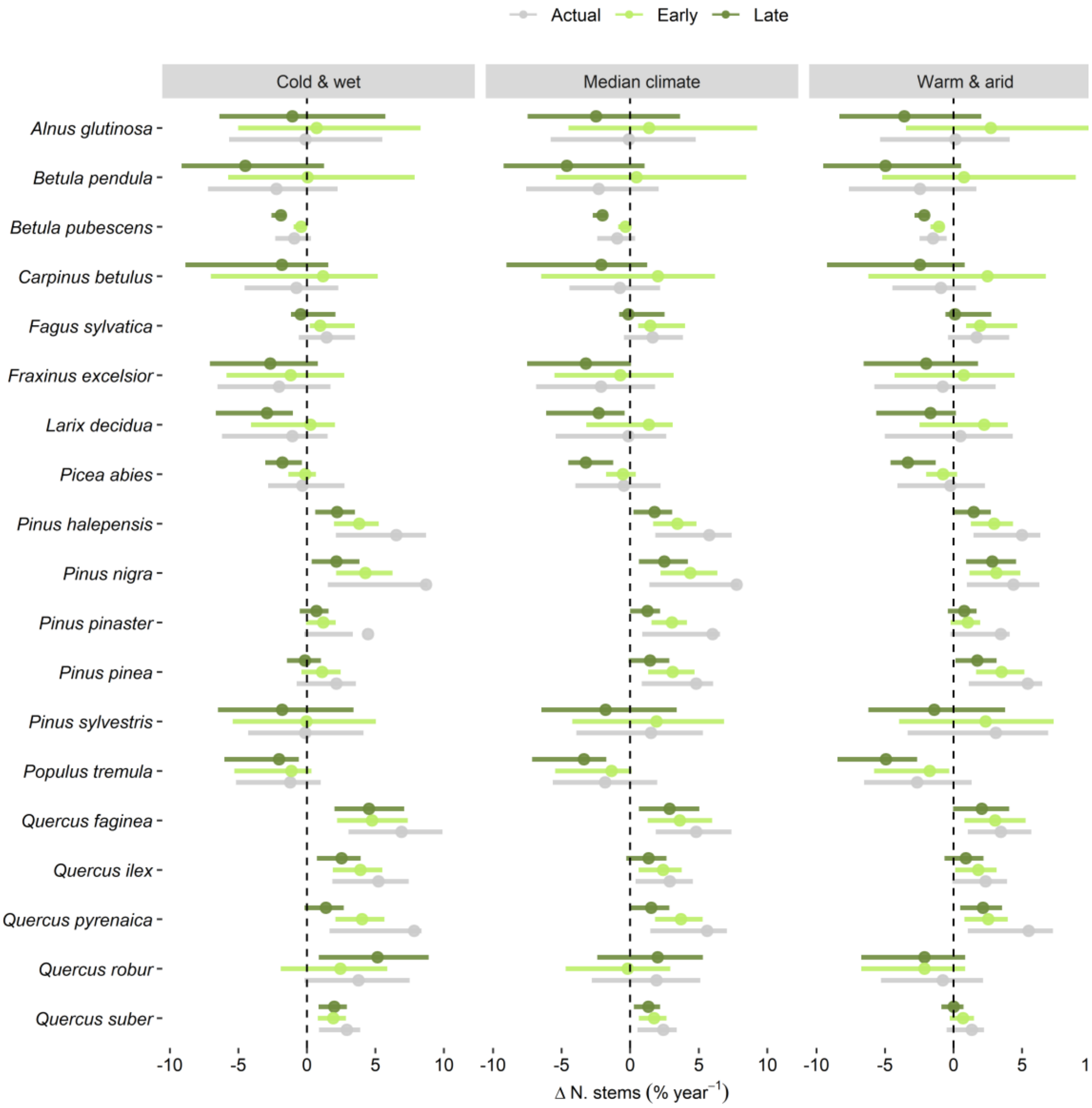


Figure 2.S4.3. Predictive distributions of changes in species abundance for European species setting minimum temperature and aridity index in cold and wet, median climate, and warm and arid regions of each species climate range, and setting forest succession in actual, early and late forest succession values (*Methods*). Points indicate mean changes and intervals 50% uncertainty.

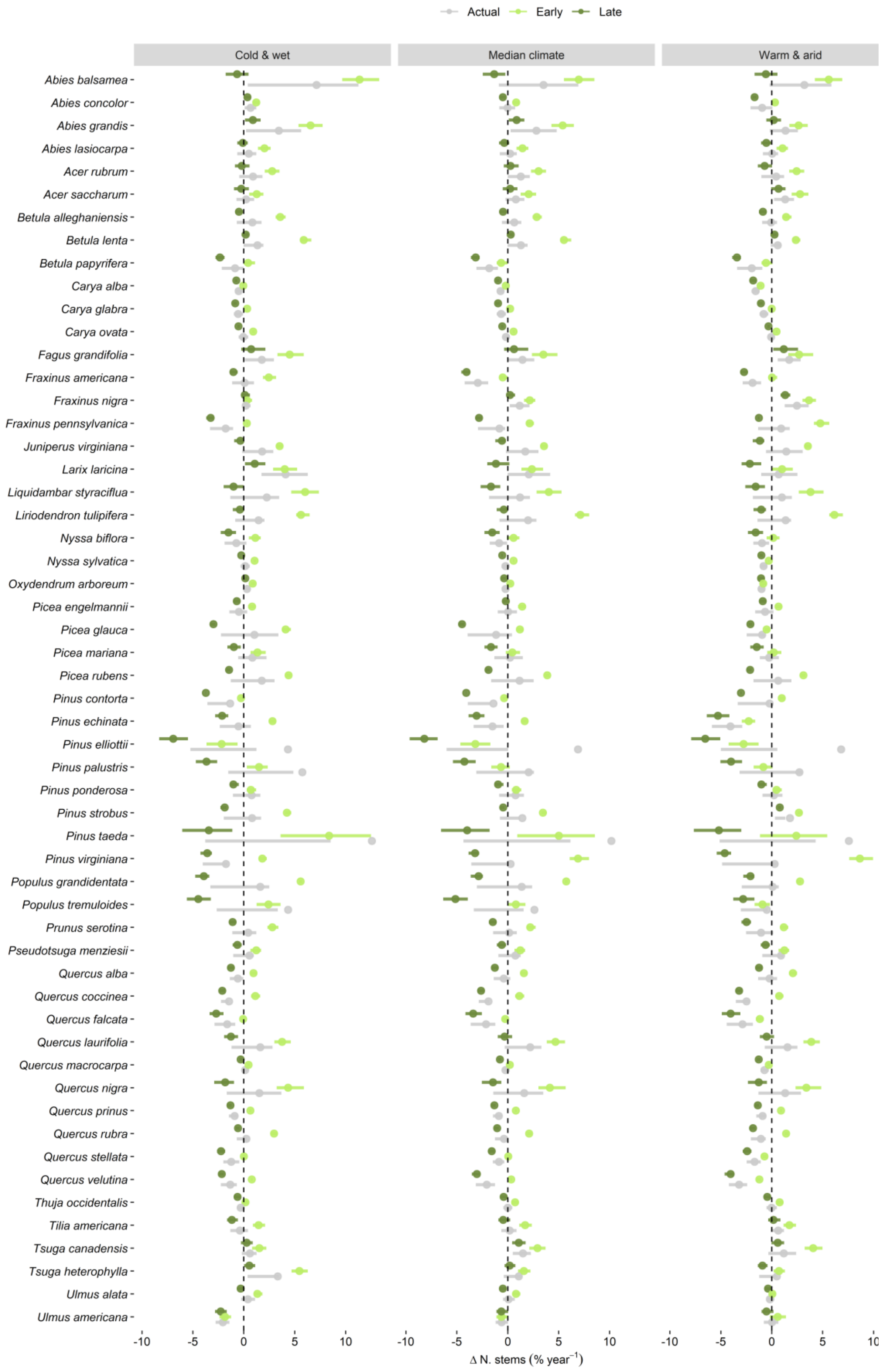


Figure 2.S4.4. Predictive distributions of changes in species abundance for U.S. species setting minimum temperature and aridity index in cold and wet, median climate, and warm

and arid regions of each species climate range, and setting forest succession in actual, early and late forest succession values (*Methods*). Points indicate mean changes and intervals 50% uncertainty.

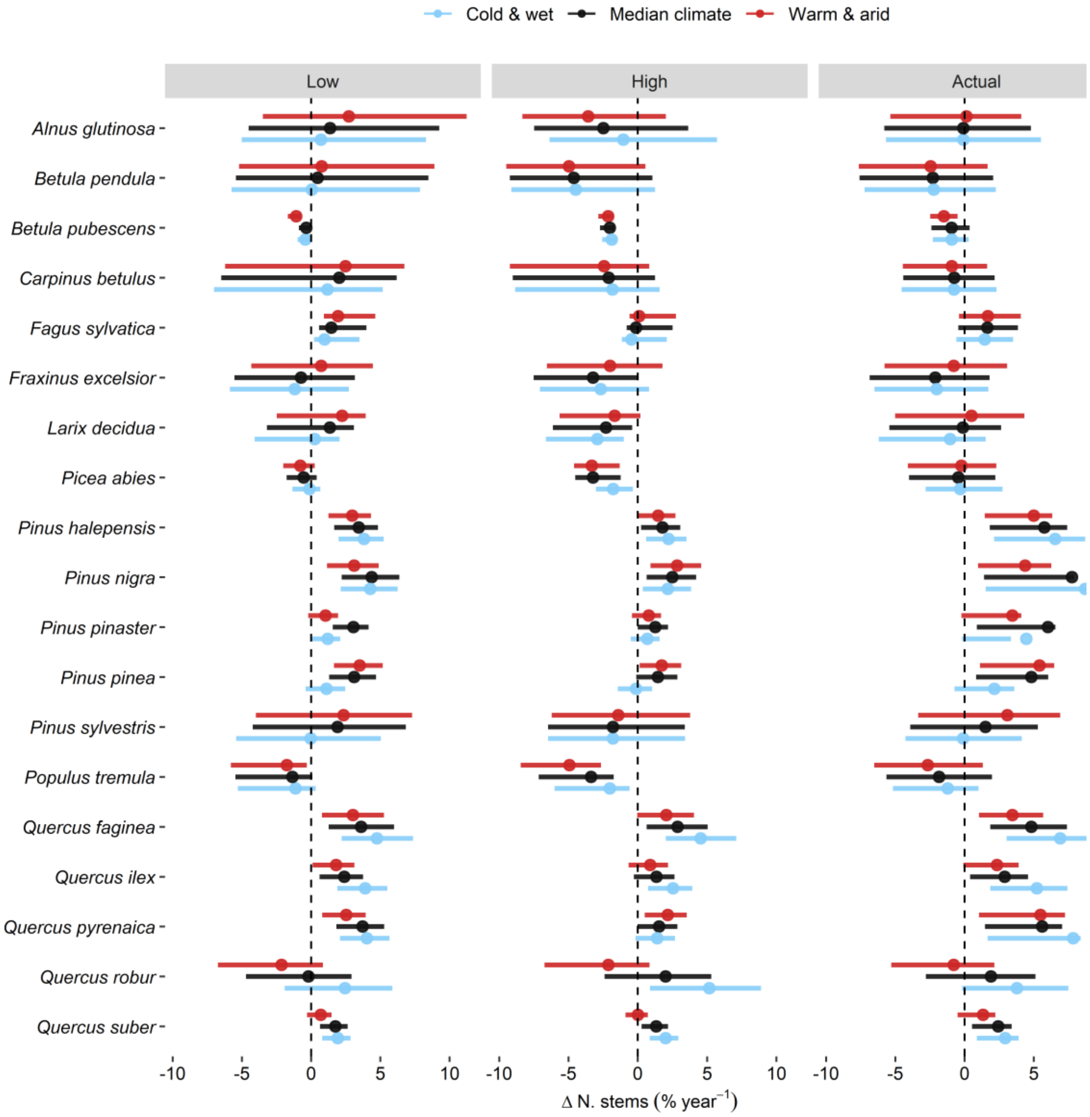


Figure 2.S4.5. Same as Figure 2.S4.3 but swapping climate and forest succession distributions to facilitate visualisation of the effect of climate on changes in species abundance.

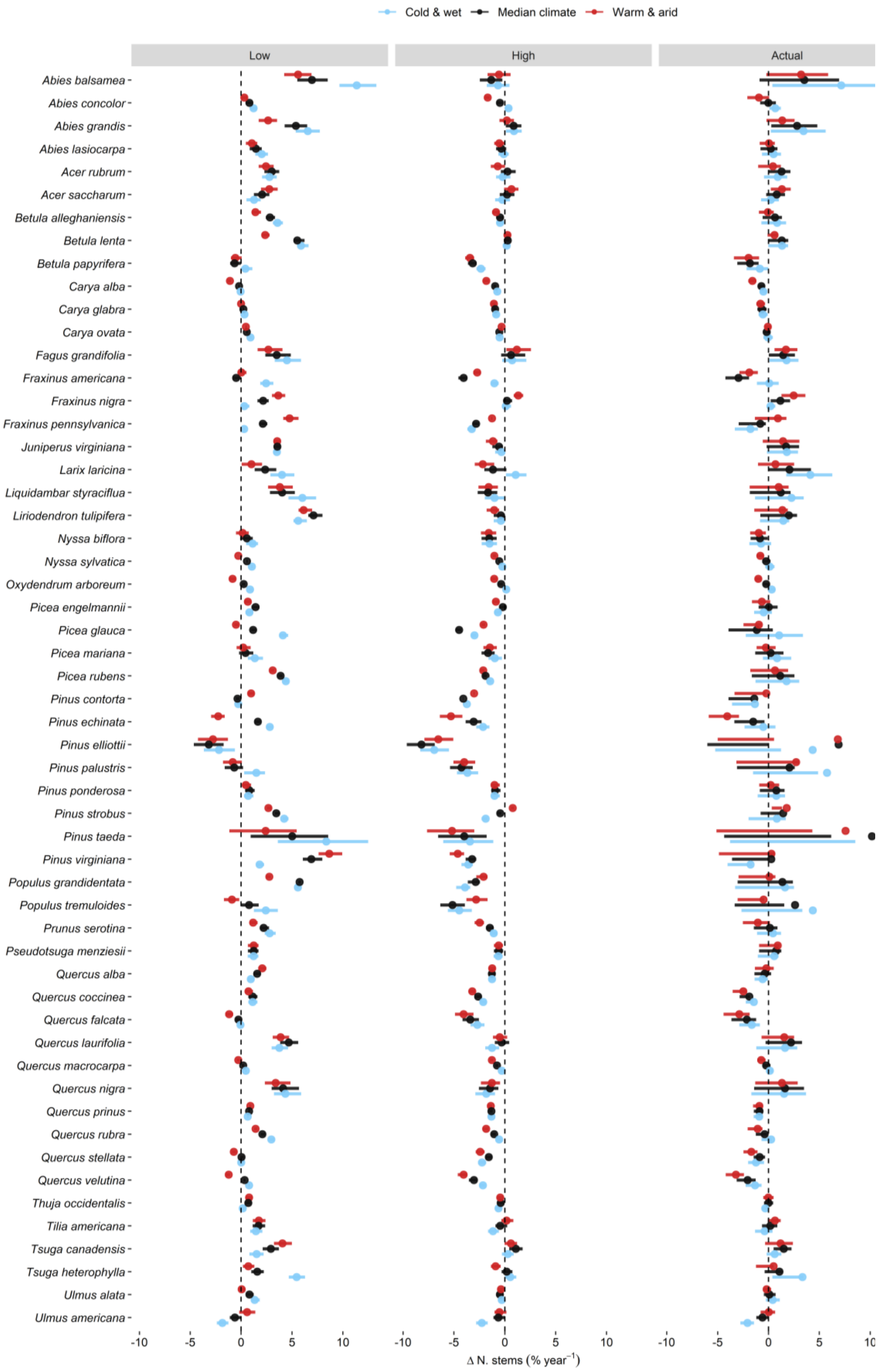


Figure 2.S4.6. Same as Figure 2.S4.4 but swapping climate and forest succession distributions to facilitate visualisation of the effect of climate on changes in species abundance.

Table 2.S4.1. Count of the number of times each cell represents the maximum and minimum value for each species.

Cell id		Count
1		
	Maximum	11
	Minimum	7
2		
	Maximum	6
	Minimum	5
3		
	Maximum	11
	Minimum	12
4		
	Maximum	13
	Minimum	7
5		
	Maximum	3
	Minimum	5
6		
	Maximum	6
	Minimum	13
7		
	Maximum	10
	Minimum	5
8		
	Maximum	9
	Minimum	5
9		
	Maximum	5
	Minimum	15

Table 2.S4.2. Species climate and forest succession sensitivity (*Methods*). The "+" in overall climate sensitivity of each species represents cases when climate has an effect on changes in species abundance greater than ± 1% year^{-1} in actual, early and late successional stage forests. The "+" in overall forest succession sensitivity represents cases when forest succession has an effect on changes in species abundance greater than ± 1% year^{-1} for cold and wet, median climate or warm and arid regions. The "+" in overall climate and forest succession sensitivity represents cases when both climate and forest succession have an effect on changes in species abundance greater than ± 1% year^{-1}. Mean climate sensitivity is calculated as the mean climate sensitivity in actual, early and late successional stage forest. Mean forest succession sensitivity is calculated as the mean forest succession sensitivity for cold and wet, median climate or warm and arid regions. Overall mean climate sensitivity as the mean of mean climate sensitivity. Overall mean forest succession sensitivity as the mean of mean forest succession sensitivity. Percentages of climate and forest succession sensitivity represent the percentage of species that climate or forest succession have an effect on changes in species abundance greater than ± 1% year^{-1}. Percentages of overall climate sensitivity, overall forest succession sensitivity, and overall climate and forest succession sensitivity represent the percentage of species that were affected by more than ± 1% year^{-1} only by climate, only by forest succession or by both climate and forest succession, respectively.

Climate sensitivity (actual)	**Climate sensitivity (early)**	**Climate sensitivity (late)**	**Forest succession sensitivity (cold & wet)**	**Forest succession sensitivity (median climate)**	**Forest succession sensitivity (warm & arid)**	**Overall climate sensitivity**	**Overall forest succession sensitivity**	**Overall climate & forest succession sensitivity**	**Mean climate sensitivity**	**Mean forest succession sensitivity**	**Overall mean climate sensitivity**	**Overall mean forest succession sensitivity**
Abies balsamea												
3.9	5.8	0.1	12.0	8.3	6.2	+	+	+	3.3	8.8	1.4	3.0
Abies concolor												
1.6	0.9	2.0	0.9	1.3	2.0	+	+	+	1.5	1.4	1.4	3.0
Abies grandis												
2.1	3.9	0.7	5.7	4.5	2.4	+	+	+	2.2	4.2	1.4	3.0
Abies lasiocarpa												
0.5	1.0	0.4	2.1	1.8	1.6	-	+	-	0.6	1.8	1.4	3.0
Acer rubrum												
0.5	0.4	0.5	3.0	2.8	3.1	-	+	-	0.4	3.0	1.4	3.0
Acer saccharum												
1.1	1.5	0.9	1.5	1.8	2.1	+	+	+	1.2	1.8	1.4	3.0
Alnus glutinosa												

0.2	2.0	2.5	1.8	3.9	6.3	+	+	+	1.6	4.0	1.4	3.0
Betula alleghaniensis												
0.9	2.2	0.4	4.0	3.3	2.3	+	+	+	1.2	3.2	1.4	3.0
Betula lenta												
0.7	3.5	0.1	5.7	5.2	2.1	+	+	+	1.5	4.3	1.4	3.0
Betula papyrifera												
1.1	1.0	1.1	2.8	2.5	2.9	+	+	+	1.1	2.7	1.4	3.0
Betula pendula												
0.2	0.7	0.5	4.5	5.1	5.7	-	+	-	0.5	5.1	1.4	3.0
Betula pubescens												
0.6	0.7	0.3	1.5	1.7	1.1	-	+	-	0.5	1.4	1.4	3.0
Carpinus betulus												
0.2	1.3	0.6	3.0	4.1	4.9	+	+	+	0.7	4.0	1.4	3.0
Carya alba												
1.1	1.1	1.1	0.7	0.8	0.7	+	-	-	1.1	0.7	1.4	3.0
Carya glabra												
0.3	0.3	0.2	1.2	1.2	1.1	-	+	-	0.3	1.1	1.4	3.0
Carya ovata												
0.0	0.5	0.2	1.4	1.1	0.8	-	+	-	0.2	1.1	1.4	3.0
Fagus grandifolia												
0.0	1.8	0.5	3.8	2.9	1.5	+	+	+	0.8	2.7	1.4	3.0
Fagus sylvatica												
0.2	1.0	0.5	1.4	1.6	1.9	-	+	-	0.6	1.6	1.4	3.0
Fraxinus americana												
2.0	2.4	1.7	3.5	3.6	2.7	+	+	+	2.0	3.3	1.4	3.0
Fraxinus excelsior												

1.2	1.9	0.7	1.5	2.5	2.7	+	+	+	1.3	2.3	1.4	3.0
Fraxinus nigra												
2.3	3.3	1.2	0.2	1.9	2.3	+	+	+	2.3	1.5	1.4	3.0
Fraxinus pennsylvanica												
2.7	4.5	2.0	3.5	5.0	6.0	+	+	+	3.1	4.8	1.4	3.0
Juniperus virginiana												
0.4	0.0	0.8	3.8	4.1	4.7	-	+	-	0.4	4.2	1.4	3.0
Larix decidua												
1.5	2.0	1.2	3.2	3.7	3.9	+	+	+	1.6	3.6	1.4	3.0
Larix laricina												
3.4	3.0	3.2	3.0	3.5	3.2	+	+	+	3.2	3.2	1.4	3.0
Liquidambar styraciflua												
1.3	2.2	0.6	7.0	5.7	5.4	+	+	+	1.4	6.0	1.4	3.0
Liriodendron tulipifera												
0.1	0.5	0.7	6.0	7.5	7.2	-	+	-	0.4	6.9	1.4	3.0
Nyssa biflora												
0.2	1.0	0.1	2.6	2.1	1.7	-	+	-	0.4	2.2	1.4	3.0
Nyssa sylvatica												
0.9	1.3	0.8	1.3	1.1	0.7	+	+	+	1.0	1.1	1.4	3.0
Oxydendrum arboretum												
1.3	1.7	1.2	0.7	0.6	0.2	+	-	-	1.4	0.5	1.4	3.0
Picea abies												
0.1	0.7	1.5	1.7	2.7	2.6	+	+	+	0.8	2.3	1.4	3.0
Picea engelmannii												
0.2	0.1	0.2	1.5	1.6	1.5	-	+	-	0.2	1.6	1.4	3.0
Picea glauca												

2.0	4.6	0.9	7.1	5.7	1.6	+	+	+	2.5	4.8	1.4	3.0
Picea mariana												
1.1	1.1	0.5	2.3	2.1	1.7	+	+	+	0.9	2.0	1.4	3.0
Picea rubens												
1.1	1.3	0.7	5.8	5.8	5.2	+	+	+	1.0	5.6	1.4	3.0
Pinus contorta												
1.1	1.3	0.7	3.5	3.7	4.0	+	+	+	1.0	3.7	1.4	3.0
Pinus echinate												
3.5	5.1	3.2	5.0	4.7	3.0	+	+	+	3.9	4.2	1.4	3.0
Pinus elliottii												
2.5	0.6	0.4	4.8	5.0	3.8	+	+	+	1.2	4.5	1.4	3.0
Pinus halepensis												
1.5	0.9	0.7	1.6	1.7	1.5	+	+	+	1.0	1.6	1.4	3.0
Pinus nigra												
4.3	1.2	0.7	2.1	1.9	0.3	+	+	+	2.1	1.4	1.4	3.0
Pinus palustris												
3.0	2.3	0.3	5.2	3.6	3.2	+	+	+	1.9	4.0	1.4	3.0
Pinus pinaster												
1.0	0.2	0.1	0.5	1.8	0.3	+	+	+	0.4	0.9	1.4	3.0
Pinus pinea												
3.3	2.4	1.9	1.3	1.7	1.8	+	+	+	2.5	1.6	1.4	3.0
Pinus ponderosa												
0.5	0.2	0.0	1.7	1.8	1.5	-	+	-	0.3	1.7	1.4	3.0
Pinus strobus												
1.0	1.6	2.7	6.1	3.9	1.9	+	+	+	1.7	4.0	1.4	3.0
Pinus sylvestris												

3.2	2.4	0.4	1.8	3.7	3.8	+	+	+	2.0	3.1	1.4	3.0
Pinus taeda												
5.0	6.0	1.8	11.8	9.0	7.6	+	+	+	4.2	9.5	1.4	3.0
Pinus virginiana												
2.1	6.8	1.0	5.4	10.1	13.3	+	+	+	3.3	9.6	1.4	3.0
Populus grandidentata												
1.5	2.8	1.8	9.5	8.6	4.9	+	+	+	2.1	7.7	1.4	3.0
Populus tremula												
1.4	0.6	2.9	0.9	2.0	3.2	+	+	+	1.7	2.0	1.4	3.0
Populus tremuloides												
4.8	3.3	1.7	6.9	5.9	1.9	+	+	+	3.3	4.9	1.4	3.0
Prunus serotina												
1.5	1.6	1.4	3.9	3.7	3.6	+	+	+	1.5	3.7	1.4	3.0
Pseudotsuga menziesii												
0.4	0.0	0.0	1.9	1.8	1.8	-	+	-	0.1	1.8	1.4	3.0
Quercus alba												
0.4	1.1	0.0	2.2	2.8	3.3	+	+	+	0.5	2.8	1.4	3.0
Quercus coccinea												
1.0	0.4	1.1	3.3	3.8	3.9	+	+	+	0.8	3.6	1.4	3.0
Quercus faginea												
3.5	1.7	2.5	0.2	0.8	1.0	+	-	-	2.5	0.6	1.4	3.0
Quercus falcata												
1.2	1.1	1.3	2.6	3.1	2.9	+	+	+	1.2	2.9	1.4	3.0
Quercus ilex												
2.9	2.1	1.6	1.4	1.1	0.9	+	+	+	2.2	1.1	1.4	3.0
Quercus laurifolia												

0.1	0.1	0.8	5.0	5.0	4.4	-	+	-	0.3	4.8	1.4	3.0
Quercus macrocarpa												
0.9	0.8	1.0	0.8	1.0	1.0	-	-	-	0.9	0.9	1.4	3.0
Quercus nigra												
0.2	1.0	0.5	6.2	5.6	4.7	-	+	-	0.6	5.5	1.4	3.0
Quercus prinus												
0.0	0.3	0.1	2.0	2.1	2.3	-	+	-	0.1	2.1	1.4	3.0
Quercus pyrenaica												
2.4	1.5	0.8	2.6	2.2	0.4	+	+	+	1.5	1.7	1.4	3.0
Quercus robur												
4.6	4.6	7.3	2.7	2.2	0.0	+	+	+	5.5	1.6	1.4	3.0
Quercus rubra												
1.3	1.5	1.3	3.5	3.1	3.3	+	+	+	1.4	3.3	1.4	3.0
Quercus stellata												
0.5	0.7	0.2	2.3	1.6	1.7	-	+	-	0.5	1.9	1.4	3.0
Quercus suber												
1.6	1.2	2.0	0.1	0.4	0.7	+	-	-	1.6	0.4	1.4	3.0
Quercus velutina												
1.9	2.0	1.9	2.9	3.4	2.8	+	+	+	1.9	3.1	1.4	3.0
Thuja occidentalis												
0.3	0.6	0.2	0.8	1.1	1.2	-	+	-	0.4	1.0	1.4	3.0
Tilia americana												
1.0	0.3	1.3	2.6	2.2	1.6	+	+	+	0.9	2.1	1.4	3.0
Tsuga canadensis												
0.6	2.5	0.3	1.2	1.8	3.5	+	+	+	1.1	2.2	1.4	3.0
Tsuga heterophylla												

2.8	4.8	1.5	4.9	1.4	1.6	+	+	+	3.0	2.6	1.4	3.0
Ulmus alata												
0.6	1.3	0.1	1.6	1.3	0.4	+	+	+	0.6	1.1	1.4	3.0
Ulmus americana												
2.1	2.4	1.7	0.4	0.0	1.1	+	+	+	2.1	0.5	1.4	3.0
Europe												
0.0	0.3	0.6	1.6	2.5	2.5	-	+	-	0.3	2.2	-	-
U.S.												
0.8	1.0	0.3	3.8	3.5	3.1	-	+	-	0.7	3.5	-	-
Percentage												
59.5	**62.2**	**41.9**	**85.1**	**91.9**	**82.4**	**5.41**	**24.32**	**68.92**	**54.5**	**86.5**	**-**	**-**

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Supporting information of Chapter 3: Evidence of non-stationary relationships between climate and forest responses: Increased sensitivity to climate change in Iberian forests

Appendix 3.S1. Further details of the Spanish Forest Inventory

Table 3.S1.1. Information of species studied. Species studied including the scientific name, forest type (BLDEC: broad-leaved deciduous; BLEVE: broad-leaved evergreen; NLDEC: needle-leaved deciduous; NLEVE: needle-leaved evergreen), family, group (angiosperm or gymnosperm), number of trees (No. trees) and number of plots used where the species is present in the Spanish Forest Inventory (No. plots).

Scientific name	Type	Family	Group	No. trees	No. plots
Pinus pinaster	NLEVE	Pinaceae	Gymnosperm	41035	2279
Pinus sylvestris	NLEVE	Pinaceae	Gymnosperm	34728	1725
Pinus halepensis	NLEVE	Pinaceae	Gymnosperm	21446	1975
Pinus nigra	NLEVE	Pinaceae	Gymnosperm	12469	928
Pinus radiata	NLEVE	Pinaceae	Gymnosperm	10577	516
Pinus pinea	NLEVE	Pinaceae	Gymnosperm	7065	746
Pinus uncinate	NLEVE	Pinaceae	Gymnosperm	5246	247
Abies alba	NLEVE	Pinaceae	Gymnosperm	1346	71
Pseudotsuga menziesii	NLEVE	Pinaceae	Gymnosperm	751	44
Larix spp.	NLDEC	Pinaceae	Gymnosperm	287	24
Chamaecyparis lawsoniana	NLEVE	Cupressaceae	Gymnosperm	264	16
Juniperus oxycedrus	NLEVE	Cupressaceae	Gymnosperm	240	105
Juniperus communis	NLEVE	Cupressaceae	Gymnosperm	145	98
Picea abies	NLEVE	Pinaceae	Gymnosperm	132	13
Cedrus atlantica	NLEVE	Pinaceae	Gymnosperm	84	9
Juniperus phoenicea	NLEVE	Cupressaceae	Gymnosperm	40	25
Cupressus sempervirens	NLEVE	Cupressaceae	Gymnosperm	38	6
Taxus baccata	NLEVE	Taxaceae	Gymnosperm	28	13
Larix decidua	NLDEC	Pinaceae	Gymnosperm	27	2
Juniperus thurifera	NLEVE	Cupressaceae	Gymnosperm	20	8
Cupressus arizonica	NLEVE	Cupressaceae	Gymnosperm	8	1
Quercus ilex	BLEVE	Fagaceae	Angiosperm	20529	2622
Quercus pyrenaica	BLDEC	Fagaceae	Angiosperm	12347	987
Quercus robur	BLDEC	Fagaceae	Angiosperm	11812	1322
Fagus sylvatica	BLDEC	Fagaceae	Angiosperm	11126	631
Eucalyptus globulus	BLEVE	Myrtaceae	Angiosperm	10134	735

Quercus suber	BLEVE	Fagaceae	Angiosperm	5991	761
Castanea sativa	BLDEC	Fagaceae	Angiosperm	5151	644
Quercus faginea	BLDEC	Fagaceae	Angiosperm	3792	573
Quercus pubescens (Q. Humilis)	BLDEC	Fagaceae	Angiosperm	2997	564
Quercus petraea	BLDEC	Fagaceae	Angiosperm	2357	289
Eucalyptus camaldulensis	BLEVE	Myrtaceae	Angiosperm	1824	182
Betula alba	BLDEC	Betulaceae	Angiosperm	1765	334
Alnus glutinosa	BLDEC	Betulaceae	Angiosperm	1645	183
Arbutus unedo	BLEVE	Ericaceae	Angiosperm	834	254
Fraxinus angustifolia	BLDEC	Oleaceae	Angiosperm	790	157
Betula spp.	BLDEC	Betulaceae	Angiosperm	699	156
Acer campestre	BLDEC	Aceraceae	Angiosperm	433	158
Populus nigra	BLDEC	Salicaceae	Angiosperm	430	67
Populus tremula	BLDEC	Salicaceae	Angiosperm	424	68
Fraxinus excelsior	BLDEC	Oleaceae	Angiosperm	393	99
Ilex aquifolium	BLEVE	Aquifoliaceae	Angiosperm	350	89
Corylus avellana	BLDEC	Betulaceae	Angiosperm	338	92
Crataegus monogyna	BLDEC	Rosaceae	Angiosperm	293	128
Betula pendula	BLDEC	Betulaceae	Angiosperm	282	53
Salix atrocinerea	BLDEC	Salicaceae	Angiosperm	265	81
Salix spp.	BLDEC	Salicaceae	Angiosperm	199	77
Populus x canadensis	BLDEC	Salicaceae	Angiosperm	183	16
Acer opalus	BLDEC	Aceraceae	Angiosperm	176	64
Quercus rubra	BLDEC	Fagaceae	Angiosperm	169	17
Acer monspessulanum	BLDEC	Aceraceae	Angiosperm	161	63
Acacia melanoxylon	BLEVE	Leguminosae	Angiosperm	152	13
Platanus hispanica	BLDEC	Platanaceae	Angiosperm	124	18
Olea europaea	BLEVE	Oleaceae	Angiosperm	118	37
Robinia pseudacacia	BLDEC	Leguminosae	Angiosperm	117	30
Ulmus minor	BLDEC	Ulmaceae	Angiosperm	114	45
Phillyrea latifolia	BLEVE	Oleaceae	Angiosperm	104	56
Populus alba	BLDEC	Salicaceae	Angiosperm	98	9
Prunus spp.	BLDEC	Rosaceae	Angiosperm	90	51
Sorbus aucuparia	BLDEC	Rosaceae	Angiosperm	82	36
Salix caprea	BLDEC	Salicaceae	Angiosperm	78	30
Other broad-leaved	BLDEC	-	Angiosperm	76	17
Sorbus aria	BLDEC	Rosaceae	Angiosperm	73	40
Pyrus spp.	BLDEC	Rosaceae	Angiosperm	71	42

Eucalyptus nitens	BLEVE	Myrtaceae	Angiosperm	67	16
Acacia dealbata	BLEVE	Leguminosae	Angiosperm	59	14
Prunus avium	BLDEC	Rosaceae	Angiosperm	59	33
Quercus canariensis	BLDEC	Fagaceae	Angiosperm	57	7
Eucalyptus gomphocephalus	BLEVE	Myrtaceae	Angiosperm	56	8
Tilia spp.	BLDEC	Tiliaceae	Angiosperm	54	20
Acacia spp.	BLEVE	Leguminosae	Angiosperm	52	11
Malus sylvestris	BLDEC	Rosaceae	Angiosperm	47	26
Juglans regia	BLDEC	Juglandaceae	Angiosperm	46	24
Salix alba	BLDEC	Salicaceae	Angiosperm	41	8
Laurus nobilis	BLEVE	Lauraceae	Angiosperm	34	16
Tilia platyphyllos	BLDEC	Tiliaceae	Angiosperm	32	12
Other *Eucalyptus*	BLEVE	Myrtaceae	Angiosperm	31	7
Frangula alnus	BLDEC	Rhamnaceae	Angiosperm	25	14
Crataegus spp.	BLDEC	Rosaceae	Angiosperm	24	15
Acer pseudoplatanus	BLDEC	Aceraceae	Angiosperm	23	11
Tilia cordata	BLDEC	Tiliaceae	Angiosperm	22	7
Sorbus torminalis	BLDEC	Rosaceae	Angiosperm	21	11
Rhamnus alaternus	BLEVE	Rhamnaceae	Angiosperm	20	7
Celtis australis	BLDEC	Ulmaceae	Angiosperm	17	9
Sorbus spp.	BLDEC	Rosaceae	Angiosperm	16	8
Buxus sempervirens	BLEVE	Buxaceae	Angiosperm	16	11
Sambucus nigra	BLDEC	Caprifoliaceae	Angiosperm	16	11
Tamarix spp.	NLEVE	Tamaricaceae	Angiosperm	14	1
Ulmus glabra	BLDEC	Ulmaceae	Angiosperm	9	5
Eucalyptus viminalis	BLEVE	Myrtaceae	Angiosperm	9	4
Salix babylonica	BLDEC	Salicaceae	Angiosperm	8	1
Ficus carica	BLDEC	Moraceae	Angiosperm	7	5
Acer negundo	BLDEC	Aceraceae	Angiosperm	5	2
Ulmus pumila	BLDEC	Ulmaceae	Angiosperm	4	2
Acer platanoides	BLDEC	Aceraceae	Angiosperm	4	3
Salix elaeagnos	BLDEC	Salicaceae	Angiosperm	4	2

Table 3.S1.2. Number of plots per region and forest type. Region, number of plots (No. plots) and number of plots for each forest type (BLDEC: broad-leaved deciduous; BLEVE: broad-leaved evergreen; NLDEC: needle-leaved deciduous; NLEVE: needle-leaved evergreen; Mixed).

Region	No. plots	BLDEC	BLEVE	NLDEC	NLEVE	Mixed
Cataluña	3,226	501	679	1	1,992	53
Extremadura	1,514	189	971	0	326	28
Galicia	2,339	919	246	0	1,015	159
Madrid	860	150	265	0	439	6
Murcia	1,014	0	28	0	979	7
País Vasco	841	439	64	6	322	10
La Rioja	739	403	93	2	239	2
Total	**10,533**	**2,601**	**2,346**	**9**	**5,312**	**265**

Appendix 3.S2. Further modelling details

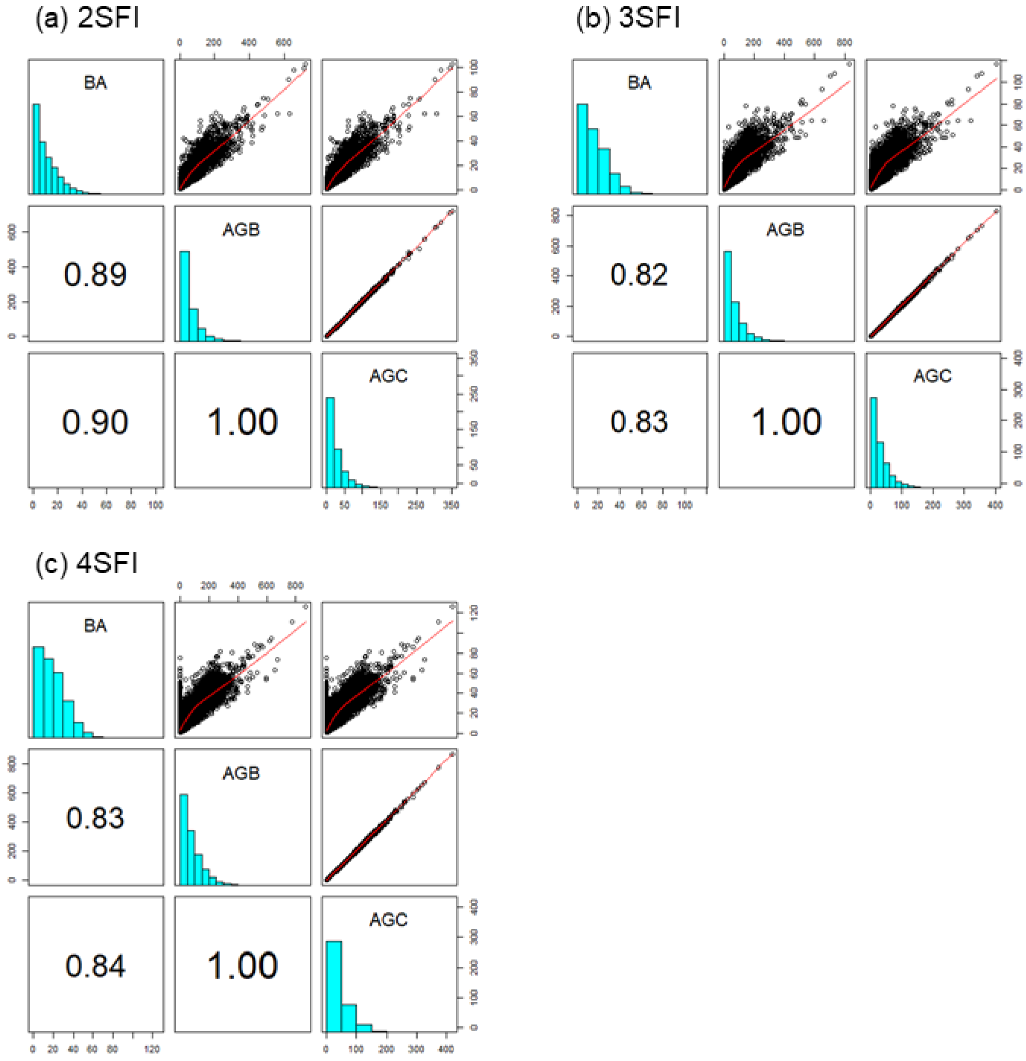


Figure 3.S2.1. Relationships between basal area, biomass and carbon storage in three consecutive forest inventories. Basal area (BA), aboveground biomass (AGB) and aboveground carbon (AGC) over the second (2SFI), third (3SFI) and fourth (4SFI) Spanish Forest Inventory including scatterplots, Pearson correlation coefficients and histograms.

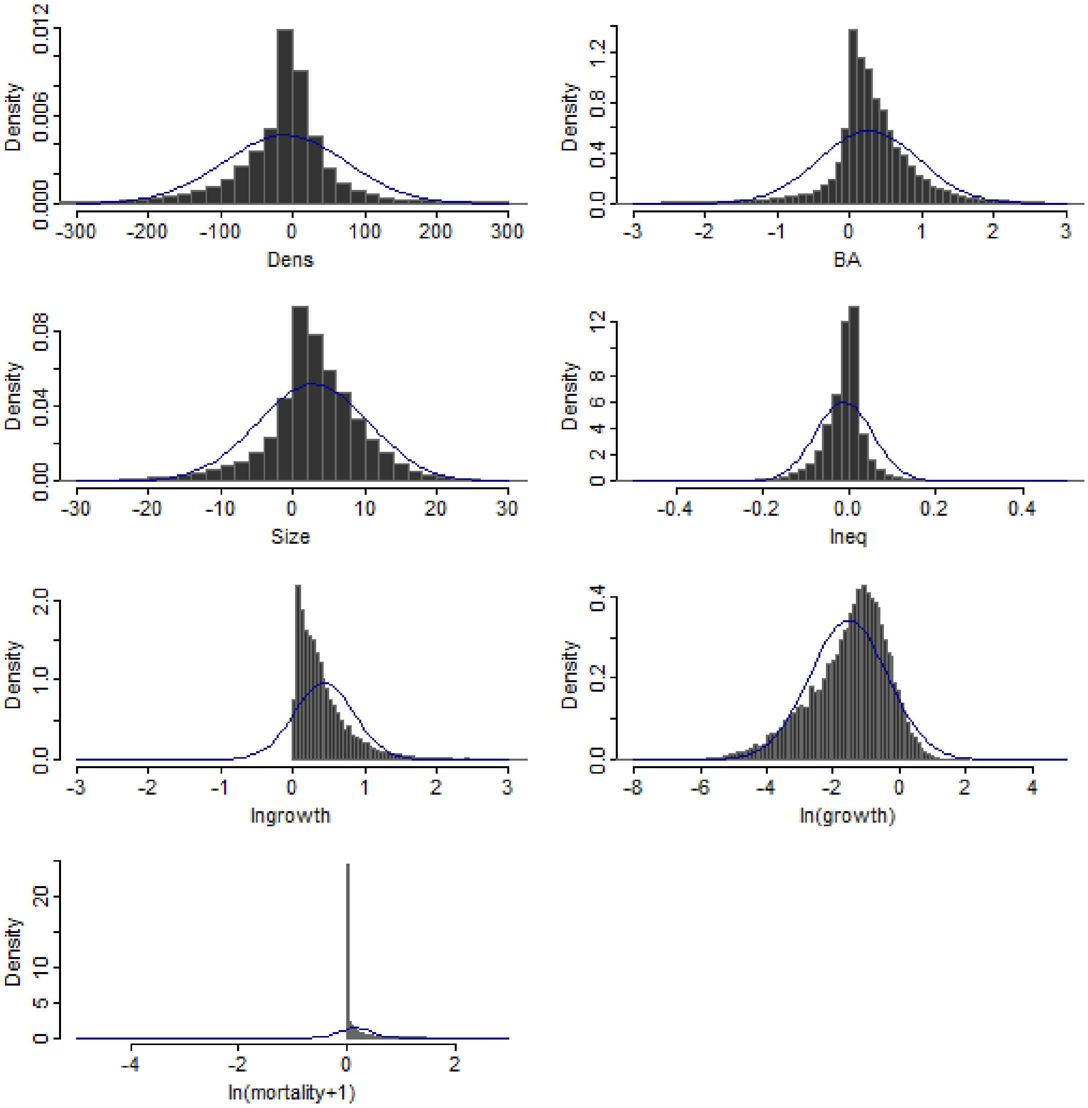


Figure 3.S2.2. Histograms of the response variables. Changes in density (*Δ*Dens), changes in basal area (*Δ*BA), changes in tree size (*Δ*Size), changes in tree size inequality (*Δ*Ineq), ingrowth, growth (ln(growth)) and mortality (ln(mortality+1)). Mortality was only modelled for values > 0 following a normal distribution (the percentage of zeros in ln(mortality+1) is 49.04%).

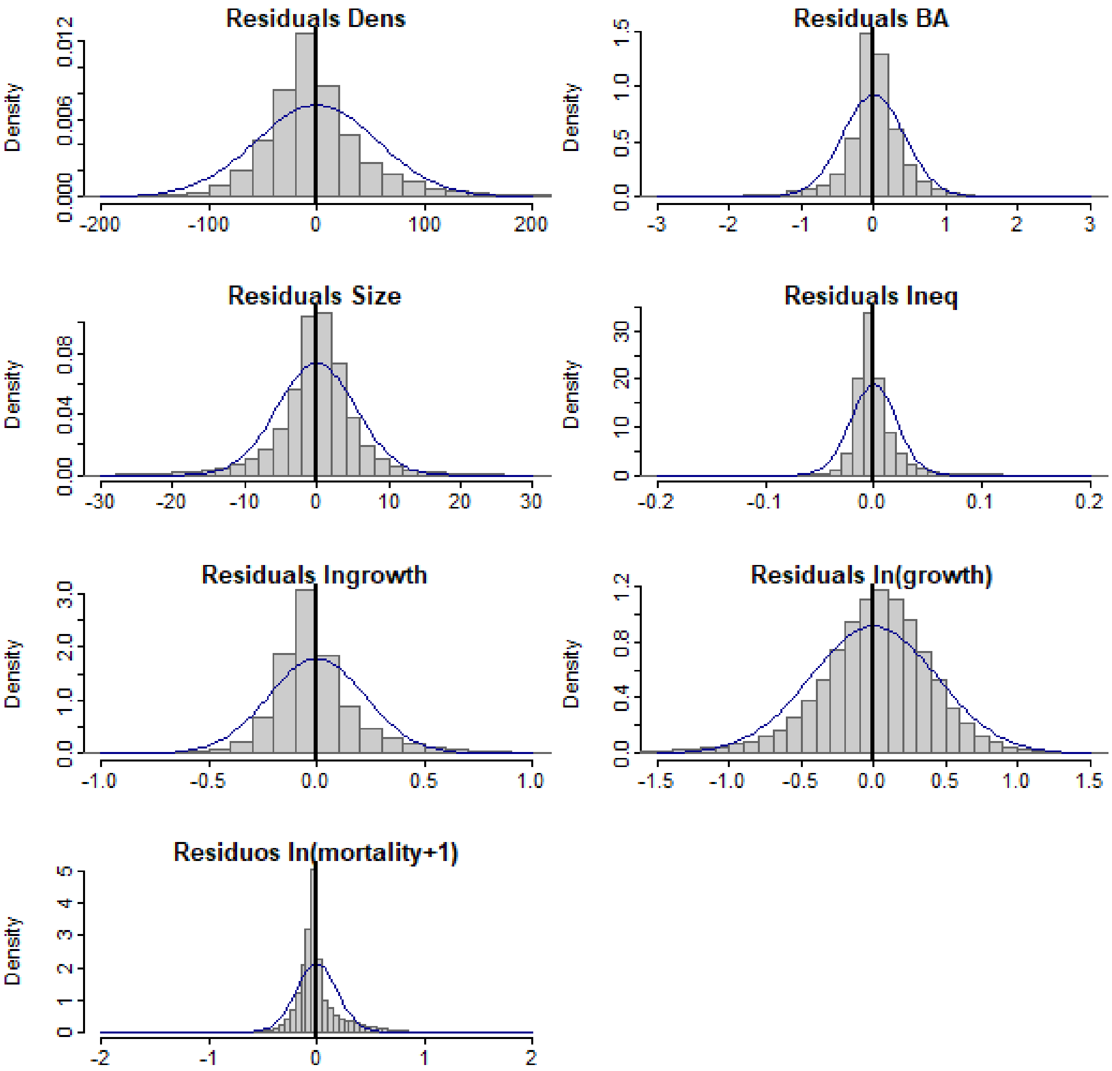


Figure 3.S2.3. Histograms of the residuals of the models. Residuals of the models of changes in density (*Δ*Dens), changes in basal area (*Δ*BA), changes in tree size (*Δ*Size), changes in tree size inequality (*Δ*Ineq), ingrowth, growth (ln(growth)) and mortality (ln(mortality+1)).

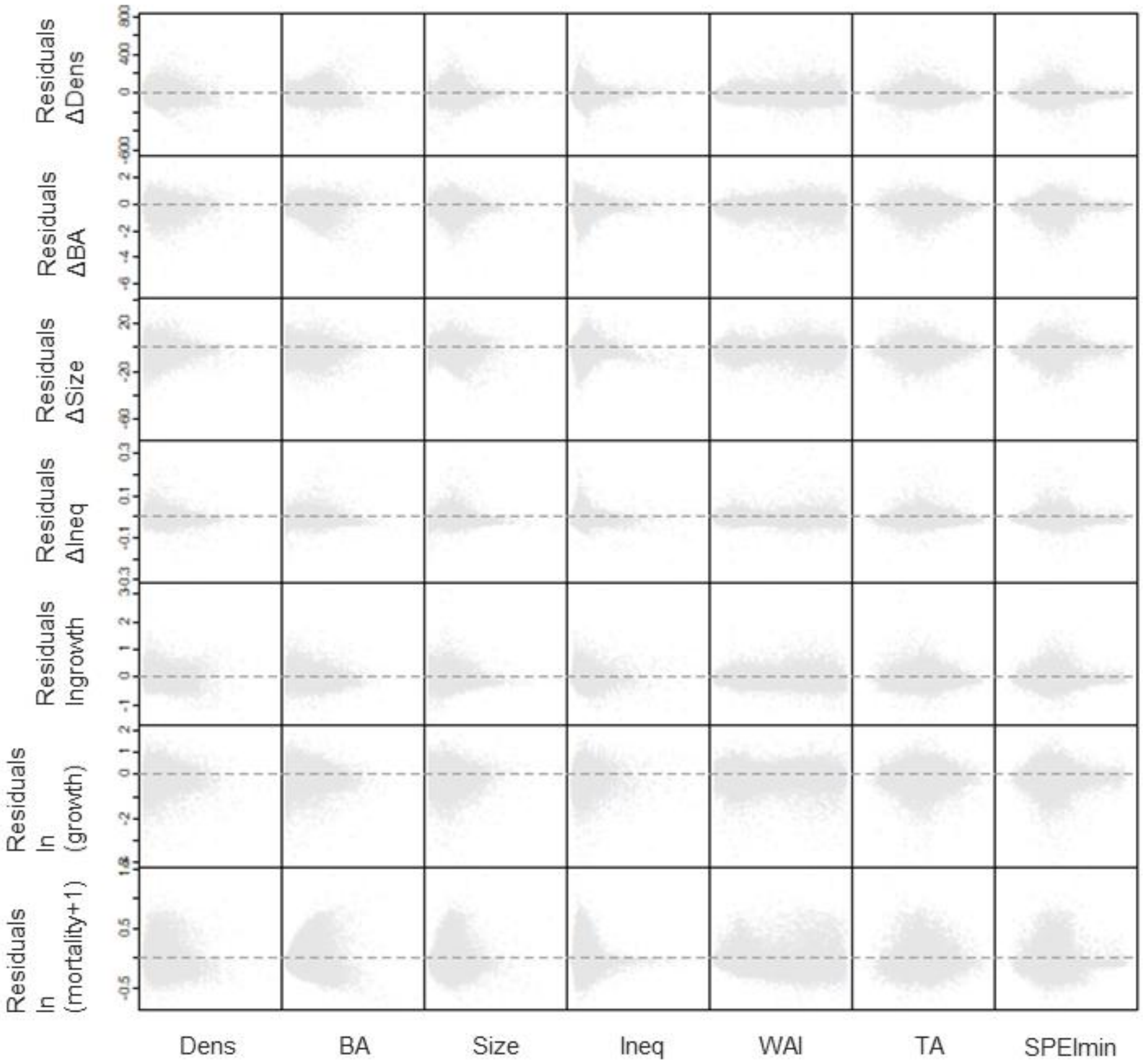


Figure 3.S2.4. Scatter plots of the models' residuals versus the explanatory variables. Partial residuals of the models of changes in density (*Δ*Dens), changes in basal area (*Δ*BA), changes in tree size (*Δ*Size), changes in tree size inequality (*Δ*Ineq), ingrowth, growth (ln(growth)) and mortality (ln(mortality+1)) versus explanatory variables of density (Dens), basal area (BA), tree size (Size), tree size inequality (Ineq), water availability (WAI), temperature anomalies (TA) and 18-month minimum SPEI (SPEImin).

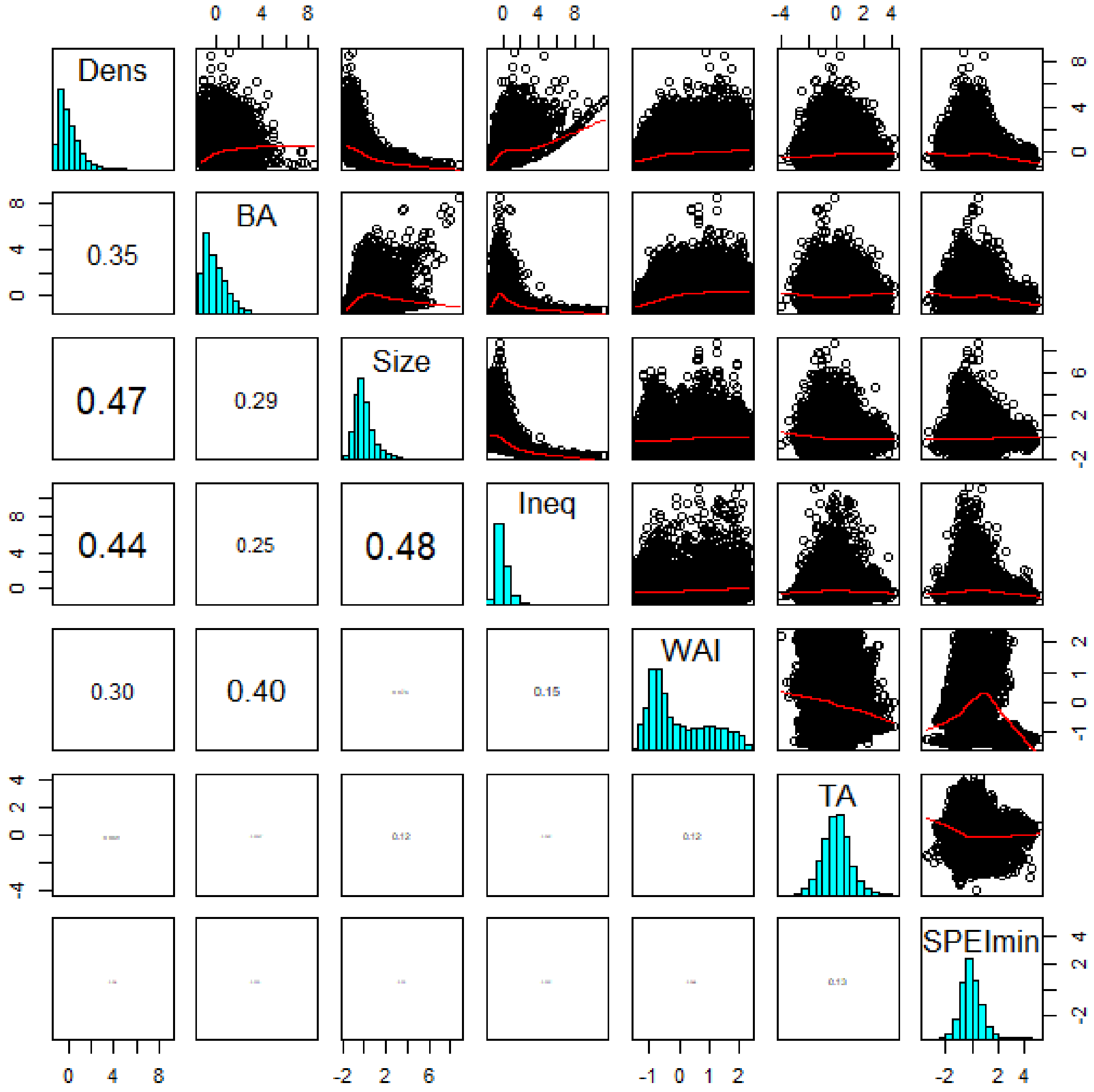


Figure 3.S2.5. Relationships between the standardised explanatory variables. Density (Dens), basal area (BA), tree size (Size), tree size inequality (Ineq), water availability (WAI), temperature anomalies (TA) and 18-month minimum SPEI (SPEImin) including scatterplots, Pearson correlation coefficients and histograms.

Table 3.S2.1. Comparisons of alternate models of changes in structure and demography to test the degree of support of the main effects and the interactions in (a) broad-leaved deciduous, (b) broad-leaved evergreen and (c) needle-leaved evergreen forests, respectively. Comparisons between models of changes in density, basal area, tree size, tree size inequality, ingrowth, growth and mortality based on Bayesian Information Criterion (BIC). The best models include the main effects and interactions between structural and climate variables supported in terms of *Δ*BIC (only the numbers of the variables that are included in the best model are shown). Structural variables are density (Dens), basal area (BA), tree size (Size), tree size inequality (Ineq); climate variables are water availability (WAI), temperature anomalies (TA) and 18-month minimum SPEI (SPEImin). The BIC of the best fitting model is compared with models in which each main effect and interaction is dropped (i.e., “No”). Therefore, the positive *Δ*BIC are shown if removing explanatory variables is not supported by BIC comparison. The combined effect of BIC when dropping all structural or climate variables

and its interactions is also shown. Marginal and conditional R^2 are indicated for the best fitting model (i.e., for the fixed and fixed plus random effects, respectively).

(a) Broad-leaved deciduous

Models	Density	Basal area	Tree size	Size inequality	Ingrowth	Growth	Mortality
Best model	0	0	0	0	0	0	0
No Dens × WAI	48	-	-	-	25	-	-
No Dens × TA	-	-	-	-	-	-	-
No Dens × SPEImin	6	-	-	-	-	-	-
No BA × WAI	8	23	-	-	-	-	7
No BA × TA	-	14	-	-	-	-	25
No BA × SPEImin	-	-	-	5	-	-	-
No Size × WAI	12	-	-	-	-	-	-
No Size × TA	-	-	-	-	-	-	-
No Size × SPEImin	-	-	-	-	-	-	-
No Ineq × WAI	-	-	-	10	-	-	-
No Ineq × TA	-	-	-	-	-	-	-
No Ineq × SPEImin	-	-	-	14	-	-	-
No Dens	1327	214	-	24	790	467	-
No BA	414	228	1	140	85	340	679
No Size	260	71	214	-	67	-	28
No Ineq	239	73	651	4340	202	310	-
No WAI	24	19	-	37	167	23	73
No TA	-	6	-	-	-	-	28
No SPEImin	7	-	-	5	-	14	-
No interactions	48	34	-	25	25	-	28
No structure	2701	760	29021	5913	1941	1755	699
No climate	-10	-13	-	22	134	46	71
R^2 marginal	0.46	0.18	0.28	0.74	0.38	0.41	0.20
R^2 conditional	0.46	0.31	0.28	0.86	0.46	0.63	0.33

(b) Broad-leaved evergreen

Models	Density	Basal area	Tree size	Size inequality	Ingrowth	Growth	Mortality
Best model	0	0	0	0	0	0	0
No Dens × WAI	164	11	-	-	26	38	-
No Dens × TA	-	-	-	-	44	-	-
No Dens × SPEImin	-	-	-	-	-	-	-

No BA × WAI	121	94	-	8	-	-	125
No BA × TA	-	7	15	-	6	-	6
No BA × SPEImin	-	5	-	-	-	-	-
No Size × WAI	13	9	72	-	23	-	-
No Size × TA	-	-	23	-	-	-	-
No Size × SPEImin	-	-	-	10	-	-	-
No Ineq × WAI	-	-	4	11	20	-	-
No Ineq × TA	16	-	-	-	-	-	-
No Ineq × SPEImin	-	-	-	-	-	-	-
No Dens	1070	391	-	-	800	324	-
No BA	532	445	57	109	86	125	720
No Size	118	2	216	25	18	80	-
No Ineq	167	-	553	2960	58	82	-
No WAI	200	176	66	101	699	146	265
No TA	15	1	63	11	36	-	3
No SPEImin	1	16	-	4	35	-	-
No interactions	200	104	91	65	118	30	119
No structure	2273	888	1450	4166	1610	1361	601
No climate	-13	94	23	49	693	100	136
R^2 marginal	0.55	0.32	0.41	0.75	0.63	0.55	0.35
R^2 conditional	0.55	0.52	0.42	0.84	0.67	0.71	0.48

(c) Needle-leaved evergreen

Models	Density	Basal area	Tree size	Size inequality	Ingrowth	Growth	Mortality
Best model	0	0	0	0	0	0	0
No Dens × WAI	48	-	-	-	-	225	-
No Dens × TA	-	-	-	-	16	-	-
No Dens × SPEImin	-	-	-	-	-	-	-
No BA × WAI	10	60	-	-	-	-	53
No BA × TA	-	-	-	-	-	-	-
No BA × SPEImin	-	-	-	-	-	-	-
No Size × WAI	14	-	13	-	-	-	-
No Size × TA	-	-	12	-	-	3	-
No Size × SPEImin	-	-	-	-	-	-	-
No Ineq × WAI	-	-	10	90	27	-	-
No Ineq × TA	-	-	-	-	-	-	-
No Ineq × SPEImin	-	-	-	-	25	-	-

No Dens	3403	1106	49	-	2507	1703	-
No BA	1623	981	95	36	264	324	1924
No Size	307	77	145	64	177	146	-
No Ineq	147	-	698	7680	179	770	-
No WAI	47	111	55	212	804	589	330
No TA	-	-	41	-	7	16	-
No SPEImin	-	-	-	-	17	-	-
No interactions	22	60	22	81	94	222	45
No structure	6601	2093	3485	11659	4748	3655	1879
No climate	19	51	69	122	731	414	276
R^2 marginal	0.54	0.24	0.35	0.74	0.53	0.53	0.32
R^2 conditional	0.57	0.42	0.41	0.82	0.63	0.76	0.42

Appendix 3.S3. Changes in forest structure and demography in Iberian forests

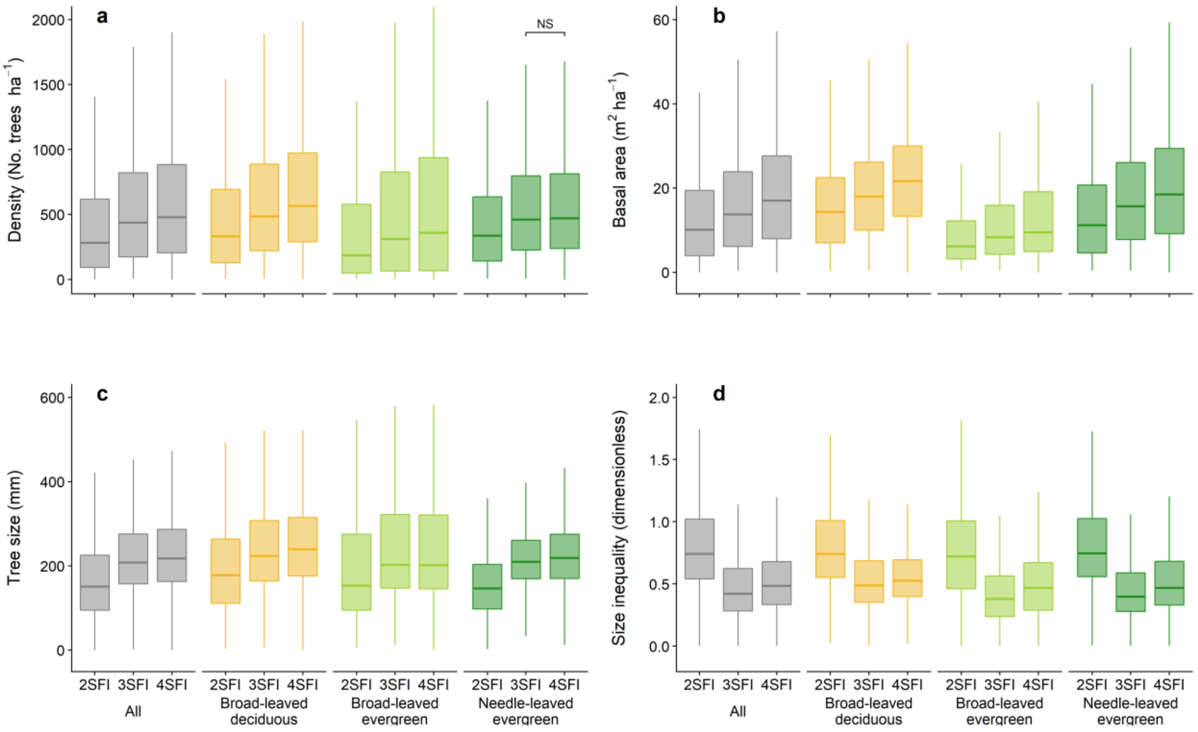


Figure 3.S3.1. Forest structure over three consecutive forest inventories by forest types. Box plots of forest structure over the second (2SFI), third (3SFI) and fourth (4SFI) Spanish Forest Inventory include (a) density, (b) basal area, (c) tree size, and (d) tree size inequality. Trends for all forests (grey box plots) and broad-leaved deciduous (orange box plots), broad-leaved evergreen (light green box plots) and needle-leaved evergreen (dark green box plots)

forests are shown. NS indicate non-significant differences from one forest inventory to another according to paired samples Wilcoxon test.

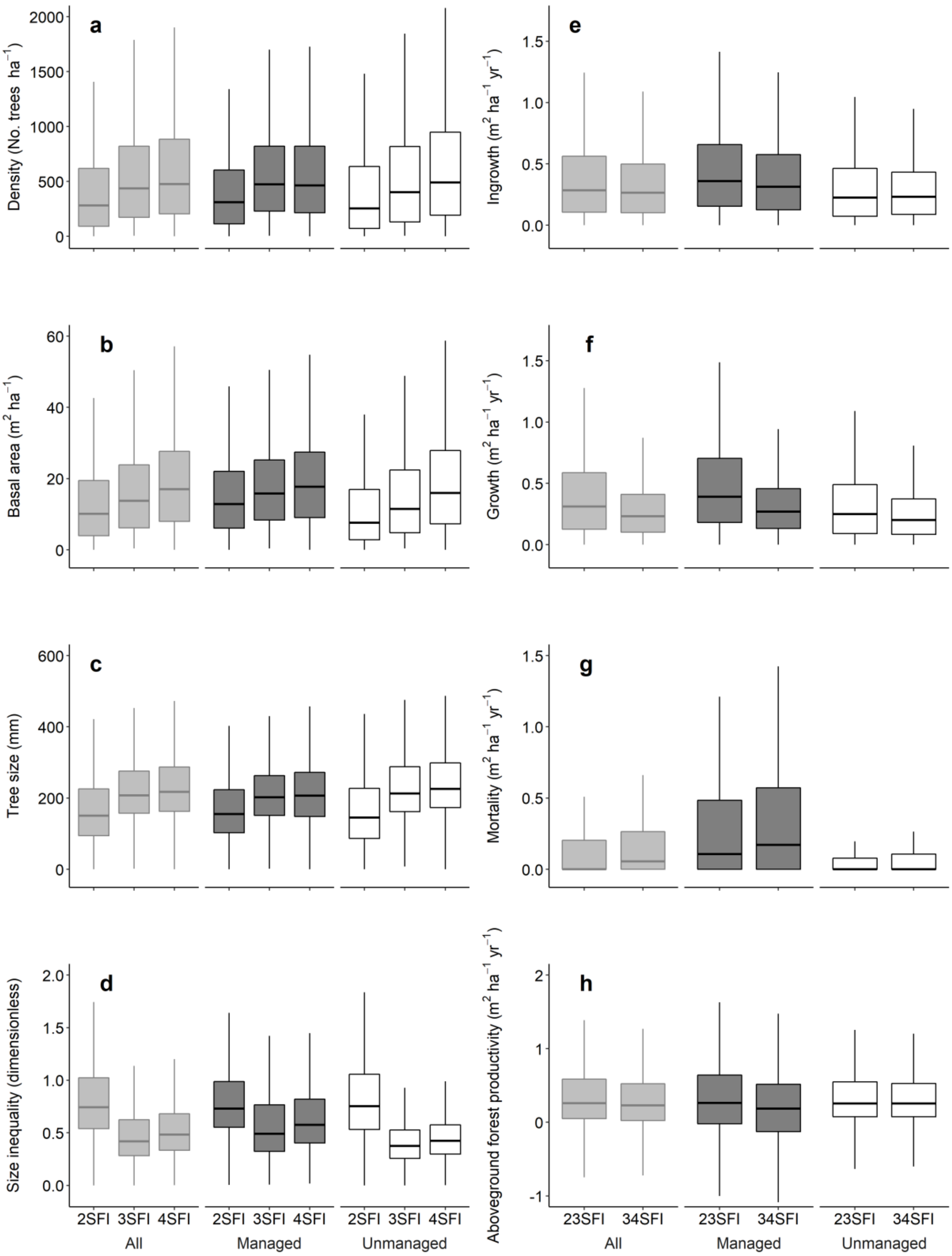


Figure 3.S3.2. Forest structure and demography over three consecutive forest inventories depending on the management status. Box plots of forest structure over the second (2SFI), third (3SFI) and fourth (4SFI) Spanish Forest Inventory include (a) density, (b) basal area, (c) tree size, and (d) tree size inequality. Box plots of forest demography from 23SFI

to 34SFI include (e) ingrowth, (f) growth, (g) mortality and (h) aboveground forest productivity. Trends for all forests (grey box plots) and managed (black box plots) and unmanaged (white box plots) forests are shown.

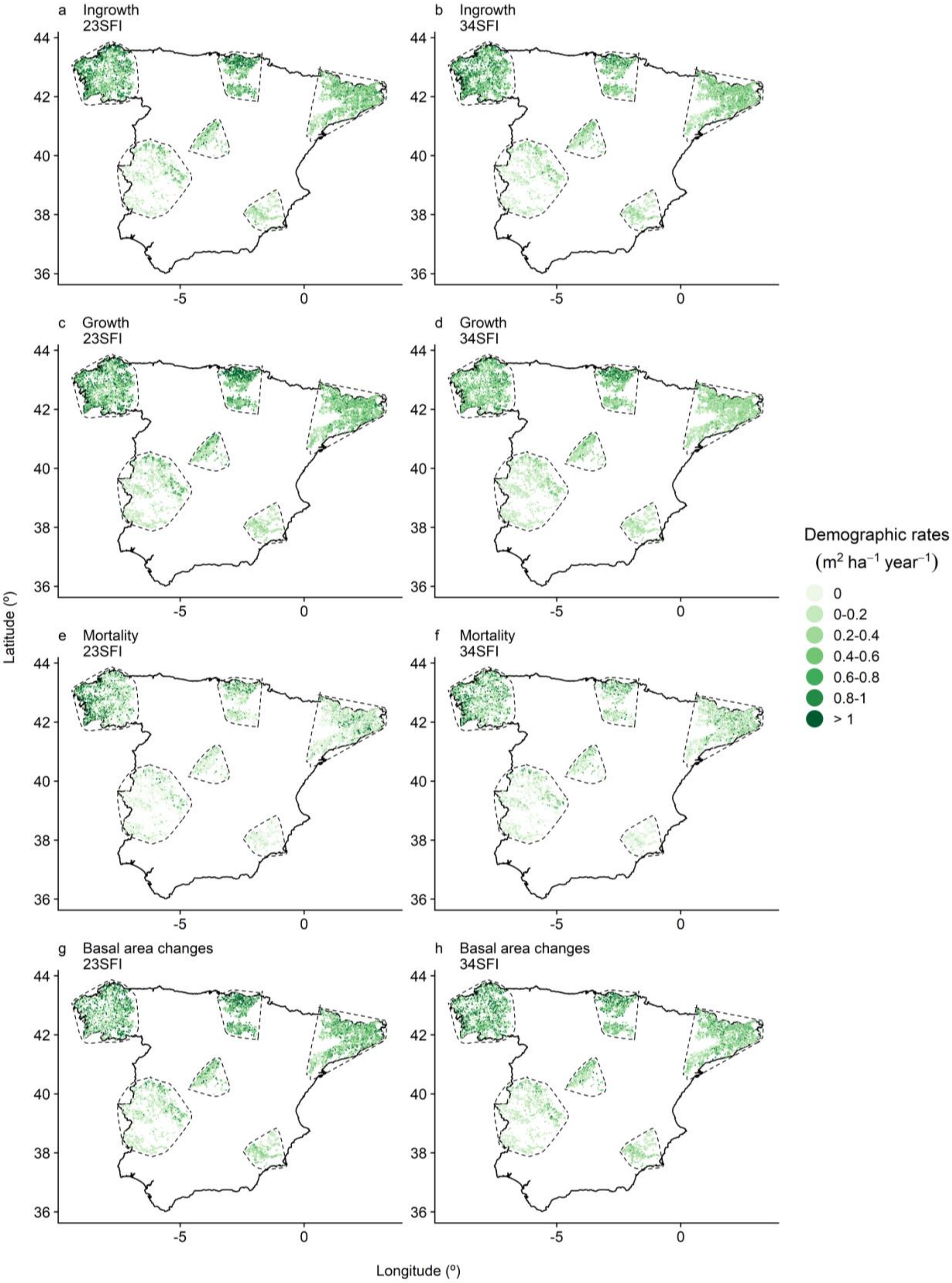


Figure 3.S3.3. Map of forest demography from 23SFI to 34SFI. (a) ingrowth 23SFI, (b) ingrowth 34SFI, (c) growth 23SFI, (d) growth 34SFI, (e) mortality 23SFI, (f) mortality 34SFI, (g) aboveground forest productivity 23SFI and (h) aboveground forest productivity 34SFI.

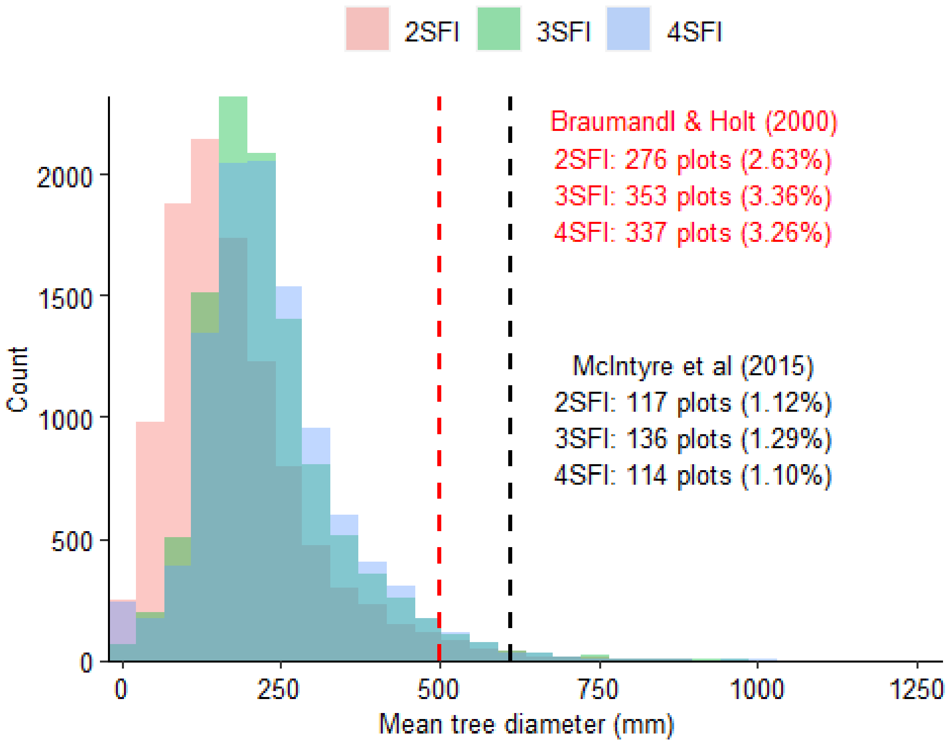


Figure 3.S3.4. Histograms of mean tree diameter during the second (2SFI), third (3SFI) and fourth (4SFI) Spanish forest Inventory. The red dashed line illustrates 500 mm of mean tree diameter established by Braumandl & Holt (2000) to identify old-growth forests and the number and percentage of plots that is greater than this size in each inventory are indicated in red. The black dashed line illustrates 610 mm of mean tree diameter established by McIntyre et al. (2015) and the number and percentage of plots that is greater than this size in each inventory are indicated in black.

Appendix S4. Detailed methods of the structural equation models to unravel the relationships between climate, forest structure, demography and productivity over two consecutive time periods

Table 3.S4.1. Evaluation of the SEM fit: Model Chi-Square, degrees of freedom (df), P-value, Comparative Fit Index (CFI), Root Mean Square Error of Approximation (RMSEA) and Standardised Root Mean Square Residual (SRMR) for all forests and each forest type (BLDEC: broad-leaved deciduous; BLEVE: broad-leaved evergreen; NLEVE: needle-leaved evergreen).

Fit measures	**All**	**BLDEC**	**BLEVE**	**NLEVE**
Chi-Square	702.304	219.464	128.586	433.430
Df	21.000	29.000	24.000	21.000
P-value	0.000	0.000	0.000	0.000
CFI	0.994	0.992	0.995	0.993
RMSEA	0.061	0.053	0.051	0.066
SRMR	0.008	0.011	0.008	0.007

Table 3.S4.2. Coefficients of multigroup structural equation models representing the effect of climate and forest structure on forest demography and aboveground forest productivity from 23SFI to 34SFI in (a) all, (b) broad-leaved deciduous, (c) broad-leaved evergreen and (d) needle-leaved evergreen forests. Regressions depict the relationships between water availability (WAI), temperature anomalies (TA), 18-month minimum SPEI (SPEImin), density (Dens), basal area (BA), tree size (Size), tree size inequality (Ineq), ingrowth (Ing), growth (Growth), mortality (Mort) and aboveground forest productivity (AFP); Period (23SFI or 34SFI); Constants (stationary effects over the two periods); Estimate; Std. error (Standard error); Z-value; and $P(>|z|)$.

(a) All

Regressions	Period	Constants	Estimate	Std. error	Z-value	$P(>\lvert z\rvert)$
Dens ~ WAI	23SFI	1	0.281	0.007	39.767	0.000
Dens ~ TA	23SFI	-	0.156	0.012	13.278	0.000
Dens ~ SPEImin	23SFI	-	-0.006	0.015	-0.392	0.695
BA ~ WAI	23SFI	2	0.383	0.007	54.769	0.000
BA ~ TA	23SFI	-	0.098	0.010	9.672	0.000
BA ~ SPEImin	23SFI	-	0.025	0.013	1.982	0.048
Size ~ WAI	23SFI	-	0.212	0.008	25.870	0.000
Size ~ TA	23SFI	3	-0.102	0.007	-14.010	0.000
Size ~ SPEImin	23SFI	4	-0.016	0.007	-2.178	0.029

Ineq ~ WAI	23SFI	-	0.013	0.010	1.279	0.201
Ineq ~ TA	23SFI	-	-0.035	0.012	-2.974	0.003
Ineq ~ SPEImin	23SFI	-	-0.062	0.015	-4.235	0.000
Ing ~ WAI	23SFI	-	0.183	0.006	29.621	0.000
Ing ~ TA	23SFI	-	0.035	0.006	5.685	0.000
Ing ~ SPEImin	23SFI	-	-0.034	0.008	-4.318	0.000
Ing ~ Dens	23SFI	-	0.865	0.008	108.282	0.000
Ing ~ BA	23SFI	-	-0.240	0.010	-24.157	0.000
Ing ~ Ineq	23SFI	-	0.342	0.007	51.600	0.000
Ing ~ Size	23SFI	-	0.275	0.009	29.145	0.000
Growth ~ WAI	23SFI	-	0.169	0.009	18.422	0.000
Growth ~ TA	23SFI	-	0.085	0.009	9.194	0.000
Growth ~ SPEImin	23SFI	-	-0.036	0.012	-3.051	0.002
Growth ~ Dens	23SFI	-	0.480	0.012	40.381	0.000
Growth ~ BA	23SFI	-	0.243	0.015	16.470	0.000
Growth ~ Ineq	23SFI	-	-0.276	0.010	-28.166	0.000
Growth ~ Size	23SFI	-	-0.085	0.014	-6.023	0.000
Mort ~ WAI	23SFI	-	0.202	0.011	18.969	0.000
Mort ~ TA	23SFI	-	-0.034	0.011	-3.128	0.002
Mort ~ SPEImin	23SFI	-	-0.019	0.014	-1.431	0.152
Mort ~ Dens	23SFI	-	-0.072	0.014	-5.238	0.000
Mort ~ BA	23SFI	-	0.550	0.017	32.855	0.000
Mort ~ Ineq	23SFI	5	-0.027	0.009	-2.987	0.003
Mort ~ Size	23SFI	-	-0.116	0.016	-7.087	0.000
AFP ~ Growth	23SFI	-	0.104	0.002	47.052	0.000
AFP ~ Mort	23SFI	6	-0.435	0.002	-283.285	0.000
AFP ~ Ing	23SFI	7	0.390	0.002	234.764	0.000
Dens ~ WAI	34SFI	1	0.281	0.007	39.767	0.000

Dens ~ TA	34SFI	-	0.068	0.008	8.501	0.000
Dens ~ SPEImin	34SFI	-	-0.069	0.007	-9.486	0.000
BA ~ WAI	34SFI	2	0.383	0.007	54.769	0.000
BA ~ TA	34SFI	-	-0.029	0.009	-3.093	0.002
BA ~ SPEImin	34SFI	-	-0.086	0.008	-10.293	0.000
Size ~ WAI	34SFI	-	0.108	0.009	11.705	0.000
Size ~ TA	34SFI	3	-0.102	0.007	-14.010	0.000
Size ~ SPEImin	34SFI	4	-0.016	0.007	-2.178	0.029
Ineq ~ WAI	34SFI	-	0.226	0.008	29.891	0.000
Ineq ~ TA	34SFI	-	0.047	0.008	6.199	0.000
Ineq ~ SPEImin	34SFI	-	-0.010	0.007	-1.522	0.128
Ing ~ WAI	34SFI	-	0.363	0.010	37.333	0.000
Ing ~ TA	34SFI	-	-0.015	0.008	-1.849	0.065
Ing ~ SPEImin	34SFI	-	0.002	0.007	0.237	0.813
Ing ~ Dens	34SFI	-	0.234	0.016	14.552	0.000
Ing ~ BA	34SFI	-	-0.072	0.012	-5.998	0.000
Ing ~ Ineq	34SFI	-	0.076	0.014	5.486	0.000
Ing ~ Size	34SFI	-	-0.099	0.012	-8.296	0.000
Growth ~ WAI	34SFI	-	0.207	0.008	25.346	0.000
Growth ~ TA	34SFI	-	-0.021	0.007	-3.141	0.002
Growth ~ SPEImin	34SFI	-	0.041	0.006	6.995	0.000
Growth ~ Dens	34SFI	-	0.156	0.013	11.606	0.000
Growth ~ BA	34SFI	-	0.490	0.010	48.787	0.000
Growth ~ Ineq	34SFI	-	-0.201	0.011	-17.550	0.000
Growth ~ Size	34SFI	-	-0.171	0.010	-17.068	0.000
Mort ~ WAI	34SFI	-	0.144	0.010	13.953	0.000
Mort ~ TA	34SFI	-	0.078	0.009	9.066	0.000
Mort ~ SPEImin	34SFI	-	0.018	0.008	2.390	0.017
Mort ~ Dens	34SFI	-	0.083	0.016	5.314	0.000

Mort ~ BA	34SFI	-	0.393	0.012	32.453	0.000
Mort ~ Ineq	34SFI	5	-0.027	0.009	-2.987	0.003
Mort ~ Size	34SFI	-	-0.033	0.013	-2.550	0.011
AFP ~ Growth	34SFI	-	0.139	0.002	59.795	0.000
AFP ~ Mort	34SFI	6	-0.435	0.002	-283.285	0.000
AFP ~ Ing	34SFI	7	0.390	0.002	234.764	0.000

(b) Broad-leaved deciduous

Regressions	Period	Constants	Estimate	Std. error	*Z*-value	$P(>\lvert z\rvert)$
Dens ~ WAI	23SFI	-	-0.008	0.022	-0.388	0.698
Dens ~ TA	23SFI	-	0.099	0.024	4.032	0.000
Dens ~ SPEImin	23SFI	1	-0.052	0.016	-3.380	0.001
BA ~ WAI	23SFI	2	0.205	0.015	13.903	0.000
BA ~ TA	23SFI	-	-0.003	0.021	-0.132	0.895
BA ~ SPEImin	23SFI	3	-0.040	0.015	-2.700	0.007
Size ~ WAI	23SFI	-	0.204	0.019	11.014	0.000
Size ~ TA	23SFI	4	-0.106	0.014	-7.397	0.000
Size ~ SPEImin	23SFI	5	0.013	0.015	0.836	0.403
Ineq ~ WAI	23SFI	-	-0.008	0.022	-0.388	0.698
Ineq ~ TA	23SFI	6	0.024	0.013	1.801	0.072
Ineq ~ SPEImin	23SFI	7	-0.023	0.014	-1.700	0.089
Ing ~ WAI	23SFI	-	0.124	0.013	9.747	0.000
Ing ~ TA	23SFI	8	0.007	0.011	0.584	0.559
Ing ~ SPEImin	23SFI	-	0.014	0.016	0.881	0.378
Ing ~ Dens	23SFI	-	0.743	0.016	45.385	0.000
Ing ~ BA	23SFI	9	-0.154	0.016	-9.332	0.000
Ing ~ Ineq	23SFI	-	0.448	0.013	33.789	0.000
Ing ~ Size	23SFI	-	0.291	0.020	14.730	0.000
Growth ~ WAI	23SFI	-	0.044	0.018	2.518	0.012
Growth ~ TA	23SFI	10	-0.002	0.011	-0.180	0.857
Growth ~ SPEImin	23SFI	11	0.007	0.012	0.549	0.583
Growth ~ Dens	23SFI	-	0.431	0.021	20.082	0.000

Growth ~ BA	23SFI	-	0.347	0.026	13.571	0.000
Growth ~ Ineq	23SFI	-	-0.307	0.019	-16.012	0.000
Growth ~ Size	23SFI	12	-0.099	0.019	-5.263	0.000
Mort ~ WAI	23SFI	13	0.142	0.015	9.749	0.000
Mort ~ TA	23SFI	-	-0.049	0.024	-2.043	0.041
Mort ~ SPEImin	23SFI	-	0.036	0.026	1.363	0.173
Mort ~ Dens	23SFI	-	-0.008	0.029	-0.289	0.772
Mort ~ BA	23SFI	-	0.496	0.034	14.393	0.000
Mort ~ Ineq	23SFI	14	-0.042	0.018	-2.379	0.017
Mort ~ Size	23SFI	-	-0.121	0.036	-3.369	0.001
AFP ~ Growth	23SFI	-	0.078	0.004	19.480	0.000
AFP ~ Mort	23SFI	-	-0.422	0.004	-104.822	0.000
AFP ~ Ing	23SFI	15	0.349	0.003	122.940	0.000
Dens ~ WAI	34SFI	-	0.081	0.020	3.994	0.000
Dens ~ TA	34SFI	-	0.009	0.016	0.537	0.591
Dens ~ SPEImin	34SFI	1	-0.052	0.016	-3.380	0.001
BA ~ WAI	34SFI	2	0.205	0.015	13.903	0.000
BA ~ TA	34SFI	-	-0.140	0.018	-7.669	0.000
BA ~ SPEImin	34SFI	3	-0.040	0.015	-2.700	0.007
Size ~ WAI	34SFI	-	0.162	0.020	7.995	0.000
Size ~ TA	34SFI	4	-0.106	0.014	-7.397	0.000
Size ~ SPEImin	34SFI	5	0.013	0.015	0.836	0.403
Ineq ~ WAI	34SFI	-	0.150	0.017	8.662	0.000
Ineq ~ TA	34SFI	6	0.024	0.013	1.801	0.072
Ineq ~ SPEImin	34SFI	7	-0.023	0.014	-1.700	0.089
Ing ~ WAI	34SFI	-	0.236	0.020	11.815	0.000
Ing ~ TA	34SFI	8	0.007	0.011	0.584	0.559
Ing ~ SPEImin	34SFI	-	-0.042	0.016	-2.567	0.010
Ing ~ Dens	34SFI	-	0.281	0.028	9.924	0.000
Ing ~ BA	34SFI	9	-0.154	0.016	-9.332	0.000
Ing ~ Ineq	34SFI	-	0.140	0.027	5.265	0.000
Ing ~ Size	34SFI	-	0.010	0.024	0.391	0.696
Growth ~ WAI	34SFI	-	0.142	0.016	8.796	0.000

Growth ~ TA	34SFI	10	-0.002	0.011	-0.180	0.857
Growth ~ SPEImin	34SFI	11	0.007	0.012	0.549	0.583
Growth ~ Dens	34SFI	-	0.226	0.024	9.276	0.000
Growth ~ BA	34SFI	-	0.466	0.019	24.734	0.000
Growth ~ Ineq	34SFI	-	-0.219	0.023	-9.659	0.000
Growth ~ Size	34SFI	12	-0.099	0.019	-5.263	0.000
Mort ~ WAI	34SFI	13	0.142	0.015	9.749	0.000
Mort ~ TA	34SFI	-	0.077	0.017	4.640	0.000
Mort ~ SPEImin	34SFI	-	-0.032	0.017	-1.930	0.054
Mort ~ Dens	34SFI	-	0.135	0.029	4.624	0.000
Mort ~ BA	34SFI	-	0.301	0.024	12.670	0.000
Mort ~ Ineq	34SFI	14	-0.042	0.018	-2.379	0.017
Mort ~ Size	34SFI	-	-0.052	0.027	-1.895	0.058
AFP ~ Growth	34SFI	-	0.120	0.004	30.352	0.000
AFP ~ Mort	34SFI	-	-0.384	0.004	-99.404	0.000
AFP ~ Ing	34SFI	15	0.349	0.003	122.940	0.000

(c) Broad-leaved evergreen

Regressions	Period	Constants	Estimate	Std. error	*Z*-value	*P*(>|*z*|)
Dens ~ WAI	23SFI	1	0.445	0.015	29.840	0.000
Dens ~ TA	23SFI	-	0.357	0.024	15.062	0.000
Dens ~ SPEImin	23SFI	-	0.099	0.025	3.996	0.000
BA ~ WAI	23SFI	-	0.317	0.019	16.588	0.000
BA ~ TA	23SFI	-	0.313	0.022	13.937	0.000
BA ~ SPEImin	23SFI	-	0.040	0.021	1.901	0.057
Size ~ WAI	23SFI	-	-0.036	0.019	-1.872	0.061
Size ~ TA	23SFI	2	-0.104	0.017	-6.186	0.000
Size ~ SPEImin	23SFI	-	-0.208	0.021	-9.960	0.000
Ineq ~ WAI	23SFI	-	0.183	0.024	7.574	0.000
Ineq ~ TA	23SFI	-	-0.129	0.026	-4.952	0.000
Ineq ~ SPEImin	23SFI	3	0.008	0.015	0.525	0.600
Ing ~ WAI	23SFI	-	0.308	0.013	24.470	0.000
Ing ~ TA	23SFI	-	-0.014	0.013	-1.094	0.274

Ing ~ SPEImin	23SFI	-	-0.034	0.013	-2.705	0.007
Ing ~ Dens	23SFI	-	0.967	0.018	52.965	0.000
Ing ~ BA	23SFI	-	-0.336	0.021	-16.123	0.000
Ing ~ Ineq	23SFI	-	0.331	0.014	22.875	0.000
Ing ~ Size	23SFI	-	0.328	0.018	18.240	0.000
Growth ~ WAI	23SFI	4	0.198	0.014	13.943	0.000
Growth ~ TA	23SFI	-	0.114	0.021	5.447	0.000
Growth ~ SPEImin	23SFI	5	-0.025	0.013	-1.988	0.047
Growth ~ Dens	23SFI	-	0.374	0.026	14.558	0.000
Growth ~ BA	23SFI	-	0.251	0.030	8.234	0.000
Growth ~ Ineq	23SFI	-	-0.247	0.022	-11.154	0.000
Growth ~ Size	23SFI	6	-0.211	0.015	-13.787	0.000
Mort ~ WAI	23SFI	-	0.279	0.024	11.681	0.000
Mort ~ TA	23SFI	-	-0.069	0.026	-2.668	0.008
Mort ~ SPEImin	23SFI	7	-0.003	0.016	-0.160	0.873
Mort ~ Dens	23SFI	-	-0.193	0.031	-6.222	0.000
Mort ~ BA	23SFI	-	0.752	0.036	21.131	0.000
Mort ~ Ineq	23SFI	8	0.118	0.021	5.530	0.000
Mort ~ Size	23SFI	9	0.023	0.019	1.210	0.226
AFP ~ Growth	23SFI	-	0.068	0.004	15.648	0.000
AFP ~ Mort	23SFI	-	-0.383	0.004	-97.986	0.000
AFP ~ Ing	23SFI	10	0.360	0.003	113.147	0.000
Dens ~ WAI	34SFI	1	0.445	0.015	29.840	0.000
Dens ~ TA	34SFI	-	0.176	0.018	9.759	0.000
Dens ~ SPEImin	34SFI	-	-0.107	0.020	-5.414	0.000
BA ~ WAI	34SFI	-	0.561	0.021	26.080	0.000
BA ~ TA	34SFI	-	0.195	0.021	9.116	0.000
BA ~ SPEImin	34SFI	-	-0.166	0.023	-7.348	0.000
Size ~ WAI	34SFI	-	-0.147	0.025	-5.927	0.000
Size ~ TA	34SFI	2	-0.104	0.017	-6.186	0.000
Size ~ SPEImin	34SFI	-	-0.000	0.026	-0.010	0.992
Ineq ~ WAI	34SFI	-	0.248	0.017	14.710	0.000
Ineq ~ TA	34SFI	-	0.086	0.016	5.285	0.000

Ineq ~ SPEImin	34SFI	3	0.008	0.015	0.525	0.600
Ing ~ WAI	34SFI	-	0.413	0.021	20.094	0.000
Ing ~ TA	34SFI	-	0.032	0.016	1.959	0.050
Ing ~ SPEImin	34SFI	-	-0.074	0.017	-4.404	0.000
Ing ~ Dens	34SFI	-	0.241	0.031	7.776	0.000
Ing ~ BA	34SFI	-	-0.053	0.023	-2.312	0.021
Ing ~ Ineq	34SFI	-	0.020	0.028	0.736	0.462
Ing ~ Size	34SFI	-	-0.086	0.018	-4.660	0.000
Growth ~ WAI	34SFI	4	0.198	0.014	13.943	0.000
Growth ~ TA	34SFI	-	0.048	0.016	3.043	0.002
Growth ~ SPEImin	34SFI	5	-0.025	0.013	-1.988	0.047
Growth ~ Dens	34SFI	-	0.085	0.029	2.937	0.003
Growth ~ BA	34SFI	-	0.448	0.021	21.022	0.000
Growth ~ Ineq	34SFI	-	-0.068	0.026	-2.631	0.009
Growth ~ Size	34SFI	6	-0.211	0.015	-13.787	0.000
Mort ~ WAI	34SFI	-	0.194	0.023	8.385	0.000
Mort ~ TA	34SFI	-	0.089	0.019	4.607	0.000
Mort ~ SPEImin	34SFI	7	-0.003	0.016	-0.160	0.873
Mort ~ Dens	34SFI	-	-0.053	0.032	-1.648	0.099
Mort ~ BA	34SFI	-	0.343	0.026	13.456	0.000
Mort ~ Ineq	34SFI	8	0.118	0.021	5.530	0.000
Mort ~ Size	34SFI	9	0.023	0.019	1.210	0.226
AFP ~ Growth	34SFI	-	0.091	0.004	22.850	0.000
AFP ~ Mort	34SFI	-	-0.350	0.004	-89.070	0.000
AFP ~ Ing	34SFI	10	0.360	0.003	113.147	0.000

(d) Needle-leaved evergreen

Regressions	Period	Constants	Estimate	Std. error	*Z*-value	*P*(>|*z*|)
Dens ~ WAI	23SFI	-	0.360	0.015	24.295	0.000
Dens ~ TA	23SFI	1	0.023	0.009	2.528	0.011

Dens ~ SPEImin	23SFI	2	-0.087	0.009	-9.574	0.000
BA ~ WAI	23SFI	3	0.414	0.009	43.823	0.000
BA ~ TA	23SFI	-	0.071	0.014	5.173	0.000
BA ~ SPEImin	23SFI	-	0.014	0.019	0.741	0.458
Size ~ WAI	23SFI	-	0.231	0.013	18.396	0.000
Size ~ TA	23SFI	-	-0.012	0.014	-0.904	0.366
Size ~ SPEImin	23SFI	-	0.094	0.019	4.922	0.000
Ineq ~ WAI	23SFI	-	-0.001	0.016	-0.055	0.956
Ineq ~ TA	23SFI	-	-0.050	0.018	-2.781	0.005
Ineq ~ SPEImin	23SFI	-	-0.103	0.025	-4.063	0.000
Ing ~ WAI	23SFI	-	0.201	0.008	25.054	0.000
Ing ~ TA	23SFI	-	0.033	0.007	4.422	0.000
Ing ~ SPEImin	23SFI	-	-0.085	0.011	-8.034	0.000
Ing ~ Dens	23SFI	-	0.937	0.010	93.437	0.000
Ing ~ BA	23SFI	-	-0.332	0.013	-25.186	0.000
Ing ~ Ineq	23SFI	-	0.296	0.008	35.594	0.000
Ing ~ Size	23SFI	-	0.313	0.013	23.877	0.000
Growth ~ WAI	23SFI	4	0.211	0.009	24.315	0.000
Growth ~ TA	23SFI	-	0.049	0.012	4.215	0.000
Growth ~ SPEImin	23SFI	-	-0.109	0.016	-6.626	0.000
Growth ~ Dens	23SFI	-	0.547	0.015	35.535	0.000
Growth ~ BA	23SFI	-	0.139	0.020	6.825	0.000
Growth ~ Ineq	23SFI	5	-0.299	0.011	-26.619	0.000
Growth ~ Size	23SFI	-	-0.039	0.020	-1.941	0.052
Mort ~ WAI	23SFI	-	0.227	0.014	16.261	0.000
Mort ~ TA	23SFI	-	-0.049	0.013	-3.715	0.000
Mort ~ SPEImin	23SFI	-	-0.060	0.019	-3.244	0.001
Mort ~ Dens	23SFI	-	-0.095	0.018	-5.410	0.000
Mort ~ BA	23SFI	-	0.532	0.023	23.178	0.000
Mort ~ Ineq	23SFI	6	-0.019	0.013	-1.452	0.146
Mort ~ Size	23SFI	-	-0.068	0.023	-2.959	0.003
AFP ~ Growth	23SFI	-	0.119	0.003	37.204	0.000

AFP ~ Mort	23SFI	-	-0.450	0.003	-141.700	0.000
AFP ~ Ing	23SFI	7	0.392	0.003	155.045	0.000
Dens ~ WAI	34SFI	-	0.285	0.012	24.509	0.000
Dens ~ TA	34SFI	1	0.023	0.009	2.528	0.011
Dens ~ SPEImin	34SFI	2	-0.087	0.009	-9.574	0.000
BA ~ WAI	34SFI	3	0.414	0.009	43.823	0.000
BA ~ TA	34SFI	-	-0.065	0.013	-5.229	0.000
BA ~ SPEImin	34SFI	-	-0.150	0.011	-13.631	0.000
Size ~ WAI	34SFI	-	0.180	0.013	13.456	0.000
Size ~ TA	34SFI	-	-0.093	0.012	-7.830	0.000
Size ~ SPEImin	34SFI	-	-0.011	0.011	-1.047	0.295
Ineq ~ WAI	34SFI	-	0.175	0.009	18.991	0.000
Ineq ~ TA	34SFI	-	0.041	0.008	4.969	0.000
Ineq ~ SPEImin	34SFI	-	-0.006	0.008	-0.850	0.395
Ing ~ WAI	34SFI	-	0.394	0.013	29.702	0.000
Ing ~ TA	34SFI	-	-0.051	0.010	-4.919	0.000
Ing ~ SPEImin	34SFI	-	-0.017	0.009	-1.853	0.064
Ing ~ Dens	34SFI	-	0.208	0.025	8.325	0.000
Ing ~ BA	34SFI	-	-0.064	0.018	-3.602	0.000
Ing ~ Ineq	34SFI	-	0.014	0.024	0.576	0.565
Ing ~ Size	34SFI	-	-0.066	0.018	-3.742	0.000
Growth ~ WAI	34SFI	4	0.211	0.009	24.315	0.000
Growth ~ TA	34SFI	-	-0.061	0.009	-6.610	0.000
Growth ~ SPEImin	34SFI	-	-0.008	0.008	-0.927	0.354
Growth ~ Dens	34SFI	-	0.217	0.019	11.577	0.000
Growth ~ BA	34SFI	-	0.413	0.014	29.107	0.000
Growth ~ Ineq	34SFI	5	-0.299	0.011	-26.619	0.000
Growth ~ Size	34SFI	-	-0.101	0.015	-6.662	0.000
Mort ~ WAI	34SFI	-	0.174	0.015	11.528	0.000
Mort ~ TA	34SFI	-	0.042	0.012	3.435	0.001
Mort ~ SPEImin	34SFI	-	0.017	0.011	1.576	0.115
Mort ~ Dens	34SFI	-	0.119	0.025	4.688	0.000

Mort ~ BA	34SFI	-	0.394	0.019	20.855	0.000
Mort ~ Ineq	34SFI	6	-0.019	0.013	-1.452	0.146
Mort ~ Size	34SFI	-	-0.008	0.021	-0.365	0.715
AFP ~ Growth	34SFI	-	0.165	0.004	43.741	0.000
AFP ~ Mort	34SFI	-	-0.483	0.003	-149.014	0.000
AFP ~ Ing	34SFI	7	0.392	0.003	155.045	0.000

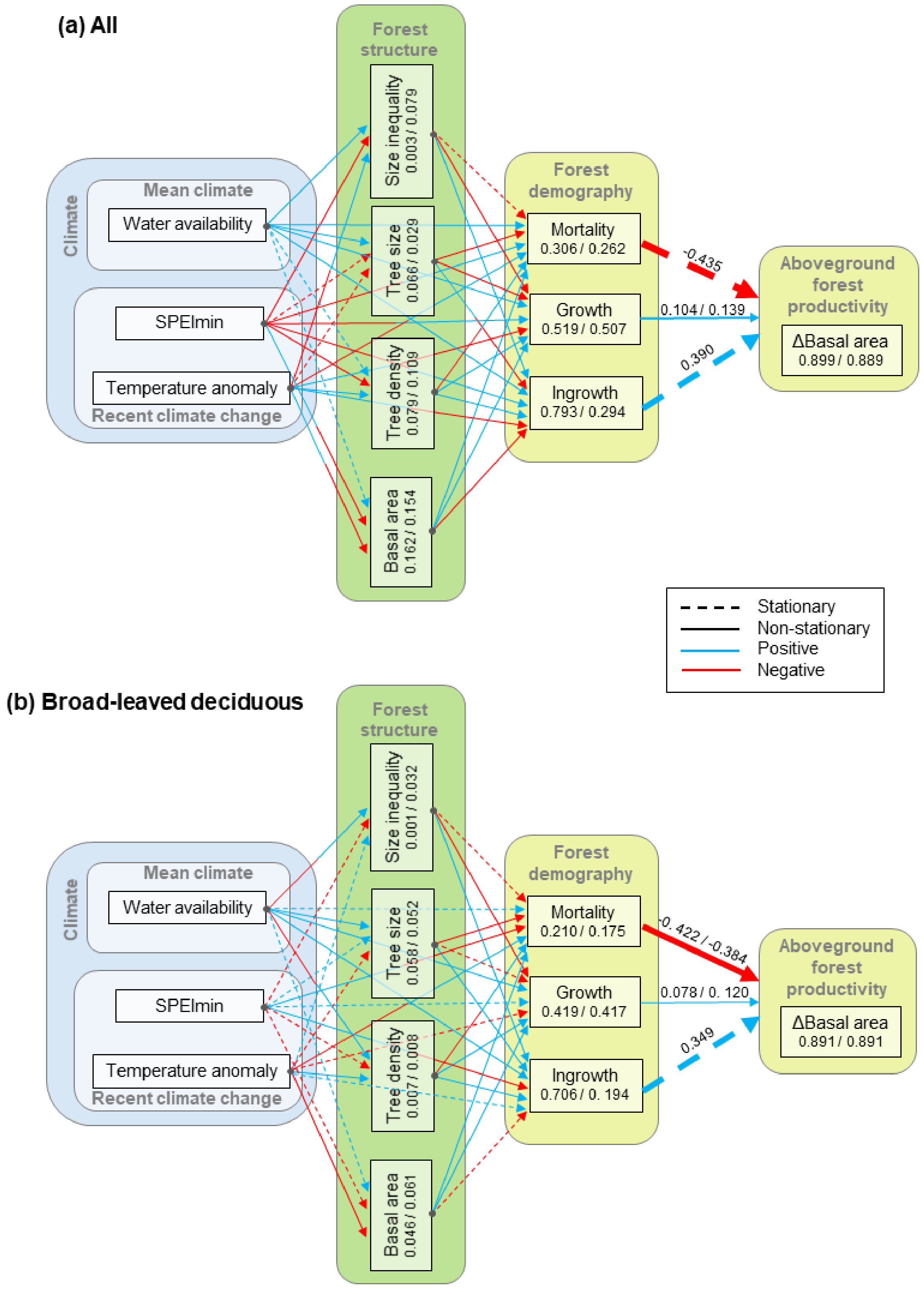
Table 3.S4.3. Direct and indirect effects of (a) water availability (WAI), (b) temperature anomalies (TA), and (c) 18-month minimum SPEI (SPEImin) in ingrowth, growth and mortality over two consecutive time periods: 23SFI and 34SFI. The indirect effects are modulated by forest structure: density (Dens), basal area (BA), tree size (Size) and tree size inequality (Ineq). The total effects for each period are the sum of the direct (Dir) and indirect effects.

(a) WAI23				**WAI34**			
	Ingrowth	Growth	Mortality		Ingrowth	Growth	Mortality
Dens	0.243	0.135	-0.020	Dens	0.066	0.044	0.023
BA	-0.092	0.093	0.211	BA	-0.028	0.188	0.151
Size	0.058	-0.018	-0.025	Size	-0.011	-0.018	-0.004
Ineq	0.004	-0.004	0.000	Ineq	0.017	-0.045	-0.006
Dir	0.183	0.169	0.202	Dir	0.363	0.207	0.144
Total23	**0.397**	**0.375**	**0.367**	**Total34**	**0.408**	**0.375**	**0.308**

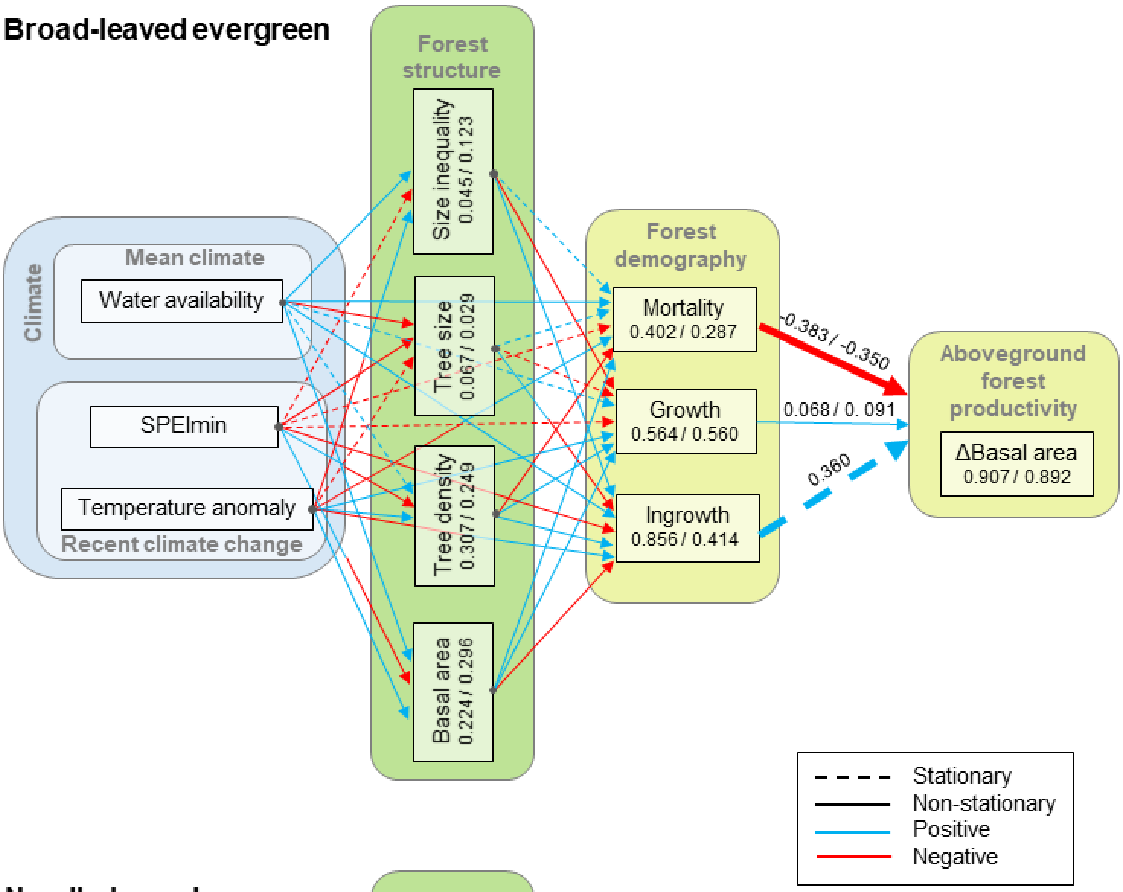
(b) TA 23SFI				**TA 34SFI**			
	Ingrowth	Growth	Mortality		Ingrowth	Growth	Mortality
Dens	0.135	0.075	-0.011	Dens	0.016	0.011	0.006
BA	-0.024	0.024	0.054	BA	0.002	-0.014	-0.011
Size	-0.028	0.009	0.012	Size	0.010	0.017	0.003
Ineq	-0.012	0.010	0.001	Ineq	0.004	-0.009	-0.001
Dir	0.035	0.085	-0.034	Dir	-0.015	-0.021	0.078
Total23	**0.106**	**0.202**	**0.021**	**Total34**	**0.017**	**-0.017**	**0.074**

(c) SPEImin 23SFI				**SPEImin 34SFI**			
	Ingrowth	Growth	Mortality		Ingrowth	Growth	Mortality
Dens	-0.005	-0.003	0.000	Dens	-0.016	-0.011	-0.006

BA	-0.006	0.006	0.014	BA	0.006	-0.042	-0.034
Size	-0.004	0.001	0.002	Size	0.002	0.003	0.001
Ineq	-0.021	0.017	0.002	Ineq	-0.001	0.002	0.000
Dir	-0.034	-0.036	-0.019	Dir	0.002	0.041	0.018
Total23	**-0.071**	**-0.014**	**-0.001**	**Total34**	**-0.007**	**-0.007**	**-0.021**


(a) All
Forest structure
Size inequality 0.003 / 0.079
Tree size 0.066 / 0.029
Tree density 0.079 / 0.109
Basal area 0.162 / 0.154
Climate
Mean climate
Water availability
SPEImin
Temperature anomaly
Recent climate change
Forest demography
Mortality 0.306 / 0.262
Growth 0.519 / 0.507
Ingrowth 0.793 / 0.294
-0.435
0.104 / 0.139
0.390
Aboveground forest productivity
ΔBasal area 0.899 / 0.889
Stationary
Non-stationary
Positive
Negative
(b) Broad-leaved deciduous
Forest structure
Size inequality 0.001 / 0.032
Tree size 0.058 / 0.052
Tree density 0.007 / 0.008
Basal area 0.046 / 0.061
Climate
Mean climate
Water availability
SPEImin
Temperature anomaly
Recent climate change
Forest demography
Mortality 0.210 / 0.175
Growth 0.419 / 0.417
Ingrowth 0.706 / 0. 194
-0. 422 / -0.384
0.078 / 0. 120
0.349
Aboveground forest productivity
ΔBasal area 0.891 / 0.891

(c) Broad-leaved evergreen



(d) Needle-leaved evergreen

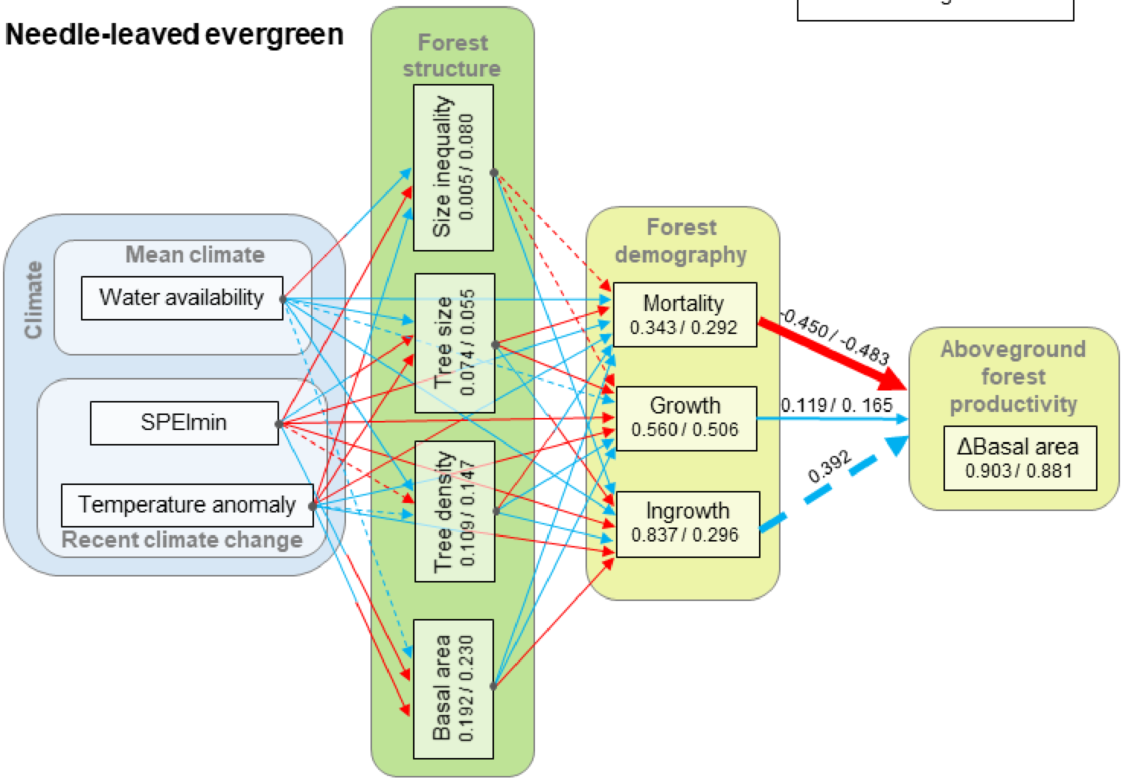


Figure 3.S4.1. Multigroup structural equation models representing the relationships between climate, forest structure, demography and aboveground productivity from 23SFI to 34SFI in (a) all, (b) broad-leaved deciduous, (c) broad-leaved evergreen and (d)

needle-leaved evergreen forests. Variables are grouped in four categories characterising climate (blue box), forest structure (green box), forest demography and aboveground forest productivity (yellow boxes). Arrows indicate causal relationships between variables based on the theoretical model (Fig. 3.1). Dashed lines illustrate stationary effects (i.e., time stable effects from 23SFI to 34SFI) and continuous lines indicate the opposite. Blue lines show positive effects and red lines show negative effects. Note that the same arrow represents the time stability from 23SFI to 34SFI so an arrow can change magnitude and sign (e.g., showing two colours). The estimated coefficients for ingrowth, growth and mortality are provided above their corresponding arrows and the thickness of these arrows have been scaled based on those magnitudes. The R^2 of the models in each period are shown below each response variables (i.e., R^2, 23SFI / 34SFI)

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Supporting information of Chapter 4: Anthropogenic legacies underpin climate change-related risks to forests

The case study of Scots pine (*Pinus sylvestris* L.)

Spanish Forest Inventory and climate data

We selected all trees in permanent stands in the third Spanish Forest Inventory census in which *Pinus sylvestris* had ≥ 50% of basal area (142340 *Pinus sylvestris* trees in 5418 stands, representing 14.7% of all trees). We obtained the natural or planted character of each stand using the Spanish Regions of Provenance for Forest Species (hereafter SRP, see Alía et al. 2005). This database determines the origin of the species (i.e., natural or planted during the 20th century) based on historical information (Ceballos 1966) and available phenotypic, genetic, and environmental information (Alía et al. 2009). Thus, joining the selected *Pinus sylvestris* stands with the SRP database, we determined the natural or planted origin of the stands (Ruiz-Benito, Gómez-Aparicio, and Zavala 2012) (96241 natural individuals located in 3966 stands and 46099 planted individuals located in 1452 stands).

We obtained forest structure variables using information from the second and third Spanish Forest Inventory censuses. This allowed us to have the broadest possible structural representation of the analysed stands. We calculated stand-level tree density (No. trees ha^{-1}), basal area (m^2 ha^{-1}), mean d.b.h. (mm), mean height (m), coefficient of variation of d.b.h. (adimensional), coefficient of variation of height (adimensional), the ratio height:d.b.h (adimensional), species richness (No. of species), recruitment (No. trees ha^{-1}) and tree vigour (categorical variable ranging from one, meaning healthy tree, to six, meaning dead standing but non-rotten tree, calculated as the mean value from the tree level quality index, see Moreno-Fernández et al. 2019). Using all forest structure variables, we performed a cluster analysis considering all planted and natural stands (clusters thereafter are referred as forest structural typologies). Then, we obtained a variable that related the natural or planted origin of the stand and the forest structural typology to which that stand belonged (thereafter legacy type).

Drought conditions were characterised using 12-month SPEI for the period between the inventory censuses (adimensional) with a 0.5 degrees spatial resolution from SPEIbase v2.5 (Vicente-Serrano, Beguería, and López-Moreno 2010) (Fig. 4.S5a). Water availability index was calculated as the difference between annual precipitation and potential evapotranspiration with respect to potential evapotranspiration (i.e. (annual precipitation – PET) / PET, %) for the period 1970-2000 with a 1 km^2 spatial resolution using data from WorldClim 2 (Fick and Hijmans 2017) and Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2 (Trabucco and Zomer 2019) (Fig. 4.S5b).

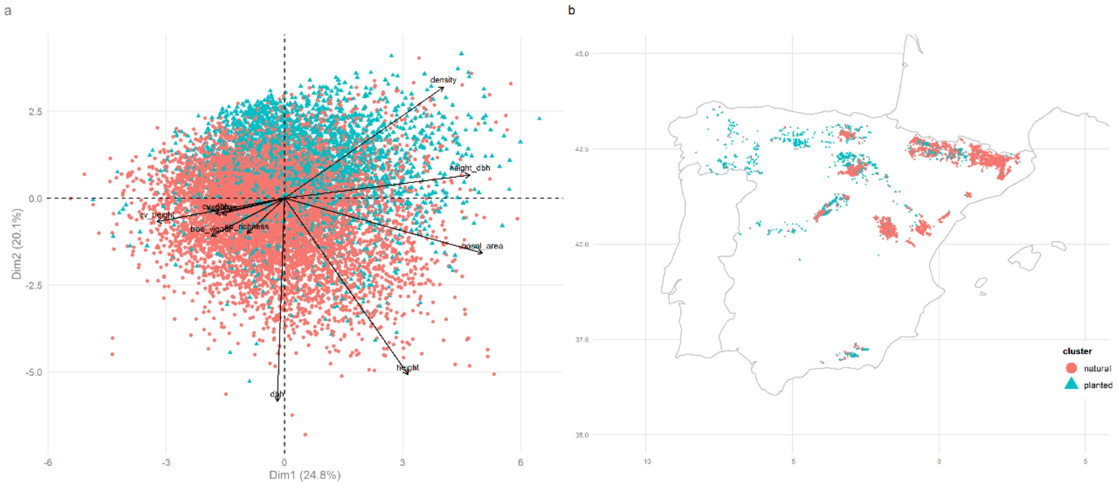

Figure 4.S1. (a) Distribution of inventory plots (classified according to SRP) over the two first dimensions of the cluster analyses for forest structural variables. The contribution of each variable to each dimension is shown by the direction and length of the arrows. (b) Map showing the geographic distribution of SRPs.

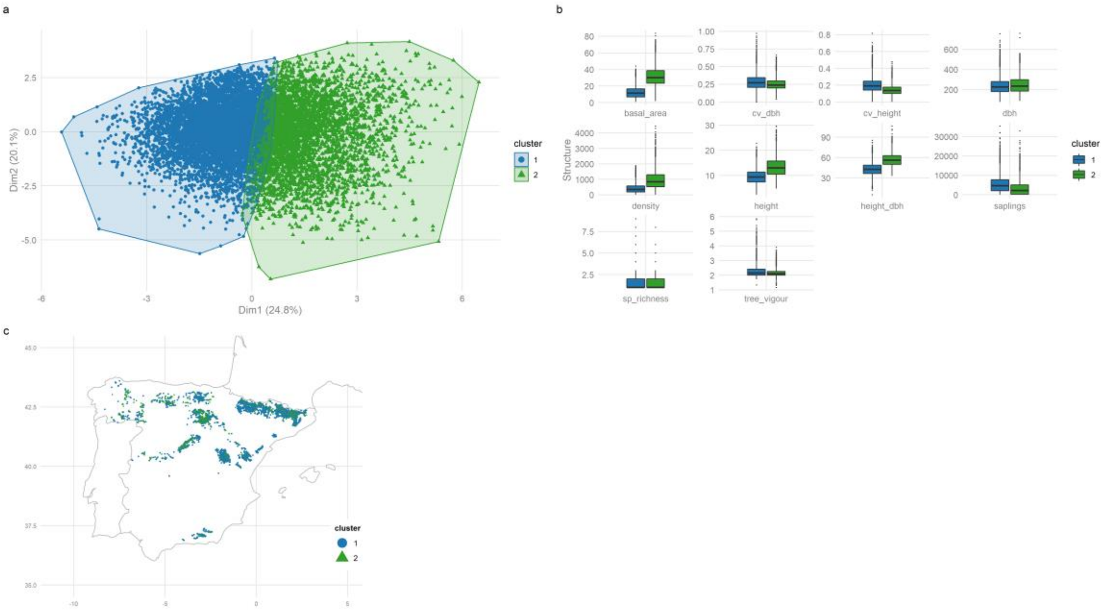

Figure 4.S2. (a) Distribution of inventory plots (classified according to the two main forest structural typologies) over the two first dimensions of the cluster analyses for forest structural variables. (b) Boxplots showing the distribution of forest structural variables within each forest structural typology. (c) Geographic distribution of inventory plots classified according to their corresponding forest structural typology.

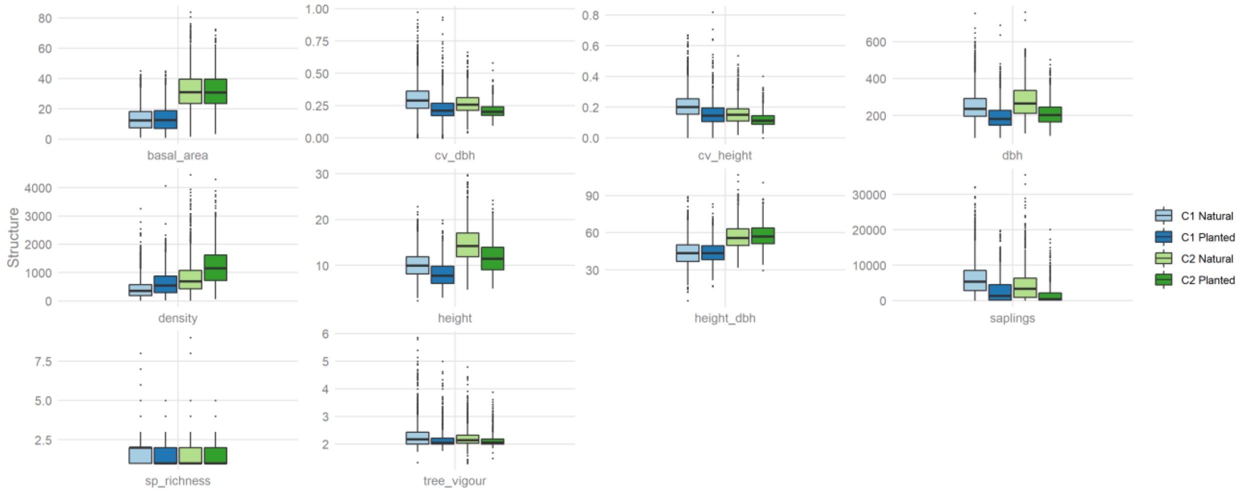

Figure 4.S3. Boxplots showing the distribution of forest structural variables within each legacy type (stand character × forest structural typology).

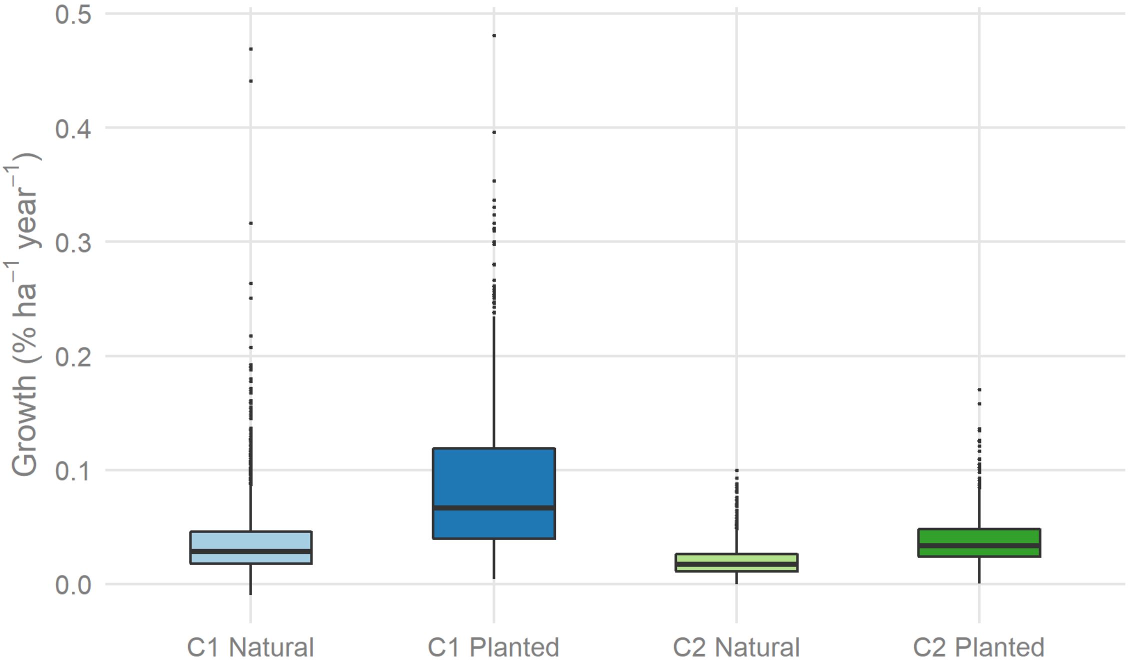

Figure 4.S4. Growth rate for each legacy type (stand character × forest structural typology) during the study period.

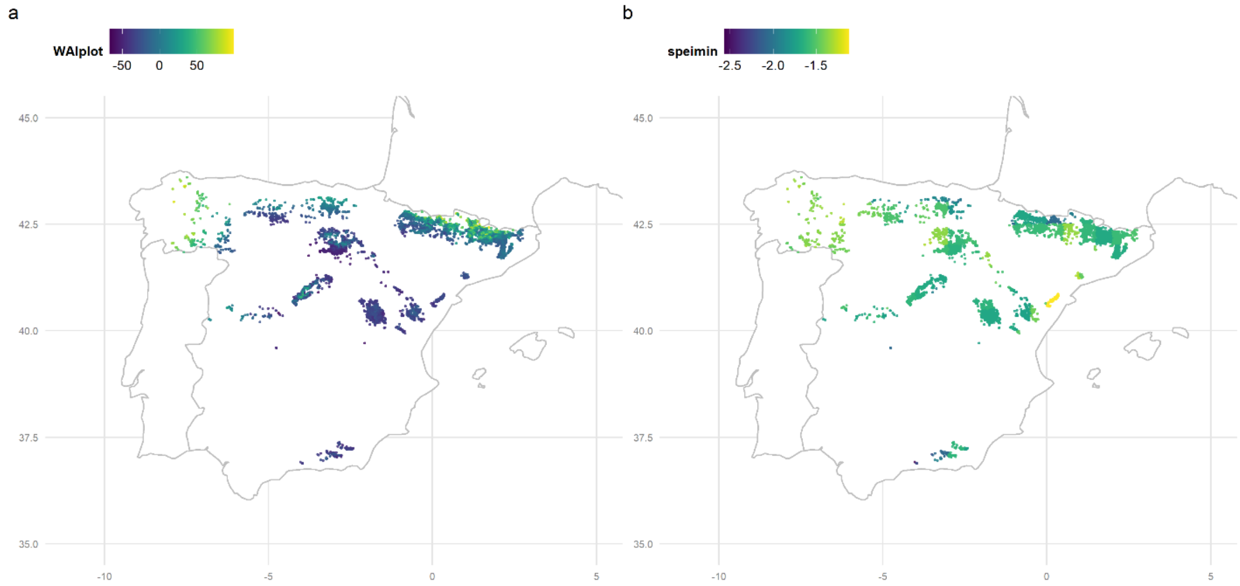

Figure 4.S5. Geographic distribution of climatic variables: (a) water availability index (WAIplot, %), (b) drought (SPEImin).

Statistical models of tree mortality depending on anthropogenic legacy effects and climate

We fitted hurdle-gamma models using the *glmmTMB* R package (Brooks et al. 2022). We modelled tree mortality in each stand relative to the initial basal area of the stand and considering the time elapsed between consecutive censuses as a function of legacy type, water availability index, SPEI and their interactions with a *ziGamma* conditional error distribution using a log link. We filtered plots with more than one individual. On stands where there was no evidence of cuts between consecutive censuses, mortality of absent and present trees was used and on stands where there was evidence of cuts between censuses only mortality of present trees was used. We included a zero-inflation model with the same fixed variables as for the conditional model. The predictor variables were not strongly collinear (Fig. 4.S6) and model residuals were diagnosed using *DHARMa* R package (Hartig 2022) (Fig. 4.S7).

We used predictive comparisons by applying a reduction of 18.435 of water availability index and 0.069 of SPEI to all the current stand conditions (Gelman and Pardoe 2007). Units for reducing the water availability index and SPEI were selected as the difference between the median and the first quantile of each variable when analysing all stands together. We also compared the observed mortality with the predicted mortality of the model for each legacy type (Fig. 4.3A in Box 4.1).

We analysed transitions between structural typologies between the second and the third Spanish Forest Inventory censuses (Table 4.S1) and we found that transitions mainly occurred from C1 to C2. Thus, we made predictions accounting for a scenario of stand development (i.e., setting all natural and planted stands as C2) while reducing water availability index and SPEI by 18.435 and 0.069, respectively (Fig. 4.3B in Box 4.1) and compared these predictions to the observed tree mortality.

All analyses were performed using R Statistical Software (v4.2.0; R Core Team 2022) and in addition to the above-mentioned R packages we also used *tidyverse* (Wickham 2021), *here* (Müller 2020), patchwork (Pedersen 2020), *sf* (Pebesma 2022), *viridis* (Garnier 2021), *corrr*

(Kuhn, Jackson, and Cimentada 2020), *bbmle* (Bolker and R Development Core Team 2022), *MASS* (Ripley 2022), *performance* (Lüdecke et al. 2022), *ggdist* (Kay 2022), *RColorBrewer* (Neuwirth 2022), *testthat* (Wickham 2022), *factoextra* (Kassambara and Mundt 2020), *RColorBrewer* (Neuwirth 2022), *ggh4x* (van den Brand 2021), *janitor* (Firke 2021), *gt* (Iannone, Cheng, and Schloerke 2022) packages for data processing, analyses and visualisation.

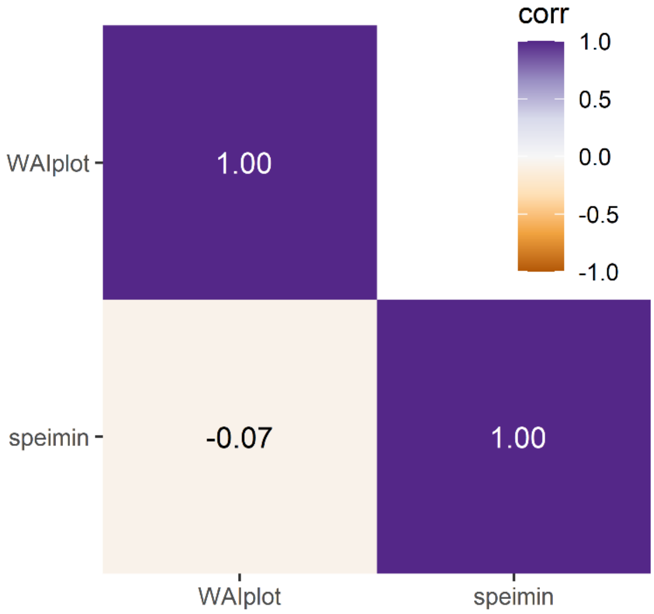

Figure 4.S6. Correlations between water availability index and drought (WAIplot and SPEImin) used as covariates in the statistical analyses.

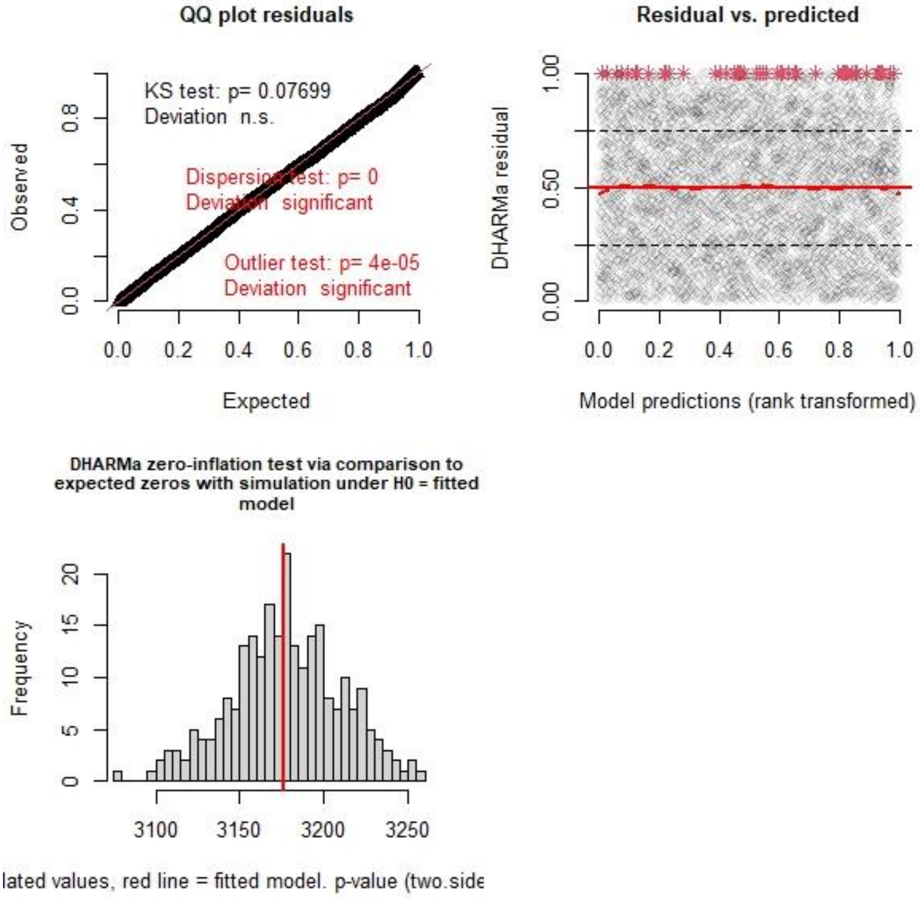

Figure 4.S7. Model evaluation of the tree mortality model when regressed on anthropogenic legacies and climate showing a qqplot of the residuals, residuals versus predicted and a zero-inflation test.

Table 4.S1. Number of plots with transitions among forest structural typologies from the first to the second forest inventory census.

	3SFI C1	3SFI C2
2SFI C1	2787	643
2SFI C2	148	1584

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Supporting information of Chapter 5: Land- and forest-use legacies modulate tree growth synchrony in response to climate change through changes in forest structural diversity

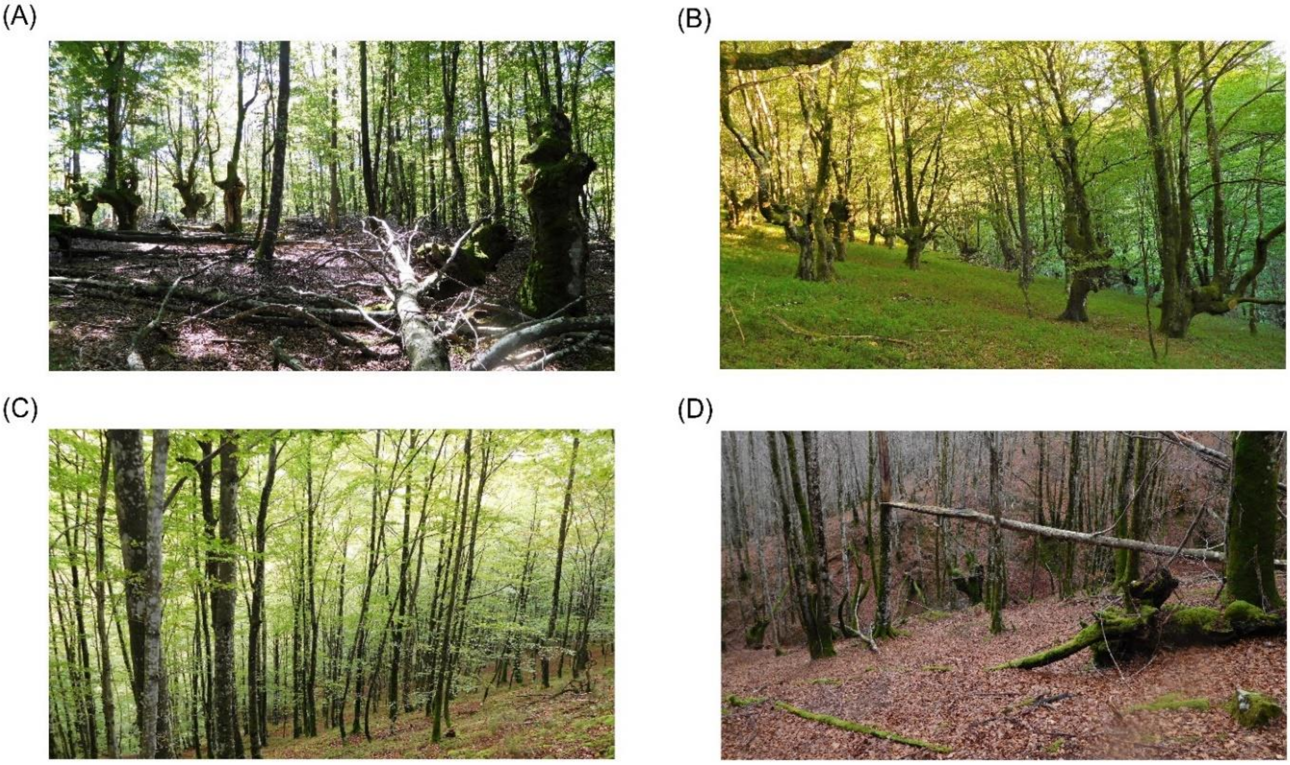
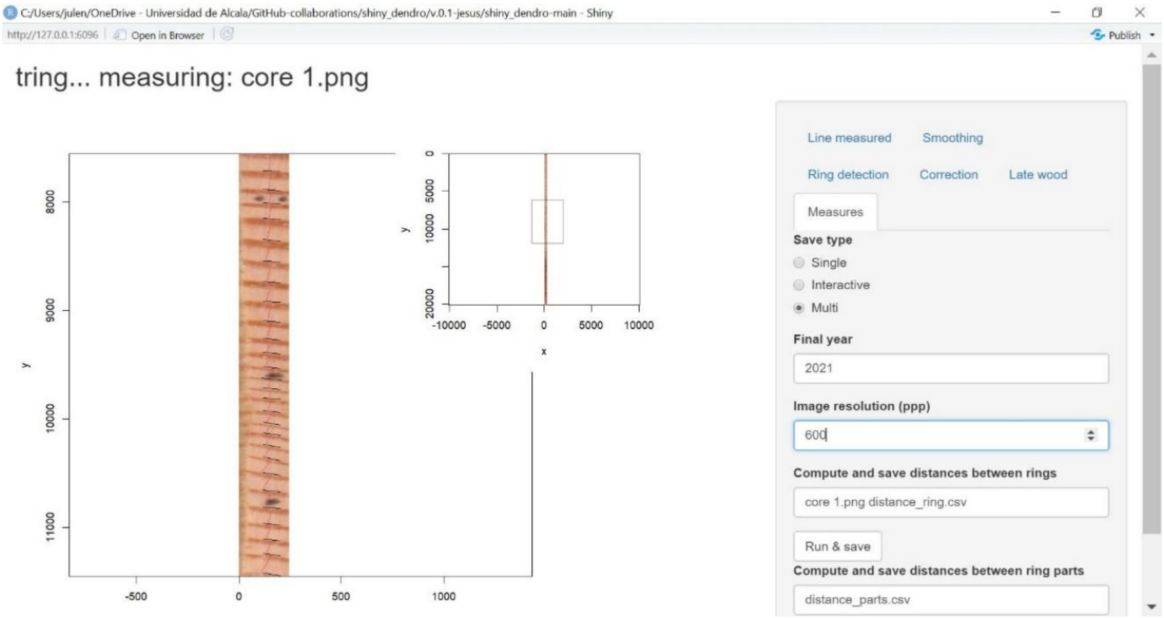


Figure 5.S1. Examples of (A) recently-pruned pollard; (B) long-pruned pollard; (C) recently-established; and (D) long-established stands.



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http://127.0.0.1:6096

tring... measuring: core 1.png

Save type

○ Single

○ Interactive

● Multi

Final year: 2021

Image resolution (ppp): 600

Compute and save distances between rings: core 1.png distance_ring.csv

Compute and save distances between ring parts: distance_parts.csv

Figure 5.S2. Example of a tree core measured with *trini* R package (Astigarraga et al., 2022).

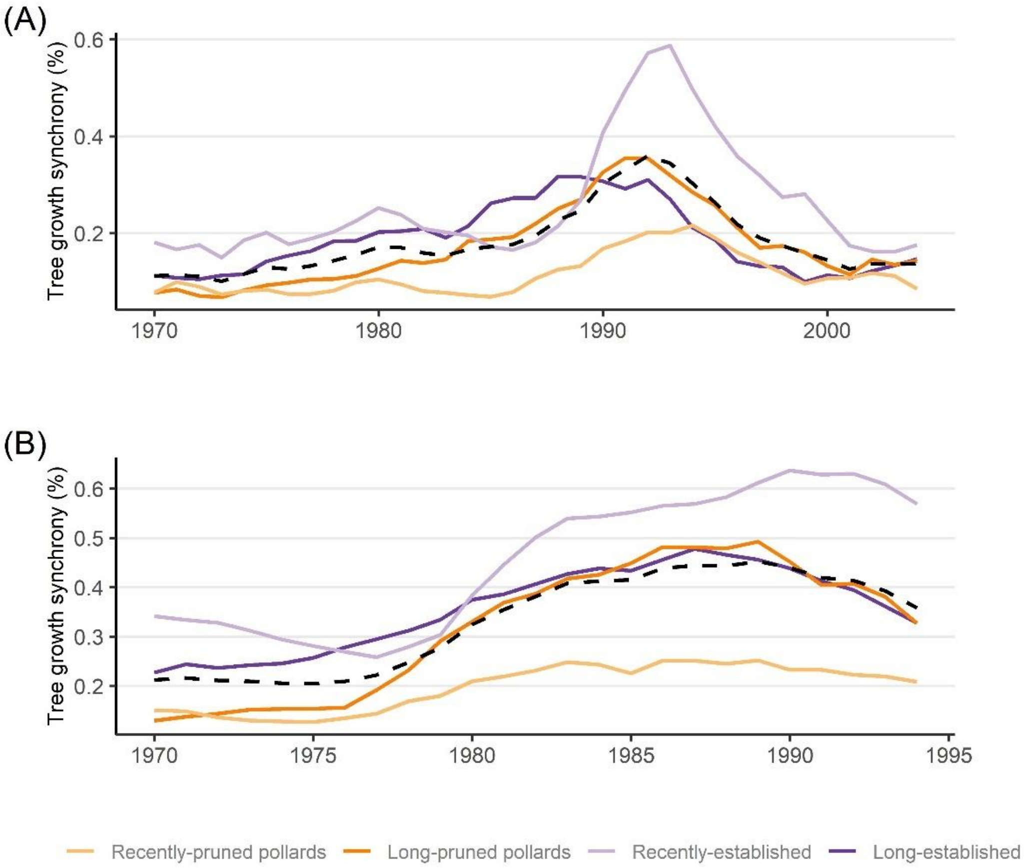

Figure 5.S3. Tree growth synchrony with (A) 15-years; and (B) 25-years time windows.

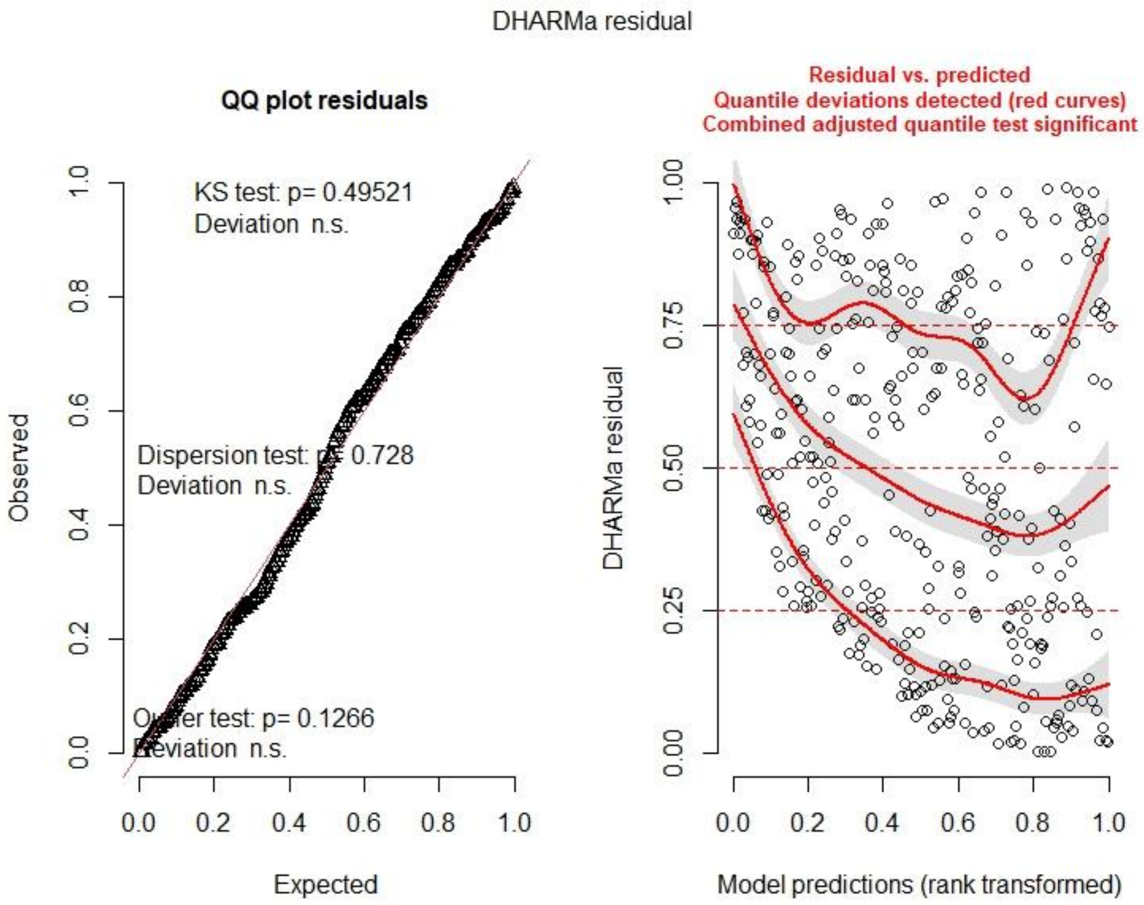

Figure 5.S4. Model evaluation of tree growth synchrony model when regressed on number of late spring frosts, number of heatwaves, total precipitation, tree size heterogeneity and mean tree size showing a qqplot of the residuals and residuals versus predicted.

References

Astigarraga, J., Calatayud, J., & Cruz-Alonso, V. (2022). *trini*. Zenodo. https://doi.org/10.5281/zenodo.7193360

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Julen

Curriculum vitae

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Land line phone:	**688618777**

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Academic & research training

2019-present	**PhD in Ecology, Conservation and Ecosystem Restoration.** Universidad de Alcalá. FPI fellowship of the Department of Education of the Basque Government (Programa Predoctoral de Formación de Personal Investigador No Doctor del Departamento de Educación del Gobierno Vasco)
2017-2019	**MSc in Ecology.** 9.1/10. Extraordinary Prize. Universidad Autónoma de Madrid and Universidad Complutense de Madrid
2018	**Research assistant in Charles Darwin University's Research Institute for the Environment and Livelihoods** (Darwin, Australia). Global training scholarship of the Basque Government
2012-2016	**Bachelor’s Degree in Geography and Land Use.** 8.2/10. Universidad del País Vasco / Euskal Herriko Unibertsitatea
2016	**Internship at Aranzadi Science Society**
2015	**Erasmus + scholarship at the University of Eastern Finland**

Short stays at research institutions

2022	**Facultad de Biología. Universidad de Sevilla.** Sevilla. Spain. 18/04/2022-18/07/2022 (3 months). Tutor: Francisco Rodríguez Sánchez. Analysis of North American and European forest inventory data. Data preparation of European beech growth synchrony
2021	**University of Birmingham. School of Geography, Earth and Environmental Sciences.** Birmingham. United Kingdom. 07/06/2021-07/09/2021 (3 months). Tutors: Adriane Esquivel Muelbert and Thomas Pugh. Conceptualisation and exploratory analyses of North American and European forest inventory data

Publications

Articles with Science Citation Index published

- **Astigarraga, J.**, Andivia, E., Zavala, M. A., Gazol, A., Cruz-Alonso, V., Vicente-Serrano, S. M., & Ruiz-Benito, P. (2020). Evidence of non-stationary relationships between climate and forest responses: Increased sensitivity to climate change in Iberian forests. *Global Change Biology*, *26*(9), 5063–5076. https://doi.org/10.1111/gcb.15198
- **Astigarraga, J.**, & Cruz-Alonso, V. (2022). ¡Se puede entender cómo funcionan Git y GitHub! *Ecosistemas*, *31*(1). https://doi.org/10.7818/ECOS.2332
- Tijerín-Triviño, J., Moreno-Fernández, D., Zavala, M. A., **Astigarraga, J.**, & García, M. (2022). Identifying Forest Structural Types along an Aridity Gradient in Peninsular Spain: Integrating Low-Density LiDAR, Forest Inventory, and Aridity Index. *Remote Sensing*, *14*(1), 235. https://doi.org/10.3390/rs14010235
- Ruiz-Benito, P., Andivia, E., Archambeaou, J., **Astigarraga, J.**, Barrientos, R., Cruz-Alonso, V., Florencio, M., Gómez, D., Martínez-Baroja, L., Quiles, P., Rohrer, Z., Santos, A. M. C., Velado, E., Villén-Pérez, S., & Morales-Castilla, I. (2018). Ventajas de la estadística bayesiana frente a la frecuentista: ¿por qué nos resistimos a usarla? *Ecosistemas*, *27*(2), 136–139. https://doi.org/10.7818/ECOS.1591

Articles submitted or to be submitted

- Vilà-Cabrera, A.*, **Astigarraga, J.***, Jump, A. S., Zavala, M. A., Seijo, F., Sperlich, D., & Ruiz-Benito, P.* (under review). Anthropogenic Legacies Underpin Climate Change-Related Risks to Forests. *Trends in Plant Science*. * These authors led the manuscript
- **Astigarraga, J.**, Esquivel-Muelbert, A., Ruiz-Benito, P., Rodríguez-Sánchez, F., Zavala, M. A., Gazol, A., Vilà-Cabrera, A., Schelhaas, M. J., Cienciala, E., Dahlgren, J., Govaere, L., König, L., Kunstler, G., Lehtonen, A., Talarczyk, A., Woodall, C. W., & Pugh, T. A. P. In preparation. Recent dynamics of Northern Hemisphere tree species along climatic and successional gradients (target journal: *PNAS*)
- **Astigarraga, J.**, Calatayud, J., Ruiz-Benito, P., Madrigal-González, J., Rodríguez-Sánchez, F., Tijerín-Triviño, J., Zavala, M. A., Andivia, E., & Herrero, A. In preparation. Land- and forest-use legacies modulate tree growth synchrony in response to climate change through changes in forest structural diversity (target journal: *Ecosystems* / *Agricultural and Forest Meteorology*)
- **Astigarraga, J.**, Calatayud, J., & Cruz-Alonso, V. (2022). *trini*. Zenodo. https://doi.org/10.5281/zenodo.7193360

- Cruz-Alonso, V., Pucher, C., Ratcliffe, S., Ruiz-Benito, P., **Astigarraga, J.**, Neumann, Hasenauer, H., & Rodríguez-Sánchez, F. (under review). The *easyclimate* R package: easy access to high-resolution daily climate data for Europe. *Environmental Modelling and Software*
- Esquivel-Muelbert, A.… Ruiz Benito, P, Zavala, M. A., **Astigarraga, J.**, & Pugh. T.A.M. In preparation. Remarkable disequilibrium across Earth's forests (target journal: *Science*)
- Bordin, K. M., Müller, S.C., Pugh, T. A. M., Phillips O. L., Fortunel, C., Schietti, J., Needham, J. F., Woodall, C. W., **Astigarraga, J.**, Bialic-Murphy, L., Liu, D., Suvanto, S., & Esquivel-Muelbert, A. In preparation. Growth-mortality strategies across temperate tree species and their relationship with functional traits (target journal: *Nature Ecology and Evolution / PNAS*)
- Bernardo-Madrid, R., González-Suárez, M., **Astigarraga, J.**, Rueda, M., & Calatayud, J. In preparation. Biogeographical roles: novel biodiversity patterns emerging at bioregion scale converging across the tree of life (target journal: *Nature Ecology and Evolution / Nature communications*)
- Serra-Malaquer, X., Godoy, O., Ruiz-Benito, P., Rodríguez-Sánchez, F., González-Díaz, P., **Astigarraga, J.**, Tijerín-Triviño, J., & Rueda, M. In preparation. Tree biodiversity and ecosystem function across North America (target journal: *PNAS*)
- Rebollo Orozco, P., Moreno-Fernández, D., Cruz-Alonso, V., Zavala, M. A., Gazol, A., Gómez-Aparicio, L., Andivia, E., **Astigarraga, J.**, & Ruiz Benito, P. In preparation. The role of climate and structural characteristics in spatial patterns of tree mortality and damage in Mediterranean forests (target journal: *Agricultural and Forest Meteorology*)

Books

- González-Díaz, P., Ruiz-Benito, P., **Astigarraga, J.**, Cruz-Alonso, V., Moreno-Fernández, D., Herrero, A., Gosálbez, J., & Zavala, M. A. (2020): *Los bosques españoles como soluciones naturales frente al cambio climático: herramientas de análisis y modelización*. Oficina Española de Cambio Climático. Ministerio para la Transición Ecológica y el Reto Demográfico, Madrid

Software

- **Astigarraga, J.**, Calatayud, J., & Cruz-Alonso, V. (2022). *trini*. Zenodo. https://doi.org/10.5281/zenodo.7193360
- Cruz-Alonso, V., Pucher, C., Ratcliffe, S., Ruiz-Benito, P., **Astigarraga, J.**, Neumann, Hasenauer, H., & Rodríguez-Sánchez, F. (under review). The easyclimate R package: easy access to high-resolution daily climate data for Europe. *Environmental Modelling and Software*

Other non-SCI publications

- Herrero, A., **Astigarraga, J.**, Cruz-Alonso, V. (2021). Zuhaitz motzak: iraganeko ustiapenaren aztarnak gaurko basoetan. Árboles trasmochos: el legado del manejo del pasado en los bosques actuales. *Pyrenaica*. 284, ISSN 0212-5676

Participation in research projects

- *Forest management legacies as a modulator of tree growth responses to climate change*. Municipality of Oñati. 2020-2023. PI: **J. Astigarraga**. 4,155.72€
- *IBerian FORest responses to climate change across spatio-temporal scales: hotspots and roles of structural and functional RESilience (IB-ForRes)*. Subproject 1: “Combinando inventarios y trabajo de campo para identificar las causas y consecuencias de los puntos calientes de cambio climático / Combining inventories and field data to identify causes and consequences of hotspots to climate change (LARGE)”. Ministerio de Ciencia e Innovación. Proyectos Generación de Conocimiento 2021. 2022-2025. PI: P. Ruiz Benito, Miguel A. Zavala Gironés. Total subproject 1: 133,100 €
- *Effect of climate change on the structure and dynamics of Iberian forests*. Becas Leonardo a Investigadores y Creadores Culturales 2018, Fundación BBVA. 2018-2020. PI: P. Ruiz Benito. 38,989.67€
- *Data-driven models of forest drought vulnerability and resilience across spatial and temporal scales: application to the Spanish climate change adaptation strategy (DARE)*. Ministerio de Ciencia, Innovación y Universidades. Proyecto Retos Coordinados. 2019-2022. PI: M. A. Zavala. 96,000€
- *Evaluación de la dinámica espacio-temporal de los daños forestales en bosques ibéricos*. Ayudas para la realización de Proyectos para Potenciar la Creación y Consolidación de Grupos de Investigación. Programa propio de la Universidad de Alcalá 2020. 2020-2021. PI: P. Ruiz Benito. 6,000€

Assisted conferences

As speaker

- **Astigarraga, J.**, Andivia, E., Zavala, M. A., Gazol, A., Cruz-Alonso, V., & Ruiz-Benito P. Temporal changes in Iberian forest structure, dynamics and composition in the last 35 years. In: *I Sibecol Meeting and XIV AEET meeting*. Barcelona. 2019.
- **Astigarraga, J.**, Andivia, E., Zavala, M. A., Gazol, A., Cruz-Alonso, V., Vicente-Serrano, S. M., & Ruiz-Benito, P. Evaluación de los cambios en la estructura, la dinámica y la composición de los bosques ibéricos españoles. In: *SECF. IV reunión del grupo de Ecología, Ecofisiología y Suelos forestales*. Alcalá de Henares. 2019

- **Astigarraga, J.**, Andivia, E., Zavala, M. A., Gazol, A., Cruz-Alonso, V., Vicente-Serrano, S. M., & Ruiz-Benito, P. Evaluation of changes in the structure and dynamics of Spanish Iberian forests using 30 years of information from Spanish Forest Inventory. In: *Jornada científico-técnica del Grupo de trabajo Ibérico de Inventario y Teledetección*. Madrid. 2019
- **Astigarraga J.**, Zavala, M. A., Seijo, F., Vilà-Cabrera, A., & Ruiz-Benito, P. Anthropogenic forest-use legacies underlie Mediterranean forest vulnerability to climate change. In: *Managing Forests in the 21st century*. Potsdam. 2020
- **Astigarraga, J.**, Esquivel-Muelbert, A., Ruiz-Benito, P., Zavala, M. A., Gazol, A., Schelhaas, M. J., Cienciala, E., Dahlgren, J., Govaere, L., König, L., Kunstler, G., Lehtonen, A., Talarczyk, A., Woodall, C. W., & Pugh, T. A. M. Climatic influence on tree species demographic performance across temperate forests. In: *XV Congreso Nacional de la AEET*. Plasencia. 2021
- **Astigarraga, J.**, Esquivel-Muelbert, A., Ruiz-Benito, P., Rodríguez-Sánchez, F., Zavala, M. A., Gazol, A., Vilà-Cabrera, A., Schelhaas, M. J., Cienciala, E., Dahlgren, J., Govaere, L., König, L., Kunstler, G., Lehtonen, A., Talarczyk, A., Woodall, C. W., & Pugh, T. A. M. Tree species climatic affiliation determines demographic balance across mature Northern Hemisphere forests. In: *Transforming our understanding of global forests - 2022 BIFoR sixth annual Community Meeting*. Birmingham. 2022

As co-author

- Vilà-Cabrera, A., **Astigarraga, J.**, Jump, A. S., Zavala, M. A., Seijo, F., Sperlich, D., & Ruiz-Benito, P. Forest Management Legacies in a Warming World. In: *XV Congreso Nacional de la AEET*. Plasencia. 2021
- Cruz-Alonso, V., **Astigarraga, J.**, Ratcliffe, S., Rodríguez-Sánchez, F., Ruiz-Benito, P., Andivia, A., Ballesteros-Cánovas, J. A., Herrero, A., Madrigal, J., & Calatayud, J. (2021) tring and easyclimate: two R packages to analyze long-term responses of forest ecosystems. Poster. In: *XV Congreso Nacional de la AEET*. Plasencia. 2021
- Herrero, A., Jiménez-Martínez, C., Medina-Villar, S., Cruz-Alonso, V., **Astigarraga, J.**, Laskurain, N. A. Resiliencia forestal tras el paso de un tornado: efecto de los legados materiales en la capacidad de regeneración. Poster. In: *XV Congreso Nacional de la AEET*. Plasencia. 2021
- Herrero, A., Jiménez-Martínez, C., Medina-Villar, S., Cruz-Alonso, V., **Astigarraga, J.**, Laskurain, N. A. Forest resilience after extreme winds: effect of material legacies on tree regeneration capacity. Poster. In: *64th Annual Symposium of International Association for Vegetation (IAVS).* Madrid. 2022
- Nadal-Sala, D., et al. Do Landsat satellite estimates of canopy disturbance reproduce tree mortality rates observed from forest inventories across Spain? BG3.2 – Present and future global vegetation dynamics and carbon stocks from observations and models. In: *EGU*. Vienna. 2022

- Suvanto, S., et al. Observation-based quantification of forest management in Europe. BG3.2 – Present and future global vegetation dynamics and carbon stocks from observations and models. In: *EGU*. Vienna. 2022
- Pugh, T. A. M., Scheel, M., Suvanto, S., **Astigarraga, J.**, Esquivel-Muelbert, A., Lindeskog, M., Olin, S., Papastefanou, P., Ruiz-Benito, P., Schelhaas, M.-J., Smith, B., Zavala, M. A., & the TreeMort collaboration. Drivers of changing forest dynamics in Europe. In: *Swedish Climate Symposium*. Norrköping. 2022

As listener

- SFÉ²-AEET. Conference for Early Career Scientists. Online. 2021
- AEET. I jornadas de investigadores en etapas tempranas de la carrera (ECR). Huelva. 2022

Taught courses

As teaching assistant (160 hours)

Undergraduate (146 hours)

- 2018-2019. Ecology. In: Environmental Sciences. Universidad de Alcalá
- 2018-2019. Applied techniques to fieldwork. In: Environmental Sciences. Universidad de Alcalá
- 2019-2020. Ecology. In: Environmental Sciences. Universidad de Alcalá
- 2019-2020. Applied techniques to fieldwork. In: Environmental Sciences. Universidad de Alcalá
- 2019-2020. Management and conservation of natural resources. In: Environmental Sciences. Universidad de Alcalá
- 2019-2020. Ecology and human well-being. In: Health biology. Universidad de Alcalá
- 2020-2021. Environmental criminalistics. In: Criminalistics: Sciences and Forensic Technologies. Universidad de Alcalá
- 2020-2021. Ecology. In: Environmental Sciences. Universidad de Alcalá
- 2020-2021. Applied techniques to fieldwork. In: Environmental Sciences. Universidad de Alcalá
- 2020-2021. Management and conservation of natural resources. In: Environmental Sciences. Universidad de Alcalá
- 2021-2022. Practical data science: solving environmental problems through projects. In: Optional course of Biological Sciences, Environmental Sciences, Criminalistics: Forensic Sciences and Technologies, Chemistry, Health Biology. Universidad de Alcalá

Postgraduate (14 hours)

- 2019-2020. Advanced programming. In: Master's in Geographical Information Technologies. Universidad de Alcalá

As lecturer (28 hours)

- 2020. Introduction to *R Markdown*. Coding club of the University of Birmingham. Online (1.5 hour)
- 2021. Introduction to *tidyverse*. Coding club of the University of Birmingham. Online (1.5 hour)
- 2021. Introduction to Git & GitHub. Coding club of the University of Birmingham. Online (1.5 hour)
- 2021. Introducción a Git y GitHub, dos herramientas para una ecología más colaborativa y reproducible. XV Congreso Nacional de la AEET. Plasencia (4 hours)
- 2021. Git and GitHub: tools for collaborative work and reproducible projects. Real Colegio Complutense Postdoc Seminar at Harvard University. Online (1.5 hour)
- 2022. Data handling and visualisation in R. Escuela de Doctorado de la Universidad de Alcalá. Online (8 hours)
- 2022. Introducción al análisis de datos con *tidyverse*. Ciclo de mesas redondas de estudiantes de doctorado de la Estación Biológica de Doñana. Sevilla (1.5 hour)
- 2022. Sacando el máximo partido a *tidyverse*. Grupo de usuarios de R de Sevilla. Sevilla (1.5 hour)
- 2022. Fundamentos de Git y GitHub y su aplicación en proyectos colaborativos y reproducibles en R y RStudio. Fundación Centro de Estudios Andaluces (CENTRA). Online (7 hours)

Final Bachelor's Degree Project

- 2020-2021. Impacts of climate change on European forest functions. 7.9/10. Student: Carlos García Vázquez. Supervisors: Paloma Ruiz Benito & **Julen Astigarraga Urcelay**. Universidad de Alcalá.
- 2021-2022. Forest responses to climate change and legacy. 8.5/10. Student: Alejandro Valencia Sanz. Supervisors: Paloma Ruiz Benito, **Julen Astigarraga Urcelay** & Albert Vilà Cabrera. Universidad de Alcalá.

Received courses (223 hours)

- 2018. Análisis de datos y modelos lineales en R. Universidad de Alcalá (24 hours)
- 2019. Estrategias de búsqueda y gestión de la información. Universidad de Alcalá (5 hours)
- 2019. How to write a literature review for academic researchers. Charlesworth Knowledge (5 hours)
- 2019. Introducción a *R Markdown* y *Sweave*. Universidad de Alcalá (8 hours)
- 2019. Herramientas para la visualización y presentación de datos científicos en *ggplot*. Universidad de Alcalá (20 hours)
- 2019. Optimizando el uso de R para análisis en ecología. AEET. Universidad de Girona (30 hours)
- 2019. Curso superior universitario en análisis de redes ecológicas. Universidad Rey Juan Carlos (36 hours)
- 2019. Ecología del despoblamiento rural en el contexto del cambio climático. Universidad de Zaragoza (20 hours)
- 2019. Escritura de artículos científicos. AEET. Universidad de Sevilla (24 hours)
- 2019. Introduction to Agent Based-Models Using NetLogo. Transmitting Science. Barcelona (35 hours)
- 2021. Software Carpentry Git. University of Birmingham (4 hours)
- 2021. Introduction to Linux. University of Birmingham (4 hours)
- 2021. Introduction to BlueBEAR. University of Birmingham (4 hours)

Participation in evaluation committees

Evaluator in the evaluation processes of official university degrees

- 2019-2022. Agencia para la Calidad del Sistema Universitario de Castilla y León (ACSUCYL)
- 2021. Agencia de Calidad y Prospectiva Universitaria de Aragón (ACPUA)

Reviewing experience

- 2019. *Agricultural and Forest Meteorology*: 1
- 2020. *Agricultural and Forest Meteorology*: 1
- 2020. *Agricultural and Forest Meteorology*: 1
- 2021. *Agricultural and Forest Meteorology*: 1
- 2021. *Forest systems*: 1

- 2022. *Journal of Vegetation Science*: 1

Coordination activities

- 2021-present. Grupo de Ecoinformática de la Asociación Española de Ecología Terrestre (AEET)

Outreach

- Klima aldaketaren eragina XXI. mendeko basoetan / Effects of climate change on forests in the 21st century. Speaker in*: XXV. Oñatiko Ingurumen Jardunaldiak / 25th Oñati Environmental Conference.* 2022. Watch video in: https://www.youtube.com/watch?v=4DYl6HGmmrM
- El círculo letal del cambio climático en los bosques*. El País. 2020. https://elpais.com/ciencia/2020-07-20/el-circulo-letal-del-cambio-climatico-en-los-bosques.html*
- *Onda Cero Alcalá. 2020. https://www.ondacero.es/emisoras/comunidad-madrid/alcala-de-henares/audios-podcast/mas-de-uno-alcala-13072020_202007155f0ea027f5f4b20001b97f1a.html*
- Klima basoen birsortzean / Climate in forest regeneration*. Berria. 2020. https://www.berria.eus/paperekoa/1885/016/001/2020-11-18/klima-basoen-birsortzean.htm*