







## RESEARCH ARTICLE OPEN ACCESS

# Historic Land Use Modifies Impacts of Climate and Isolation in Rear Edge European Beech (*Fagus sylvatica* L.) Populations

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## ABSTRACT

Legacies of human land use have the potential to impact demographic responses to climate. However, few studies have investigated the interactive effects of land use legacies and climate change on tree demography. The demographic performance of rear edge populations in particular is an important determinant of a species' long-term persistence. In this study, we investigated whether human land use legacies affect demographic responses to climate and population isolation in rear edge European beech populations (*Fagus sylvatica* L.) at the temperate-Mediterranean transition zone in the NE Iberian Peninsula. We utilised data from the Spanish Forest Inventory and generalised linear mixed models to compare the potential interactions across four different demographic rates (tree growth, survival probability, new adult recruitment and sapling recruitment). We found that the demographic rates were affected by the combination of land use legacies, climate and population isolation in different ways, which could potentially lead to complex shifts in future population dynamics under climate change. We identified that intense historic management either magnified negative relationships between tree demography and climate or population isolation, or reduced demographic performance in favourable climates to levels observed in unfavourable climates. Through either form of interaction, we found that intense historic forest management had a negative impact on tree demography, which has the potential to compromise future carbon stocks and long-term population viability. Overall, we show that disentangling human and environmental factors can enable us to better understand heterogeneous demographic performance across the rear edge of species distributions.

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## 1 | Introduction

Alterations to the geographic distributions of species are a major ecological impact of anthropogenic climate change (Parmesan 2006; Walther et al. 2002). Due to increasing global temperatures, many species distributions are shifting poleward and uphill (Chen et al. 2011; Parmesan and Yohe 2003), including tree species (Harsch et al. 2009). Forests cover approximately 30% of global land area and are important for carbon and hydrological cycles, microclimatic regulation and soil preservation, in addition to providing many social, cultural, health and well-being benefits (Bonan 2008; Kirschbaum 2000). Tree species play a critical role in ecological regulation by providing habitats and stable conditions for other organisms (Ellison et al. 2005). Changes to the distribution of dominant tree species may, therefore, cause cascading effects for numerous other dependent species (Dyderski et al. 2018).

A key mechanism through which species distribution shifts resulting from climate change are typically expected to occur is range retraction at the rear edge (the equatorial or low altitude margins; Jump, Mátyás, and Peñuelas 2009). This expectation of rear edge population decline follows the 'centre-periphery' hypothesis that population abundance, demographic performance and within-population genetic diversity decrease from the distribution centre towards range margins due to reduced environmental suitability. This hypothesis is based on the assumption that the periphery of species distributions represents the limits of the species' environmental tolerance, that is, assumed concordance between geographic range limits (geographic marginality) and environmental niche limits (environmental marginality; Brown 1984; Hengeveld and Haack 1982; Hutchinson 1957; Pironon et al. 2017, 2015; Sexton et al. 2009). However, in contrast with expectations of spatially consistent extinction at rear edge margins due to climate change, some evidence shows heterogeneous patterns of population performance (Jump, Mátyás, and Peñuelas 2009; Sánchez de Dios et al. 2021). Understanding the drivers of heterogeneous population performance at rear edge margins is critical to improving future predictions of species distributions, as rear edge populations can be highly locally adapted, often to warmer temperatures (Hampe and Jump 2011; Hampe and Petit 2005). Extinction of rear edge populations could therefore reduce the potential of the entire distribution to persist under climate change (Habibzadeh et al. 2021).

In contrast to the main assumption of the centre-periphery hypothesis, recent research has shown that environmental and geographic marginality can have differential effects on demographic performance (Pironon et al. 2015, 2017; Vilà-Cabrera, Premoli, and Jump 2019) and genetic diversity (Lee-Yaw, Fracassetti, and Willi 2018; Casazza et al. 2021; Picard et al. 2022). These findings suggest that the geographic distribution of species may potentially not be in equilibrium with the environmental preferences of that species, and that rear edge populations may not necessarily be performing at the limit of their environmental tolerances (Oldfather et al. 2019; Vilà-Cabrera, Premoli, and Jump 2019). Rear edge populations typically occur in bioclimatic transition zones with complex topography and high microclimatic variability (Hampe and Petit 2005; Jump, Mátyás, and Peñuelas 2009), and indices of environmental and geographic marginality may therefore not

be equivalent at the local scale (Vilà-Cabrera, Premoli, and Jump 2019; Picard et al. 2022). Considering environmental and geographic marginality as separate (if interacting) indices may therefore help to disentangle the underlying drivers of observed heterogeneity in rear edge population performance (Oldfather et al. 2019; Vilà-Cabrera, Premoli, and Jump 2019).

Legacies of human land use may further impact the disequilibrium between the environmental and geographic limits of species distributions (García-Valdés et al. 2015, 2013). For example, forest distributions across Europe and North America were heavily restricted prior to the 20th century due to agricultural intensification and deforestation. This range restriction was then somewhat reversed during the late 20th century following afforestation and reductions in agricultural practices, leading to forest expansion (Winkler et al. 2021). Agricultural abandonment may be impacting the response of tree distributions to climate change, as exemplified by significantly greater treeline advances in the Pyrenees in areas of previous human land use compared to locations with natural treelines (Ameztegui et al. 2016). Forest management through logging may also cause spatial variation in species' distributional responses to climate change, such as accelerating species' colonisation by reducing competition and promoting regeneration (Wang et al. 2019). Despite an abundance of research showing the direct effects of land use legacies on forest dynamics, few studies investigating the effect of global environmental change on ecosystems have explicitly tested the potentially modulating effect of differing land use legacies (Perring et al. 2016; Vilà-Cabrera et al. 2023).

Alterations to demographic rates (growth, survival, reproduction and dispersal) are the processes through which drivers of change influence tree species range dynamics (Clark et al. 2011; Holt and Keitt 2005). Modifications to plant demography are already occurring in response to global change drivers, including increased mortality and variable changes to recruitment and growth (McDowell et al. 2020). For example, canopy mortality in European temperate forest doubled between 1984 and 2016, likely due to changes in climate and land use (Senf et al. 2018). In addition, trees in newly established forests growing on abandoned farmland often have higher growth rates than those in long established forests due to increased soil nutrient availability (Alfaro-Sánchez et al. 2019; Mausolf et al. 2018; Vilà-Cabrera et al. 2017). Global change drivers can also affect different aspects of demography in opposing directions (Astigarraga et al. 2020; McDowell et al. 2020). When scaled up across populations, changes to demographic rates manifest in extinction and colonisation events, which are the underlying mechanisms of changes to species distributions (Hansen et al. 2001). Improving our understanding of the impact of global change drivers on demography will therefore improve our ability to understand heterogeneous performance of rear edge populations.

In this study, we focus on rear edge populations of European beech (*Fagus sylvatica* L.) at the temperate-Mediterranean transition zone in the NE Iberian Peninsula. Although demographic decline in European beech is observed at the regional scale across the rear edge (Peñuelas and Boada 2003; Jump, Hunt, and Peñuelas 2006; Peñuelas et al. 2007, 2008), population-level responses to environmental change are variable (Vilà-Cabrera and Jump 2019; Vilà-Cabrera, Premoli, and Jump 2019). European

beech is an ideal species with which to investigate potentially interacting drivers of demographic performance because both climate and distance to neighbouring populations have been shown to influence population performance for this species (Cavin and Jump 2016; Hacket-Pain et al. 2016; Vilà-Cabrera, Premoli, and Jump 2019). Rear edge beech forests have also been impacted by anthropogenic land use through historic coppicing and range expansions following abandonment of farmland (Alfaro-Sánchez et al. 2019; Guerrieri et al. 2021). We used four climate variables and an index of population isolation to characterise environmental and geographic marginality respectively. To improve our understanding of heterogeneous demographic performance in rear edge European beech, we aimed to (1) compare how the effects of climate, population isolation and land use legacies differ across multiple demographic rates (growth, survival, new adult recruitment and sapling recruitment), and (2) determine whether and how land use legacies interact with climate and population isolation to impact demography.

## 2 | Methods

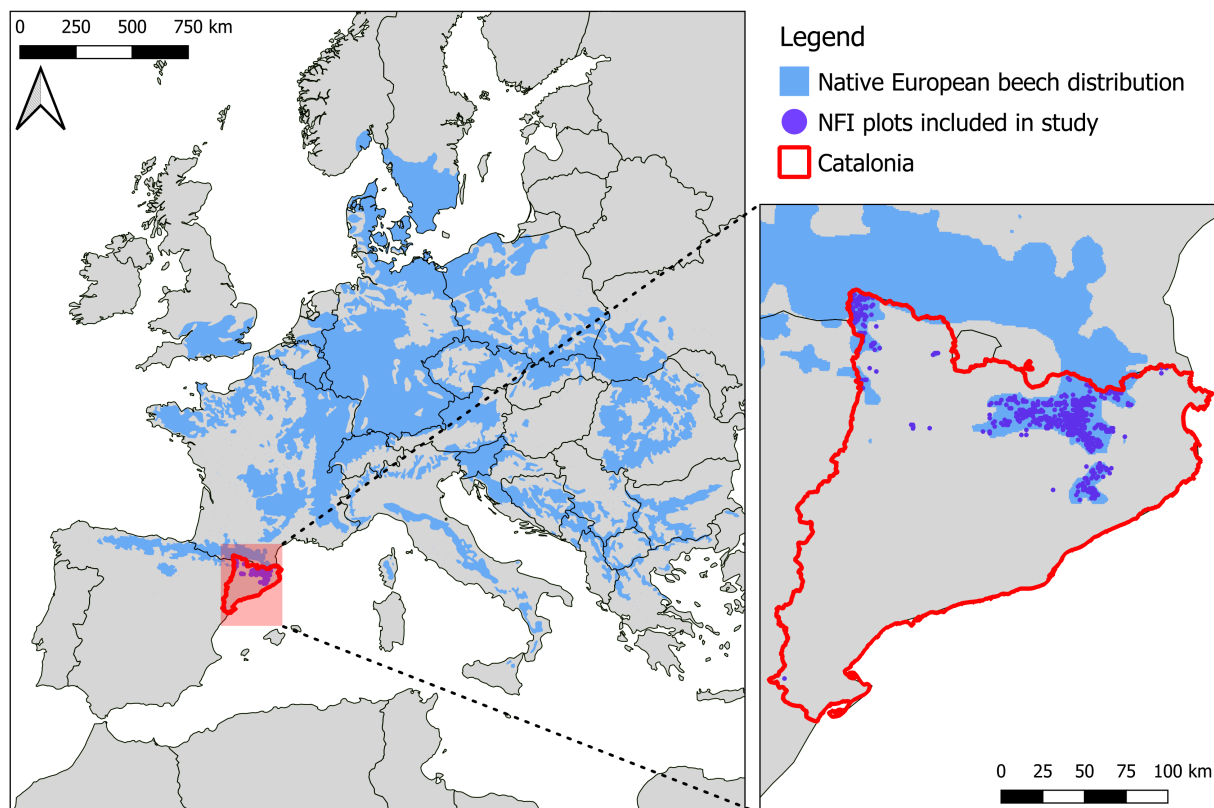
We used statistical models to relate a range of demographic rates to climate, population isolation and land use legacies, alongside additional variables known to affect beech demography.

### 2.1 | Response Variables

We evaluated individual growth rate and survival probability of adult trees (i.e., diameter at breast height (DBH)  $\geq 7.5$  cm and

a height of  $\geq 130$  cm), new adult abundance (trees that have successfully transitioned from juveniles to adults) and sapling abundance (trees between 2.5 and 7.4 cm DBH). Demographic data were obtained from the Spanish National Forest Inventory (NFI; Villaescusa and Díaz 1998; Alberdi et al. 2016). NFI plots are positioned at the nodes of a 1 km<sup>2</sup> square grid covering forested land in Spain and are censused approximately every 10 years (Villaescusa and Díaz 1998). NFI plots comprise four concentric rings of radii 5, 10, 15 and 25 m, within which trees of DBH  $\geq 7.5$ , 12.5, 22.5 and 42.5 cm respectively to the ring radii are recorded. Individual trees are censused across inventory periods. Recorded information includes species identity, status (dead, alive or new recruit), height and DBH. New adult and sapling abundance is measured in the innermost ring (5 m radius). We used data from the second (NFI2; 1986–1995), third (NFI3; 1997–2007) and fourth (NFI4; 2008–2018) inventories across Catalonia (as NFI4 data were not available outside of Catalonia). Data from the first inventory (dates ranging between 1965 and 1974) are not comparable with subsequent inventories and were therefore not included in this study. We included plots that were remeasured across at least two consecutive inventory periods with a presence of adult beech and located more than 3 km away from the Catalan border (to minimise edge effects within the calculation of the population isolation index), shown in Figure 1 (409 plots).

The annual increment in tree growth (mm year<sup>-1</sup>) of individual adult trees alive between consecutive inventories (5184 trees) was calculated as the absolute change in DBH divided by the number of growing seasons between the inventories (May–August; see Kunstler et al. (2020) for a similar approach). We



**FIGURE 1** | Approximate native European beech distribution (Caudullo, Welk, and San-Miguel-Ayanz 2017) and Spanish National Forest Inventory (NFI) plots included in the study. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

modelled survival of individual adult trees between consecutive inventories as a binary outcome (121 of 5311 trees died; 2.28% trees died). New adult and sapling abundance per plot were modelled for each inventory.

## 2.2 | Predictor Variables

Table 1 details the model predictors. To represent environmental marginality, we used mean climate, climate anomaly, topography (which may influence microclimate) and landscape-level biome type (Vilà-Cabrera, Premoli, and Jump 2019). We used vapour pressure deficit (VPD) to characterise climate, averaged between the inventory start and end date plus the two previous years to account for potential lagged effects, as also done in Ruiz-Benito et al. (2014). We used topographic position index (TPI; Weiss 2001) describing fine-scale topography as a proxy for microclimatic variation and drainage. Finally, we used tree species composition as a proxy for the wider bioclimatic context ('biome transition index', a dimensionless index representing the gradient between temperate and transitional temperate-Mediterranean climates existing within the study area). Lower and higher values of biome transition index represented plots located in more temperate or Mediterranean climates respectively. See Appendix S1 for further information on the calculation of model predictors.

To represent geographic marginality, we calculated a dimensionless index of population isolation for each NFI plot, determined by the cover and proximity of beech in the surrounding landscape as represented by an 8-m resolution land cover map of European beech in Catalonia (CREAF 2009). Population isolation ( $I_j$ ) of each NFI plot  $j$  was formulated as below (Moilanen and Nieminen 2002):

$$S_j = \sum_{i \in N, i \neq j} B_i \exp\left(\frac{-d_{ij}}{100}\right) \quad (1)$$

$$I_j = \max(S) - S_j \quad (2)$$

Where  $S_j$  represents the connectivity of NFI plot  $j$  and  $I_j$  represents the population isolation of the plot  $j$ .  $N$  included all mapped cells within a 3-km radius of  $j$  (Kunstler, Curt, and Lepart 2004).  $B_i$  was the beech cover in cell  $i$  (1 for presence or 0 for absence),  $d_{ij}$  was the distance between  $i$  and  $j$  in metres and this was divided by 100 m as a mean seed dispersal distance (see Appendix S1). We subtracted  $S_j$  from the maximum value of  $S$  to give  $I_j$ . The highest and lowest isolation values represented the most and least isolated plots within the study area respectively.

We included two types of land use legacy in the model. First, agricultural abandonment was represented by forest age, which was estimated using aerial imagery. Forest age of individual NFI plots was classified as either 'long established forest' or 'newly established forest' by comparing aerial images of the NFI forest plots from 1945, 1956 and 2005 (ICGC 2022); see Guerrieri et al. (2021) and Alfaro-Sánchez et al. (2019) for a similar method. Plots were classified as 'long established' if forest cover already existed in 1956, and 'newly established' if, in 1956, the

patch was either cropland, shrubland or newly establishing forest (i.e., present in 1956 but absent in 1945). 346 plots (84.6%) and 4887 adult trees (92%) were categorised as long established forest, and 63 plots (15.4%) and 424 adult trees (8%) were categorised as newly established forest. Plots with uncertain forest age (19 plots) due to poor aerial image quality were excluded from further analysis. Second, we used the proportion of trees resprouting from tree stumps (of any species) as a proxy to represent the intensity of historic management. A higher intensity of historic management would have resulted in more stumps due to greater amounts of felling, and therefore higher resprouting. As the NFI does not provide information regarding stump origin, we assumed that all resprouts from stumps resulted from historic management.

We included initial stand basal area ( $\text{m}^2\text{ha}^{-1}$ ) as a proxy for biotic competition and potential differences in stand development between long and newly established forests. A categorical variable (managed/unmanaged) was included to account for evidence of human management since the previous inventory. This variable represented the existence of recent management (i.e., between inventories), whereas the proportion of resprouting trees represented the degree of historic management. For the individual-level models (growth and survival), tree DBH (mm) was included to account for tree size.

We standardised all continuous predictor variables to a mean of zero and a standard deviation of 1 to enable the comparison of effect sizes between predictors (Schielzeth 2010). Further information on the calculation of model predictors is provided in the Appendix S1.

## 2.3 | Statistical Analysis

### 2.3.1 | Model Structures

We performed all statistical analysis in R v 4.1.2 (R Core Team 2021). We developed four separate models for growth, survival, new adult abundance and sapling abundance of beech using the predictors in Table 1. We included quadratic effects for TPI and tree size as intermediate values were considered likely to be associated with optimum demographic performance (Fernández-de-Uña et al. 2023; Geßler et al. 2007; Gómez-Aparicio et al. 2011; Ruiz-Benito et al. 2013). We included a random effect for plot identity to account for the nested sampling design of the NFI in all models except for survival, as no mortality was recorded in the majority of plots.

To quantify whether land use legacies interact with climate and population isolation to impact demography, we included pairwise interactions between the two land use legacy variables and the climate and population isolation variables. As only five individual trees died in newly established forest, we were not able to include interactions with forest age in the survival model. See Appendix S2 for further methodological details.

**2.3.1.1 | Growth.** We modelled growth of individual adult trees between two consecutive inventories with a linear mixed



**TABLE 1** | Model predictors of forest demography.

Category	Predictor	Definition	Source
Environmental marginality	Mean VPD	Vapour pressure deficit (kPa), i.e., difference between saturation and actual vapour pressure, used as a proxy for mean climate (low mean VPD = cold and wet; high VPD = warm and dry)	Air and dewpoint temperature from ERA5-Land (Muñoz-Sabater et al. 2021), downscaled using R package <i>KrigR</i> (Kusch and Davy 2022)
	VPD anomaly	Standardised VPD anomaly (kPa) from 1951 to 1980 baseline, used to represent degree of climate anomaly	As above
	TPI	Topographic position index, used as proxy for topographic variation influencing microclimate	Derived from Catalonia Digital Terrain Model (ICGC 2018)
	Biome transition index	Community weighted mean $P_{50}$ drought tolerance index of key tree species within 1-km radius. Used to represent location of forest plot on a gradient from temperate to transitional temperate-Mediterranean environments	Tree land cover map (CREAF 2009) and $P_{50}$ data from Sanchez-Martinez et al. (2020) & García-Valdés et al. (2021)
Geographic marginality	Population isolation	Degree of spatial isolation of NFI plot relative to other beech forest	European beech land cover map (CREAF 2009)
Land use legacy: Agricultural abandonment	Forest age	Factor-level indicator of forest age (long established forest or newly established forest)	Catalonia 1956/2005 aerial images (ICGC 2022)
Land use legacy: Historic forest management	Resprouting proportion	Proportion of measured adult trees in plot (of any species) with evidence of having resprouted from tree stumps, indicating historic management through logging	Spanish National Forest Inventory (Alberdi et al. 2016; Villalencusa and Díaz 1998)
Biotic	Tree size	Diameter at breast height (mm) of individual tree	As above
	Stand basal area	Total basal area of all trees in plot ( $\text{m}^2 \text{ha}^{-1}$ ), used as a proxy for biotic competition	As above
Recent management	Recent management	Evidence of management since previous inventory (managed or unmanaged)	As above

model using the R package *lmerTest* (Kuznetsova and Brockhoff 2017). The log-modulus transformation was applied to annual tree growth following Equation 3:

$$\log \text{ modulus } (x) = \text{sign}(x) \times \log(|x| + 1) \quad (3)$$

The log-modulus transformation allows a logarithmic transformation whilst preserving the sign of the data, permitting the inclusion of negative and zero growth measurements (John and Draper 1980). Although these presumably arise from measurement error, such error will occur across the whole range of

growth values, so removing only the negative growth would introduce bias to the model.

**2.3.1.2 | Survival.** We modelled survival of individual adult trees between consecutive inventories using a generalised linear model with a binomial error distribution. A complementary log-log link with an offset was included to account for variable time periods between surveys (as also done in Archambeau et al. 2020; Kunstler et al. 2020). Model probability estimates therefore represent estimated annual survival probabilities. We could not include the random effect for plot identity in the survival model as the majority of plots

had no tree mortality, preventing estimation of the random effect (Kunstler et al. 2020).

**2.3.1.3 | Recruitment.** We represented recruitment using the number of new adults and saplings recorded per plot, which were modelled using generalised linear mixed models with Poisson and negative binomial error distributions, respectively, using the *glmmTMB* R package (Brooks et al. 2017).

### 2.3.2 | Model Selection on Interaction Terms

To test the significance of interactions between land use legacies and climate or population isolation, for each interaction, we compared a full model (including all interactions) and a sub-model (in which one interaction term was dropped) using a likelihood ratio test (LRT) and the difference in Akaike information criteria ( $\Delta AIC$ ). Interaction terms were retained in the final model if the LRT p-value was  $<0.05$  and removal of the term caused AIC to increase by  $\geq 2$  (Burnham and Anderson 2002). For the linear growth model, we used a Maximum Likelihood estimator for selecting interactions and refitted the final model using Restricted Maximum Likelihood (Bolker 2015). We did not perform model selection on the fixed effects as these were included as predictors known to potentially affect beech demography.

## 3 | Results

### 3.1 | Direct Effects of Climate, Population Isolation and Land Use Legacies on Beech Demography

We found no significant direct relationship between mean VPD or biome transition index and any demographic rate (Figures 2 and 3A). VPD anomaly was associated with reduced tree growth, but we found no significant relationship with survival, new adult abundance or sapling abundance. Intermediate values of TPI were associated with higher tree growth and increased abundance of new adults, with optimum TPI values at approximately zero (flat ground) for growth and 1.5 (upper slopes) for new adult abundance (Figure 3A).

We found a strong relationship between population isolation and most demographic rates (except survival probability). Population isolation was associated with increased tree growth but lower abundance of new adults and saplings (Figures 2 and 3B). Increased intensity of historic management was associated with reduced survival probability and sapling abundance, but we found no significant direct relationship with tree growth or new adult abundance. We found no association of forest age with any tested demographic rate (Figures 2 and 3C).

Marginal effects of stand basal area, tree size and recent management are shown in Appendix S3, as these predictors were not related to our main research aims (but were included as factors known to affect beech demography).

### 3.2 | Interactive Effects Between Land Use Legacies and Climate or Population Isolation on Beech Demography

We found evidence supporting six interactions between land use legacies and climate or population isolation (Figure 4), comprising at least one for each demographic variable. All six of the interactions supported by the model selection procedure related to historic management intensity, while we found no interactions with forest age.

Overall, the supported interactions between historic management intensity and climate or population isolation can be categorised as one of two main forms. For the first form, intense historic management exacerbated the negative relationship between demography and climate or population isolation. This occurred for tree growth (Figure 4A) and sapling abundance (Figure 4F), in which the magnitude of the negative slopes of VPD anomaly and population isolation, respectively, were magnified under high intensities of historic management compared to low intensities.

For the second form, intense historic management flattened the negative relationship between climate and demography by reducing demographic performance in favourable climates to similar levels observed in unfavourable climates. This occurred for the relationships between biome transition index and survival probability (Figure 4B), biome transition index and new adult abundance (Figure 4D) and VPD anomaly and sapling abundance (Figure 4E).

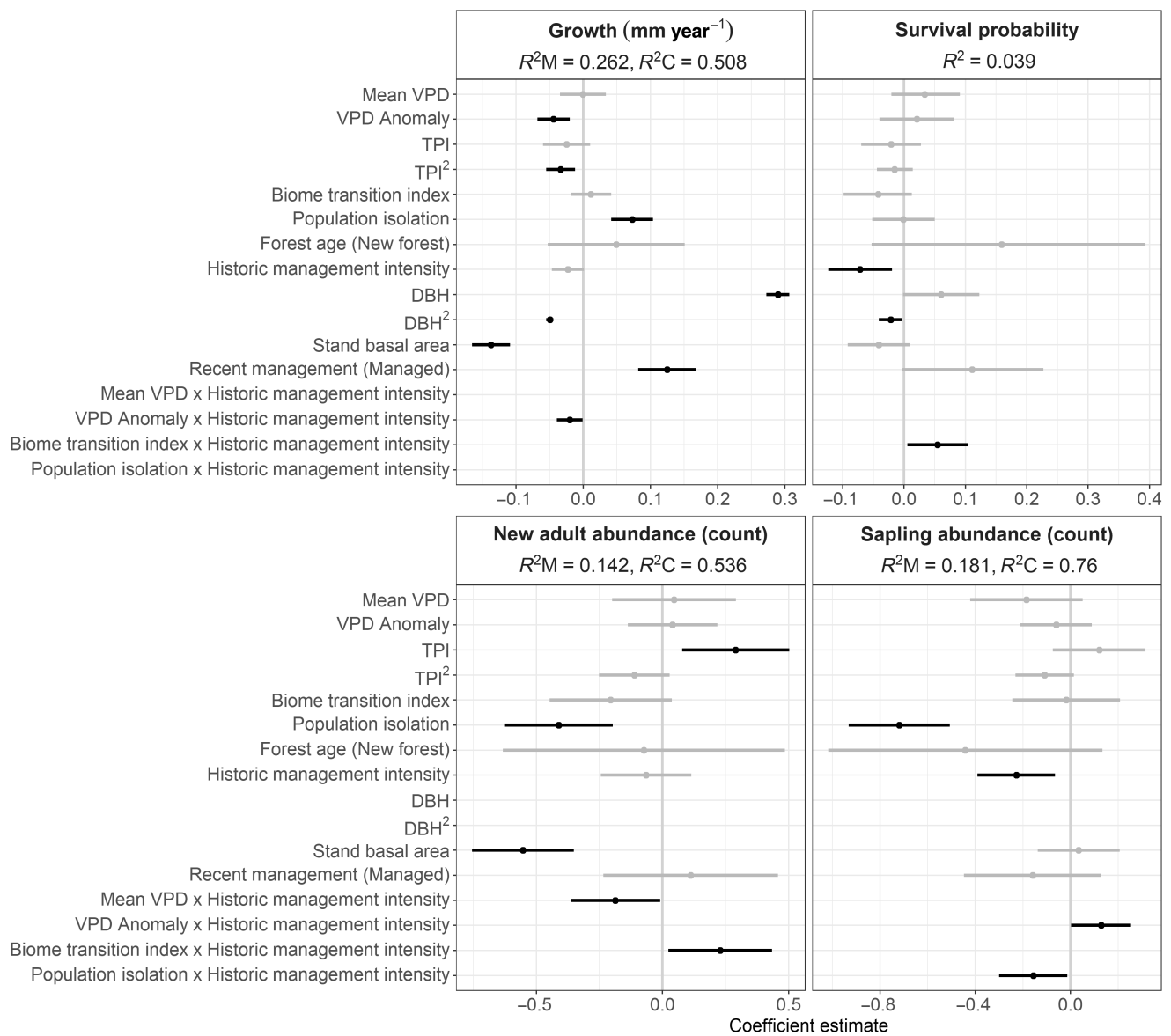
The interactive effect of historic management intensity and mean VPD on new adult abundance followed a different form: mean estimates of the slope of the relationship were positive with low historic management intensity but negative with high management intensity (Figure 4C). However, confidence intervals overlapped at all values of mean VPD, likely due to high uncertainty in the main effect of mean VPD on new adult abundance (Figure 2).

## 4 | Discussion

In this study of beech at its rear edge in NE Iberian Peninsula, we found that demographic rates showed different responses to the combination of climate, population isolation and land use legacies, which could potentially lead to complex shifts in future population dynamics under climate change. Importantly, we identified two main forms of interactions between land use legacies and climate or population isolation: intense historic management either magnified negative relationships between demography and climate or population isolation, or reduced demographic performance in favourable climates to levels observed in unfavourable climates.

### 4.1 | Direct Effects of Climate, Population Isolation and Land Use Legacies on Beech Demography

We found no significant relationship between mean VPD (representing current climate conditions) or biome transition

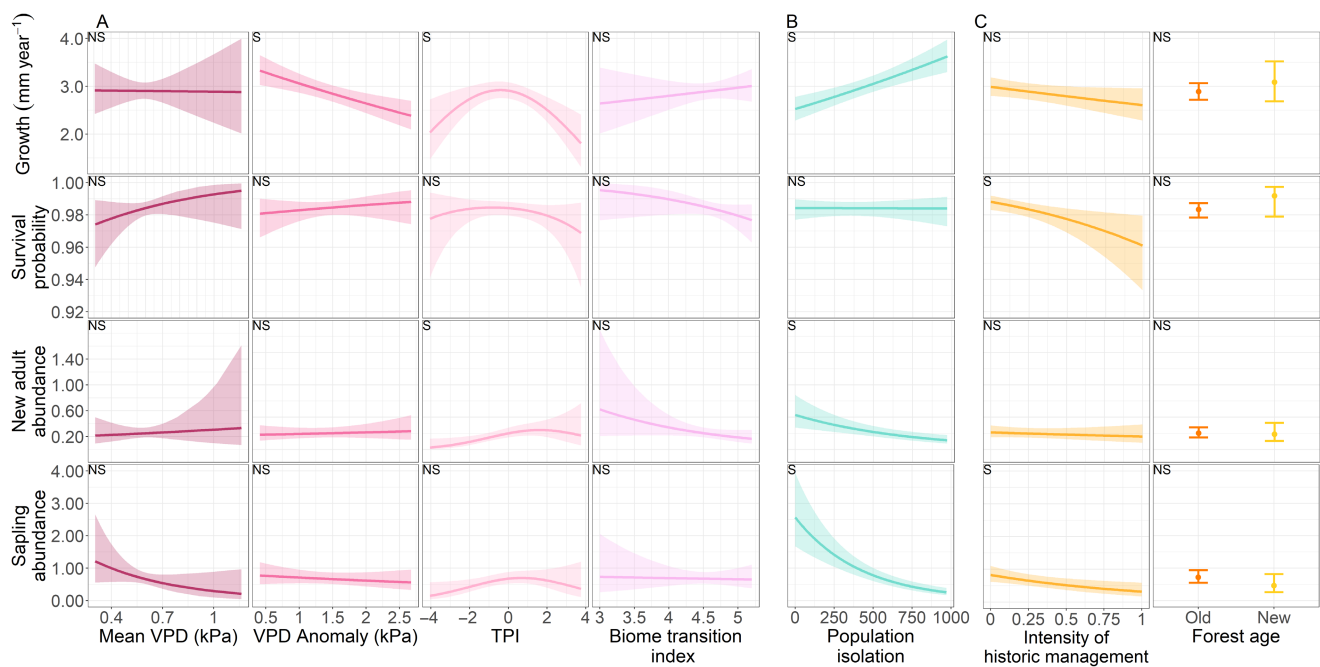


**FIGURE 2** | Coefficient estimates of growth, survival, new adult abundance and sapling abundance models. Interactions shown are those retained in at least one model following model selection. Points and lines represent mean estimates and 95% confidence intervals. Points and bars are grey where confidence intervals overlap zero.  $R^2M$  = marginal  $R^2$  (fixed effects only);  $R^2C$  = conditional  $R^2$  (fixed and random effects). Model selection results and tabular final model results are included in the Appendix S3.

index and demography, a negative relationship between VPD anomaly (representing climate anomaly) and tree growth, and an intermediate optimum TPI (flat ground) for tree growth and new adult abundance. Our finding that no demographic rate was associated with current climate conditions is in agreement with and supplements recent findings that the growth responses of European beech to drought are not necessarily more sensitive at the rear edge than in more favourable climates across the species range (Cavin and Jump 2016; Vilà-Cabrera and Jump 2019; Muffler et al. 2020). However, our finding that increasing VPD anomaly (i.e., hotter and drier than the baseline climate) was related to reduced tree growth indicates that climate change might be negatively affecting tree demography across the rear edge, supporting recent findings that climate stress has exceeded tree species compensating mechanisms such as adaptation or plasticity in rear edge populations (Anderegg et al. 2019). We also found a strong

relationship between TPI and both tree growth and new adult abundance, illustrating the key role of local conditions in determining plant cover and demographic performance (e.g., Elliott and Cowell 2015; Graae et al. 2018; Príncipe et al. 2022; Rita et al. 2023).

We found that population isolation (representing geographic marginality) was positively related to tree growth and negatively related to recruitment of adults and saplings, but had no relationship with survival. The positive relationship between population isolation and tree growth was unexpected because fragmented populations typically have reduced performance due to ecological edge effects and reduced genetic diversity (Murcia 1995; Frankham, Ballou, and Briscoe 2010). However, potential reasons could be that highly isolated populations may be situated in more favourable microclimates or are potentially locally adapted to unfavourable environmental



**FIGURE 3** | Mean predicted marginal effects and 95% confidence intervals of demographic responses according to (A) climate, (B) population isolation and (C) land use legacy fixed effects. NS, not significant and S, significant, based on whether 95% confidence intervals for coefficient estimation do or do not overlap zero. Survival represents predicted probabilities over the mean duration between surveys (12 years).

conditions (Hampe and Petit 2005; Oldfather et al. 2019; Vilà-Cabrera, Premoli, and Jump 2019). The distribution of European beech in Catalonia is also geographically clustered, with more isolated patches in the northwest where the regional climate is of Atlantic influence, which may result in higher tree growth in this fragmented area of the species' range (Cavin and Jump 2016). In addition, supplementary analysis of our data showed that increasing population isolation was strongly associated with smaller population counts, so greater tree growth in highly isolated plots may also be a result of lessened intra-specific competition if these plots are also less dense (see Appendix S3). The negative relationship between population isolation and recruitment of new adults and saplings may also potentially be caused by smaller population sizes (and therefore reduced seed supply) in highly isolated plots. While we found no relationship between population isolation and survival probability, only 2.3% of modelled trees died during the inventory period. As a result, the predicted survival probability was very high (a common issue when modelling long-lived trees (Merow et al. 2014)), which may have made estimation of partial effects difficult.

Historic forest management (represented by the proportion of resprouting trees) was negatively related to survival and sapling abundance, but had no significant relationship with tree growth or new adult abundance. In rear edge beech stands, historic management was found to result in lower basal areas and a lack of full-size canopy trees compared to historically unmanaged or abandoned pollard stands (Merino et al. 2007). This could potentially lead to reduced microclimatic buffering of the forest canopy, exposing saplings in the understory to harsher conditions (Hollunder et al. 2024; Zellweger et al. 2020), alongside potentially lessened seed production. Supplementary analysis of our data confirmed that increased historic management intensity was significantly associated

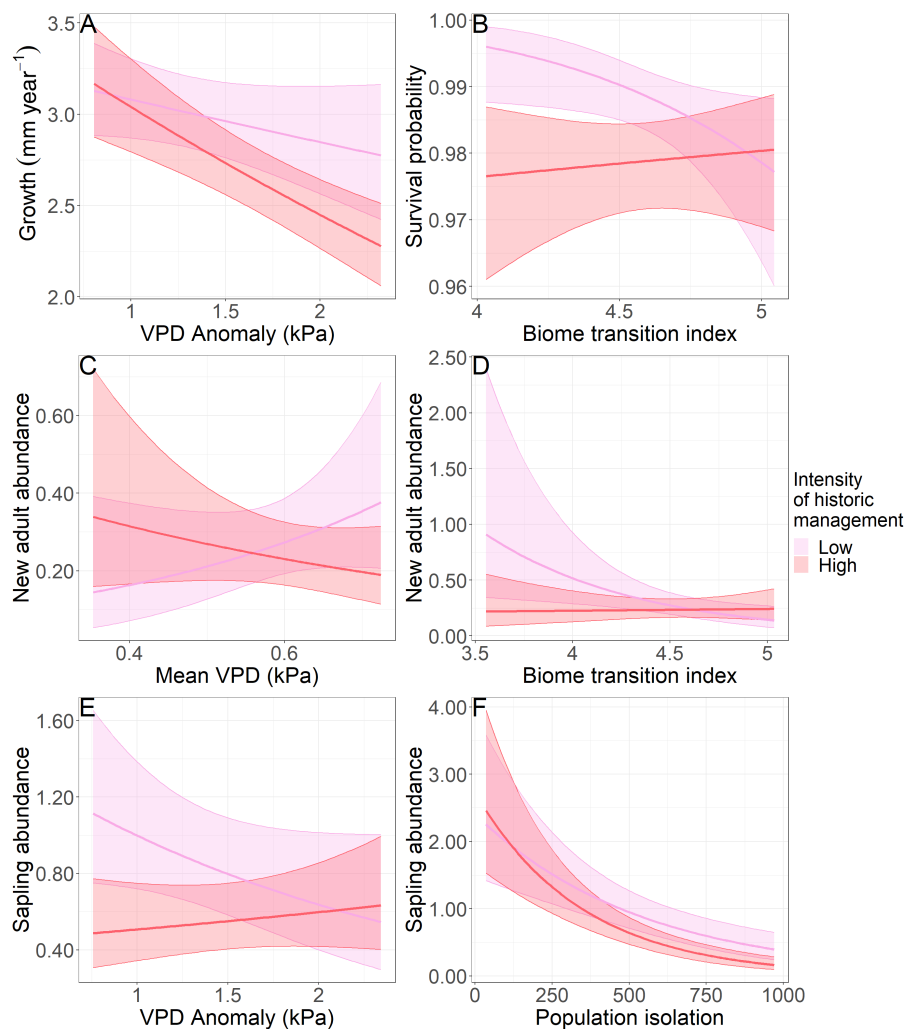
with reduced stand basal areas (see Appendix S3). It should be noted that in this study, we have assumed that all resprouts are the result of historical felling. Although some resprouts may be the result of natural causes, windthrow is likely to uproot the entire tree rather than cause stem breakage (with stem breakage at the base being particularly unusual), so it is considered probable that the majority of tree stumps would be the result of felling.

We found no clear relationship between forest age and any tested demographic rate. This contrasts with previous research showing higher tree growth in newly established forests due to increased soil nutrient availability from previous agricultural land use (Alfaro-Sánchez et al. 2019; Guerrieri et al. 2021; Mausolf et al. 2018; Vilà-Cabrera et al. 2017). However, in our dataset, only 8% of individual adult trees were located in newly established forest, despite 15% of forest plots being classified as newly established in line with previous research (Vilà-Cabrera et al. 2017). We also found that newly established forest had lower stand basal areas and higher levels of population isolation than long established forests. The potential confounding of forest age with other variables, alongside the small number of trees in newly established forest, probably accounts for the wide confidence intervals associated with the marginal effects of forest age (see Figure 2). It is therefore possible that forest age may have had a direct impact on beech demography, but we were not able to identify this effect in our dataset.

#### 4.2 | Interactive Effects Between Land Use Legacies and Climate or Population Isolation on Beech Demography

We found that the intensity of historic land use had an interactive effect on climate or population isolation for every demographic





**FIGURE 4** | Mean marginal effects and 95% confidence intervals for interactions retained after model selection, i.e. the interactions between historic management intensity and (A) VPD anomaly on tree growth; (B) biome transition index on survival; (C) mean VPD on new adult abundance; (D) biome transition index on new adult abundance; (E) VPD anomaly on sapling abundance and (F) population isolation on sapling abundance. Historic management intensity was represented by the proportion of resprouting trees which have resprouted from stumps. ‘High’ and ‘low’ intensity of historic management relates to 1 standard deviation above and below the mean value of historic management respectively.

rate tested. Interestingly, each interaction was different across the demographic rates. Overall, we found two main forms of interaction: intense historic forest management either magnified the negative relationships between climate or population isolation and demography, or reduced demographic performance in favourable climates to levels observed in unfavourable climates.

For the first form of interaction, we found that the negative relationship between VPD anomaly and tree growth was magnified under high levels of historic management (Figure 4A). Globally, VPD has risen sharply since the 1990s due to warming temperatures which cause exponential increases in atmospheric evaporative demand (Grossiord et al. 2020; Yuan et al. 2019; Zhang et al. 2015). A higher proportion of resprouting trees due to greater historic management could potentially lead to multiple-stemmed trees, causing increased competition for resources and reduced growth of individual stems (Tanentzap et al. 2012), which could potentially magnify the negative effects of increased warming and drought stress resultant of climate change on tree growth.

The negative relationship between population isolation and sapling abundance was also magnified with high forest management intensity (Figure 4F). As saplings are located in the understory, a possible explanation for this interaction may be reduced microclimatic buffering of the forest canopy due to greater historic management (Zellweger et al. 2020). Forest canopies buffer harsh temperatures, creating a cooler microclimate for understory vegetation (De Frenne et al. 2019; De Lombaerde et al. 2022; Frey et al. 2016). In the growing season, the shading effect of canopy cover greater than 50% has been found to reduce VPD by 1.1 kPa (Davis et al. 2019). Since population size was lower in more isolated plots (see Appendix S3), it is possible that canopy microclimatic buffering may be reduced in these locations (especially since beech trees cast heavy shade). As historic management may result in reduced stand basal area and fewer full-sized canopy trees (Merino et al. 2007), the reductions in microclimatic buffering in isolated plots may be exacerbated due to intense historic management, which could therefore have the potential to magnify the negative impacts of population isolation on sapling abundance.

For the second form of interaction, we found that intense historic management modified the survival response of beech along the temperate-Mediterranean transition zone, as indicated by the biome transition index (Figure 4B). In more temperate climates, survival probability was higher when historic management intensity was low. When historic management intensity was high, however, survival was reduced to (or even slightly worse than) levels observed in harsher, more Mediterranean climates. This finding suggests that intense historic management has a greater negative influence on survival in temperate climates that are typically more favourable for beech.

Similarly, the abundance of juveniles in more favourable (temperate) climates was also reduced to the levels of less favourable (temperate-Mediterranean transitional) climates under high management intensity. For new adults, high historic management reduced abundance in temperate climates to the levels in areas of biome transition (Figure 4D). For saplings, high historic management reduced abundance in locations of low VPD anomaly to the levels of locations of high VPD anomaly (Figure 4E). As juvenile trees are located in the understory, a possible explanation for these interactions may be reduced microclimatic buffering of the forest canopy due to greater historic management (Zellweger et al. 2020), reducing juvenile abundance even to the levels of less favourable climates. As the modification effect of historic management intensity was lost in transitional Mediterranean climates or locations of high VPD anomaly, this suggests the impact of harsher conditions might be unbuffered by the degree of canopy shading in extreme climates. The future climatic buffering capacity of forest canopies may be threatened by water resource limitations due to climate change (Davis et al. 2019), a possibility that could be particularly likely in rear edge beech given our finding that rising VPD was associated with reduced growth of adult trees. As the study region is predicted to experience temperature increases of 1.4°C by 2050 (Government of Catalonia 2017), canopy decline resulting from climate change could potentially limit the future shading protection afforded to juvenile beech, particularly in stands with high levels of historic management. This could potentially lead to a positive feedback mechanism whereby climate stress reduces canopy buffering (De Frenne et al. 2021), which exacerbates climate stress for the understory.

Finally, we also found evidence that the intensity of historic management has the potential to change the direction of the relationship between climate and demography. For new adult abundance, increasing mean VPD (a warmer, drier climate) had a positive relationship when historic management was low, but a negative relationship when historic management was high (Figure 4C). This could imply that when canopy shading is plentiful, increasing mean VPD may be beneficial for new adult abundance, perhaps due to higher growth rates or increased reproductive output of adults due to warmer conditions (Bogdziewicz et al. 2020). However, when the intensity of historic management is high, increasing VPD may negatively impact new adult abundance due to the reduced microclimatic buffering of the forest canopy due to fewer full-sized canopy trees (Hollunder et al. 2024; Merino et al. 2007). However, this interaction should be interpreted with caution due to the high confidence interval overlap between high and low historic management intensities at all values of mean VPD.

## 5 | Conclusions

Understanding the drivers of heterogeneous demographic performance at rear edge margins is critical to improving future predictions of species distributions (Hampe and Jump 2011; Hampe and Petit 2005). Recent work has led to the appreciation that the geographic limits of species distributions do not necessarily also represent the environmental range limits of that species, which may—at least in part—help explain observed heterogeneity in demographic performance across rear edge margins (Oldfather et al. 2019; Vilà-Cabrera, Premoli, and Jump 2019). However, our results also show that legacies of human land use have the potential to interact with gradients of marginality such as climate and population isolation to further impact population dynamics (Perring et al. 2016; Vilà-Cabrera et al. 2023).

Overall, our findings underscore two key insights. First, different demographic rates may respond differently to climate, population isolation and land use legacies, which may potentially lead to complex spatio-temporal shifts in future population dynamics under climate change. Second, the impact of climate and population isolation on forest demography may depend on the human land use legacies of the forest. We identified two main forms of interactive effects: intense historic forest management either magnified the negative relationships between demography and climate or population isolation, or reduced demographic performance in favourable climates to levels observed in unfavourable climates. Through both forms of interaction, historic forest management appears to negatively impact demography, which has the potential to compromise carbon stocks (through reduced tree growth and survival) and long-term population viability (through reduced juvenile recruitment). This could potentially lead to a positive feedback mechanism in which canopy decline reduces microclimatic buffering (De Frenne et al. 2021), leading to further forest decline through reduced juvenile abundance, which may be particularly grave in rear edge populations given their important role in a species' long-term persistence (Hampe and Petit 2005). Overall, we show that disentangling human and environmental factors can enable us to better understand heterogeneous demographic population performance across the rear edge of species distributions.

### Author Contributions

**Jazz Rhoades:** conceptualization, data curation, formal analysis, methodology, visualization, writing – original draft, writing – review and editing. **Albert Vilà-Cabrera:** conceptualization, methodology, supervision, writing – review and editing. **Paloma Ruiz-Benito:** conceptualization, data curation, methodology, supervision, writing – review and editing. **James M. Bullock:** conceptualization, methodology, supervision, writing – review and editing. **Alistair S. Jump:** conceptualization, supervision, writing – review and editing. **Daniel Chapman:** conceptualization, methodology, supervision, writing – review and editing.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data and R scripts that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.n2z34tn65>. Spanish National Forest Inventories 2, 3 and 4 are available from <https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html>. ERA5-Land climate data is available from Copernicus Climate Change Service (C3S) Climate Data Store (CDS) at <https://doi.org/10.24381/cds.e2161bac>. Catalonia aerial imagery data and Digital Terrain Model is available from <https://www.icgc.cat/en/Downloads/Open-ICGC-plugin>. Catalonia land cover data is available from [https://www.mcsc.creaf.cat/index\\_usa.htm](https://www.mcsc.creaf.cat/index_usa.htm) (version 4a).

## References

Alberdi, I., V. Sandoval, S. Condés, I. Cañellas, and R. Vallejo. 2016. "El Inventario Forestal Nacional español, una herramienta para el conocimiento, la gestión y la conservación de los ecosistemas forestales arbolados." *Ecosistemas: Revista Científica y Técnica de Ecología y Medio Ambiente* 25, no. 3: 88–97. <https://doi.org/10.7818/ECOS.2016.25-3.10>.

Alfaro-Sánchez, R., A. S. Jump, J. Pino, O. Díez-Nogales, and J. M. Espelta. 2019. "Land Use Legacies Drive Higher Growth, Lower Wood Density and Enhanced Climatic Sensitivity in Recently Established Forests." *Agricultural and Forest Meteorology* 276–277: 107630. <https://doi.org/10.1016/j.agrformet.2019.107630>.

Ameztegui, A., L. Coll, L. Brotons, and J. M. Ninot. 2016. "Land-Use Legacies Rather Than Climate Change Are Driving the Recent Upward Shift of the Mountain Tree Line in the Pyrenees." *Global Ecology and Biogeography* 25, no. 3: 263–273. <https://doi.org/10.1111/gcb.12407>.

Anderegg, W. R. L., L. D. L. Anderegg, K. L. Kerr, and A. T. Trugman. 2019. "Widespread Drought-Induced Tree Mortality at Dry Range Edges Indicates That Climate Stress Exceeds Species' Compensating Mechanisms." *Global Change Biology* 25, no. 11: 3793–3802. <https://doi.org/10.1111/gcb.14771>.

Archambeau, J., P. Ruiz-Benito, S. Ratcliffe, et al. 2020. "Similar Patterns of Background Mortality Across Europe Are Mostly Driven by Drought in European Beech and a Combination of Drought and Competition in Scots Pine." *Agricultural and Forest Meteorology* 280: 107772. <https://doi.org/10.1016/j.agrformet.2019.107772>.

Astigarraga, J., E. Andivia, M. A. Zavala, et al. 2020. "Evidence of Non-stationary Relationships Between Climate and Forest Responses:

Increased Sensitivity to Climate Change in Iberian Forests." *Global Change Biology* 26: 5063–5076. <https://doi.org/10.1111/gcb.15198>.

Bogdziewicz, M., D. Kelly, P. A. Thomas, J. G. A. Lageard, and A. Hackett-pain. 2020. "Climate Warming Disrupts Mast Seeding and Its Fitness Benefits in European Beech." *Nature Plants* 6: 88–94. <https://doi.org/10.1038/s41477-020-0592-8>.

Bolker, B. M. 2015. "Linear and Generalized Linear Mixed Models." In *Ecological Statistics: Contemporary Theory and Application*, edited by G. A. Fox, S. Negrete-Yankelevich, and V. J. Sosa, 309–333. Oxford: Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199672547.003.0014>.

Bonan, G. B. 2008. "Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests." *Science* 320, no. 5882: 1444–1449. <https://doi.org/10.1139/X09-086>.

Brooks, M. E., K. Kristensen, K. J. van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400. <https://doi.org/10.32614/RJ-2017-066>.

Brown, J. H. 1984. "On the Relationship Between Abundance and Distribution of Species." *American Naturalist* 124, no. 2: 255–279. <https://doi.org/10.2307/2461494>.

Burnham, K. P., and D. Anderson. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*. 2nd ed. New York: Springer-Verlag. <https://doi.org/10.1007/b97636>.

Cartographic and Geological Institute of Catalonia (ICGC). 2018. "Elevations Model of the Terrain of Catalonia 15×15 meters." Accessed January 11, 2021. <https://ide.cat/geonetwork/srv/cat/catalog.search#/metadata/model-digital-terreny-15x15-v2r0>.

Cartographic and Geological Institute of Catalonia (ICGC). 2022. "Open ICGC Plugin." Accessed February 6, 2023. <https://www.icgc.cat/en/Applications/Tools/Open-ICGC-plugin>.

Casazza, G., C. Macrì, D. Dagnino, et al. 2021. "When Ecological Marginality Is Not Geographically Peripheral: Exploring Genetic Predictions of the Centre-Periphery Hypothesis in the Endemic Plant *Lilium Pomponium*." *PeerJ* 9: e11039. <https://doi.org/10.7717/peerj.11039>.

Caudullo, G., E. Welk, and J. San-Miguel-Ayanz. 2017. "Chorological Maps for the Main European Woody Species." *Data in Brief* 12: 662–666. <https://doi.org/10.1016/j.dib.2017.05.007>.

Cavin, L., and A. S. Jump. 2016. "Highest Drought Sensitivity and Lowest Resistance to Growth Suppression Are Found in the Range Core of the Tree *Fagus sylvatica* L. Not the Equatorial Range Edge." *Global Change Biology* 23, no. 1: 362–379. <https://doi.org/10.1111/gcb.13366>.

Chen, I. C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated With High Levels of Climate Warming." *Science* 333, no. 6045: 1024–1026. <https://doi.org/10.1126/science.1206432>.

Clark, J. S., D. M. Bell, M. H. Hersh, and L. Nichols. 2011. "Climate Change Vulnerability of Forest Biodiversity: Climate and Competition Tracking of Demographic Rates." *Global Change Biology* 17, no. 5: 1834–1849. <https://doi.org/10.1111/j.1365-2486.2010.02380.x>.

CREAF. 2009. "Land Cover Map of Catalonia (MCSC)." [https://www.mcsc.creaf.cat/index\\_usa.htm](https://www.mcsc.creaf.cat/index_usa.htm).

Davis, K. T., S. Z. Dobrowski, Z. A. Holden, P. E. Higuera, and J. T. Abatzoglou. 2019. "Microclimatic Buffering in Forests of the Future: The Role of Local Water Balance." *Ecography* 42, no. 1: 1–11. <https://doi.org/10.1111/ecog.03836>.

De Frenne, P., J. Lenoir, M. Luoto, et al. 2021. "Forest Microclimates and Climate Change: Importance, Drivers and Future Research Agenda." *Global Change Biology* 27, no. 11: 2279–2297. <https://doi.org/10.1111/gcb.15569>.



- De Frenne, P., F. Zellweger, F. Rodríguez-Sánchez, et al. 2019. "Global Buffering of Temperatures Under Forest Canopies." *Nature Ecology & Evolution* 3, no. 5: 744–749. <https://doi.org/10.1038/s41559-019-0842-1>.
- De Lombaerde, E., P. Vangansbeke, J. Lenoir, et al. 2022. "Maintaining Forest Cover to Enhance Temperature Buffering Under Future Climate Change." *Science of the Total Environment* 810: 151338. <https://doi.org/10.1016/j.scitotenv.2021.151338>.
- Dyderski, M. K., S. Paž, L. E. Frelich, and A. M. Jagodziński. 2018. "How Much Does Climate Change Threaten European Forest Tree Species Distributions?" *Global Change Biology* 24, no. 3: 1150–1163. <https://doi.org/10.1111/gcb.13925>.
- Elliott, G. P., and C. M. Cowell. 2015. "Slope Aspect Mediates Fine-Scale Tree Establishment Patterns at Upper Treeline During Wet and Dry Periods of the 20th Century." *Arctic, Antarctic, and Alpine Research* 47, no. 4: 681–692. <https://doi.org/10.1657/AAAR0014-025>.
- Ellison, A. M., M. S. Bank, B. D. Clinton, et al. 2005. "Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems." *Frontiers in Ecology and the Environment* 3, no. 9: 479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2).
- Fernández-de-Uña, L., J. Martínez-Vilalta, R. Poyatos, M. Mencuccini, and N. G. McDowell. 2023. "The Role of Height-Driven Constraints and Compensations on Tree Vulnerability." *New Phytologist* 239, no. 6: 2083–2098. <https://doi.org/10.1111/nph.19130>.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2010. *Introduction to Conservation Genetics*. 2nd ed. Cambridge, UK: Press Syndicate for the University of Cambridge.
- Frey, S. J. K., A. S. Hadley, S. L. Johnson, M. Schulze, J. A. Jones, and M. G. Betts. 2016. "Spatial Models Reveal the Microclimatic Buffering Capacity of Old-Growth Forests." *Science Advances* 2, no. 4: e1501392. <https://doi.org/10.1126/sciadv.1501392>.
- García-Valdés, R., J. C. Svenning, M. A. Zavala, D. W. Purves, and M. B. Araújo. 2015. "Evaluating the Combined Effects of Climate and Land-Use Change on Tree Species Distributions." *Journal of Applied Ecology* 52, no. 4: 902–912. <https://doi.org/10.1111/1365-2664.12453>.
- García-Valdés, R., M. A. Zavala, M. B. Araújo, and D. W. Purves. 2013. "Chasing a Moving Target: Projecting Climate Change-Induced Shifts in Non-equilibrium Tree Species Distributions." *Journal of Ecology* 101, no. 2: 441–453. <https://doi.org/10.1111/1365-2745.12049>.
- García-Valdés, R., J. Vayreda, J. Retana, and J. Martínez-Vilalta. 2021. "Low Forest Productivity Associated with Increasing Drought-Tolerant Species Is Compensated by an Increase in Drought-Tolerance Richness." *Global Change Biology* 27, no. 10: 2113–2127.
- Geßler, A., C. Keitel, J. Kreuzwieser, R. Matyssek, W. Seiler, and H. Rennenberg. 2007. "Potential Risks for European Beech (*Fagus sylvatica* L.) in a Changing Climate." *Trees* 21, no. 1: 1–11. <https://doi.org/10.1007/s00468-006-0107-x>.
- Gómez-Aparicio, L., R. García-Valdés, P. Ruiz-Benito, and M. A. Zavala. 2011. "Disentangling the Relative Importance of Climate, Size and Competition on Tree Growth in Iberian Forests: Implications for Forest Management Under Global Change." *Global Change Biology* 17, no. 7: 2400–2414. <https://doi.org/10.1111/j.1365-2486.2011.02421.x>.
- Government of Catalonia Institute of Catalan Studies. 2017. "Climate change in Catalonia. Executive summary of the Third Report on Climate Change in Catalonia." Writing team: Xavier Duran, M. Josep Picó and Lluís Reales. Edited by Arnau Queralt. Translated by t&s – Traducciones y Tratamiento de la Documentación, S. In A. Queralt (Ed.). *cads.gencat.cat*.
- Graae, B. J., V. Vandvik, W. S. Armbruster, et al. 2018. "Stay or Go—How Topographic Complexity Influences Alpine Plant Population and Community Responses to Climate Change." *Perspectives in Plant Ecology, Evolution and Systematics* 30: 41–50. <https://doi.org/10.1016/j.ppees.2017.09.008>.
- Grossiord, C., T. N. Buckley, L. A. Cernusak, et al. 2020. "Plant Responses to Rising Vapor Pressure Deficit." *New Phytologist* 226, no. 6: 1550–1566. <https://doi.org/10.1111/nph.16485>.
- Guerrieri, R., M. Correia, I. Martín-Forés, et al. 2021. "Land-Use Legacies Influence Tree Water-Use Efficiency and Nitrogen Availability in Recently Established European Forests." *Functional Ecology* 35, no. 6: 1325–1340. <https://doi.org/10.1111/1365-2435.13787>.
- Habibzadeh, N., A. Ghoddousi, B. Bleyhl, and T. Kuemmerle. 2021. "Rear-Edge Populations Are Important for Understanding Climate Change Risk and Adaptation Potential of Threatened Species." *Conservation Science and Practice* 3, no. 5: 1–13. <https://doi.org/10.1111/csp2.375>.
- Hacket-Pain, A. J., L. Cavin, A. D. Friend, and A. S. Jump. 2016. "Consistent Limitation of Growth by High Temperature and Low Precipitation From Range Core to Southern Edge of European Beech Indicates Widespread Vulnerability to Changing Climate." *European Journal of Forest Research* 135: 897–909. <https://doi.org/10.1007/s10342-016-0982-7>.
- Hampe, A., and A. S. Jump. 2011. "Climate Relicts: Past, Present, Future." *Annual Review of Ecology, Evolution, and Systematics* 42, no. 1: 313–333. <https://doi.org/10.1146/annurev-ecolsys-102710-145015>.
- Hampe, A., and R. J. Petit. 2005. "Conserving Biodiversity Under Climate Change: The Rear Edge Matters." *Ecology Letters* 8, no. 5: 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>.
- Hansen, A. J., R. P. Neilson, V. H. Dale, et al. 2001. "Global Change in Forests: Responses of Species, Communities, and Biomes: Interactions Between Climate Change and Land Use Are Projected to Cause Large Shifts in Biodiversity." *Bioscience* 51, no. 9: 765–779. [https://doi.org/10.1641/0006-3568\(2001\)051\[0765:GCFIRO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0765:GCFIRO]2.0.CO;2).
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. "Are Treelines Advancing A Global Meta-Analysis of Treeline Response to Climate Warming." *Ecology Letters* 12: 1040–1049. <https://doi.org/10.1111/j.1461-0248.2009.01355.x>.
- Hengeveld, R., and J. Haeck. 1982. "The Distribution of Abundance. I. Measurements." *Source: Journal of Biogeography* 9, no. 4: 303–316.
- Hollunder, R. K., M. L. Garbin, F. R. Scarano, et al. 2024. "Vapor Pressure Deficit Drives the Mortality of Understorey Woody Plants During Drought Recovery in the Atlantic Forest." *Journal of Vegetation Science* 35, no. 1: 1–13. <https://doi.org/10.1111/jvs.13222>.
- Holt, R. D., and T. H. Keitt. 2005. "Species' Borders: A Unifying Theme in Ecology." *Oikos* 108, no. 1: 3–6. <https://doi.org/10.1111/j.0030-1299.2005.13145.x>.
- Hutchinson, G. E. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427.
- John, J. A., and N. R. Draper. 1980. "An Alternative Family of Transformations." *Journal of the Royal Statistical Society: Series C: Applied Statistics* 29, no. 2: 190–197. <https://www.jstor.org/stable/2986305>.
- Jump, A. S., J. M. Hunt, and J. Penuelas. 2006. "Rapid Climate Change-Related Growth Decline at the Southern Range Edge of *Fagus sylvatica*." *Global Change Biology* 12, no. 11: 2163–2174. <https://doi.org/10.1111/j.1365-2486.2006.01250.x>.
- Jump, A. S., C. Mátyás, and J. Penuelas. 2009. "The Altitude-For-Latitude Disparity in the Range Retractions of Woody Species." *Trends in Ecology & Evolution* 24, no. 12: 694–701. <https://doi.org/10.1016/j.tree.2009.06.007>.
- Kirschbaum, M. U. F. 2000. "Forest Growth and Species Distribution in a Changing Climate." *Tree Physiology* 20, no. 5–6: 309–322. <https://doi.org/10.1093/treephys/20.5-6.309>.
- Kunstler, G., T. Curt, and J. Lepart. 2004. "Spatial Pattern of Beech (*Fagus sylvatica* L.) and Oak (*Quercus pubescens* Mill.) Seedlings in Natural Pine (*Pinus sylvestris* L.) Woodlands." *European Journal of*



- Forest Research* 123, no. 4: 331–337. <https://doi.org/10.1007/s10342-004-0048-0>.
- Kunstler, G., A. Guyennon, S. Ratcliffe, et al. 2020. “Demographic Performance of European Tree Species at Their Hot and Cold Climatic Edges.” *Journal of Ecology* 1–14: 1041–1054. <https://doi.org/10.1111/1365-2745.13533>.
- Kusch, E., and R. Davy. 2022. “KrigR-a Tool for Downloading and Statistically Downscaling Climate Reanalysis Data.” *Environmental Research Letters* 17, no. 2: 024005. <https://doi.org/10.1088/1748-9326/ac48b3>.
- Kuznetsova, A., and P. Brockhoff. 2017. “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software* 82, no. 13: 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lee-Yaw, J. A., M. Fracassetti, and Y. Willi. 2018. “Environmental Marginality and Geographic Range Limits a Case Study With *Arabidopsis Lyrata*.” *Ecography* 41, no. 4: 567–712. <https://doi.org/10.1111/ecog.02869>.
- Mausolf, K., W. Härdtle, K. Jansen, et al. 2018. “Legacy Effects of Land-Use Modulate Tree Growth Responses to Climate Extremes.” *Oecologia* 187: 825–837. <https://doi.org/10.1007/s00442-018-4156-9>.
- McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, et al. 2020. “Pervasive Shifts in Forest Dynamics in a Changing World.” *Science* 368, no. 6494: eaaz9463. <https://doi.org/10.1126/science.aaz9463>.
- Merino, A., C. Real, J. G. Álvarez-González, and M. A. Rodríguez-Gutián. 2007. “Forest Structure and C Stocks in Natural *Fagus sylvatica* Forest in Southern Europe: The Effects of Past Management.” *Forest Ecology and Management* 250, no. 3: 206–214. <https://doi.org/10.1016/j.foreco.2007.05.016>.
- Merow, C., J. P. Dahlgren, C. J. E. Metcalf, et al. 2014. “Advancing Population Ecology With Integral Projection Models: A Practical Guide.” *Methods in Ecology and Evolution* 5, no. 2: 99–110. <https://doi.org/10.1111/2041-210X.12146>.
- Moilanen, A., and M. Nieminen. 2002. “Simple Connectivity Measures in Spatial Ecology.” *Ecology* 83, no. 4: 1131–1145.
- Muffler, L., R. Weigel, A. J. Hacket-Pain, et al. 2020. “Lowest Drought Sensitivity and Decreasing Growth Synchrony Towards the Dry Distribution Margin of European Beech.” *Journal of Biogeography* 47, no. 9: 1910–1921. <https://doi.org/10.1111/jbi.13884>.
- Muñoz-Sabater, J., E. Dutra, A. Agustí-Panareda, et al. 2021. “ERA5-Land: A State-Of-The-Art Global Reanalysis Dataset for Land Applications.” *Earth System Science Data* 13, no. 9: 4349–4383. <https://doi.org/10.5194/essd-13-4349-2021>.
- Murcia, C. 1995. “Edge Effects in Fragmented Forests: Implications for Conservation.” *Trends in Ecology & Evolution* 10, no. 2: 58–62. [https://doi.org/10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6).
- Oldfather, M. F., M. M. Kling, S. N. Sheth, N. C. Emery, and D. D. Ackerly. 2019. “Range Edges in Heterogeneous Landscapes: Integrating Geographic Scale and Climate Complexity Into Range Dynamics.” *Global Change Biology* 26, no. 3: 1055–1067. <https://doi.org/10.1111/gcb.14897>.
- Parmesan, C. 2006. “Ecological and Evolutionary Responses to Recent Climate Change.” *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>.
- Parmesan, C., and G. Yohe. 2003. “A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems.” *Nature* 421, no. 6918: 37–42. <https://doi.org/10.1038/nature01286>.
- Peñuelas, J., and M. Boada. 2003. “A Global Change-Induced Biome Shift in the Montseny Mountains (NE Spain).” *Global Change Biology* 9, no. 2: 131–140. <https://doi.org/10.1046/j.1365-2486.2003.00566.x>.
- Peñuelas, J., J. M. Hunt, R. Ogaya, and A. S. Jump. 2008. “Twentieth Century Changes of Tree-Ring  $\delta^{13}C$  at the Southern Range-Edge of *Fagus sylvatica*: Increasing Water-Use Efficiency Does Not Avoid the Growth Decline Induced by Warming at Low Altitudes.” *Global Change Biology* 14, no. 5: 1076–1088. <https://doi.org/10.1111/j.1365-2486.2008.01563.x>.
- Peñuelas, J., R. Ogaya, M. Boada, and A. S. Jump. 2007. “Migration, Invasion and Decline: Changes in Recruitment and Forest Structure in a Warming-Linked Shift of European Beech Forest in Catalonia (NE Spain).” *Ecography* 30, no. 6: 829–837. <https://doi.org/10.1111/j.2007.0906-7590.05247.x>.
- Perring, M. P., P. De Frenne, L. Baeten, et al. 2016. “Global Environmental Change Effects on Ecosystems: The Importance of Land-Use Legacies.” *Global Change Biology* 22, no. 4: 1361–1371. <https://doi.org/10.1111/GCB.13146>.
- Picard, N., M. Marchi, M. J. Serra-Varela, et al. 2022. “Marginality Indices for Biodiversity Conservation in Forest Trees.” *Ecological Indicators* 143, no. 109367: 109367. <https://doi.org/10.1016/j.ecolind.2022.109367>.
- Pironon, S., G. Papuga, J. Vilellas, A. L. Angert, M. B. García, and J. D. Thompson. 2017. “Geographic Variation in Genetic and Demographic Performance: New Insights From an Old Biogeographical Paradigm.” *Biological Reviews* 92, no. 4: 1877–1909. <https://doi.org/10.1111/brv.12313>.
- Pironon, S., J. Vilellas, W. F. Morris, D. F. Doak, and M. B. García. 2015. “Do Geographic, Climatic or Historical Ranges Differentiate the Performance of Central Versus Peripheral Populations?” *Global Ecology and Biogeography* 24, no. 6: 611–620. <https://doi.org/10.1111/geb.12263>.
- Príncipe, A., A. Nunes, P. Pinho, C. Aleixo, N. Neves, and C. Branquinho. 2022. “Local-Scale Factors Matter for Tree Cover Modelling in Mediterranean Drylands.” *Science of the Total Environment* 831: 154877. <https://doi.org/10.1016/j.scitotenv.2022.154877>.
- R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org/>.
- Rita, A., A. Saracino, E. Cieraad, et al. 2023. “Topoclimate Effect on Treeline Elevation Depends on the Regional Framework: A Contrast Between Southern Alps (New Zealand) and Apennines (Italy) Forests.” *Ecology and Evolution* 13, no. 1: e9733. <https://doi.org/10.1002/ece3.9733>.
- Ruiz-Benito, P., J. Madrigal-González, S. Ratcliffe, et al. 2014. “Stand Structure and Recent Climate Change Constrain Stand Basal Area Change in European Forests: A Comparison Across Boreal, Temperate, and Mediterranean Biomes.” *Ecosystems* 17: 1439–1454. <https://doi.org/10.1007/s10021-014-9806-0>.
- Ruiz-Benito, P., E. R. Lines, L. Gó Mez-Aparicio, M. A. Zavala, and D. A. Coomes. 2013. “Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition.” *PLoS One* 8, no. 2: e56843. <https://doi.org/10.1371/journal.pone.0056843>.
- Sanchez-Martinez, P., J. Martínez-Vilalta, K. G. Dexter, R. A. Segovia, and M. Mencuccini. 2020. “Adaptation and Coordinated Evolution of Plant Hydraulic Traits.” *Ecology Letters* 23, no. 11: 1599–1610.
- Sánchez de Dios, R., C. Gómez, I. Aulló, et al. 2021. “*Fagus sylvatica* L. Peripheral Populations in the Mediterranean Iberian Peninsula: Climatic or Anthropogenic Relicts?” *Ecosystems* 24, no. 1: 211–226. <https://doi.org/10.1007/s10021-020-00513-8>.
- Schielzeth, H. 2010. “Simple Means to Improve the Interpretability of Regression Coefficients.” *Methods in Ecology and Evolution* 1, no. 2: 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>.
- Senf, C., D. Pflugmacher, Y. Zhiqiang, et al. 2018. “Canopy Mortality Has Doubled in Europe's Temperate Forests Over the Last Three Decades.” *Nature Communications* 9, no. 1: 1–8. <https://doi.org/10.1038/s41467-018-07539-6>.

- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. "Evolution and Ecology of Species Range Limits." *Annual Review of Ecology, Evolution, and Systematics* 40: 415–436. <https://doi.org/10.1146/annurev.ecolsys.110308.120317>.
- Tanentzap, A. J., E. P. Mountford, A. S. Cooke, and D. A. Coomes. 2012. "The More Stems the Merrier: Advantages of Multi-Stemmed Architecture for the Demography of Understorey Trees in a Temperate Broadleaf Woodland." *Journal of Ecology* 100, no. 1: 171–183. <https://doi.org/10.1111/j.1365-2745.2011.01879.x>.
- Vilà-Cabrera, A., J. Astigarraga, A. S. Jump, et al. 2023. "Anthropogenic Land-Use Legacies Underpin Climate Change-Related Risks to Forest Ecosystems." *Trends in Plant Science* 28, no. 10: 1132–1143. <https://doi.org/10.1016/j.tplants.2023.04.014>.
- Vilà-Cabrera, A., J. M. Espelta, J. Vayreda, and J. Pino. 2017. "“New Forests” From the Twentieth Century Are a Relevant Contribution for C Storage in the Iberian Peninsula." *Ecosystems* 20: 130–143. <https://doi.org/10.1007/s10021-016-0019-6>.
- Vilà-Cabrera, A., and A. S. Jump. 2019. "Greater Growth Stability of Trees in Marginal Habitats Suggests a Patchy Pattern of Population Loss and Retention in Response to Increased Drought at the Rear Edge." *Ecology Letters* 22: 1439–1448. <https://doi.org/10.1111/ele.13329>.
- Vilà-Cabrera, A., A. C. Premoli, and A. S. Jump. 2019. "Refining Predictions of Population Decline at species' Rear Edges." *Global Change Biology* 25, no. 5: 1549–1560. <https://doi.org/10.1111/gcb.14597>.
- Villaescusa, R., and R. Díaz. 1998. *Segundo inventario forestal nacional (1986–1996)*. ICONA, Madrid: Ministerio de Medio Ambiente.
- Walther, G.-R., E. Post, P. Convey, et al. 2002. "Ecological response to recent climate change." *Nature* 416: 389–395.
- Wang, W. J., F. R. Thompson, H. S. He, J. S. Fraser, W. D. Dijk, and T. Jones-Farrand. 2019. "Climate Change and Tree Harvest Interact to Affect Future Tree Species Distribution Changes." *Journal of Ecology* 107, no. 4: 1901–1917. <https://doi.org/10.1111/1365-2745.13144>.
- Weiss, A. D. 2001. "Topographic Position and Landforms Analysis." Poster Presentation, ESRI User Conference, San Diego, CA. <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Topographic+Position+and+Landforms+Analysis#0>.
- Winkler, K., R. Fuchs, M. Rounsevell, and M. Herold. 2021. "Global Land Use Changes Are Four Times Greater Than Previously Estimated." *Nature Communications* 12, no. 1: 1–10. <https://doi.org/10.1038/s41467-021-22702-2>.
- Yuan, W., Y. Zheng, S. Piao, et al. 2019. "Increased Atmospheric Vapor Pressure Deficit Reduces Global Vegetation Growth." *Science Advances* 5, no. 8: 1–12. <https://doi.org/10.1126/sciadv.aax1396>.
- Zellweger, F., P. De Frenne, J. Lenoir, et al. 2020. "Forest Microclimate Dynamics Drive Plant Responses to Warming." *Science* 370, no. 6522: 772–775. <https://doi.org/10.1126/science.abf2939>.
- Zhang, K., J. S. Kimball, R. R. Nemani, et al. 2015. "Vegetation Greening and Climate Change Promote Multidecadal Rises of Global Land Evapotranspiration." *Scientific Reports* 5: 1–9. <https://doi.org/10.1038/srep15956>.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section.