



Less suitable climatic conditions and pests increase tree defoliation in Spanish Iberian Peninsula forests

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ABSTRACT

Forest vulnerability to climate change is expected to differ between species and across species ranges. Therefore, it is important to develop tools that can standardize the variability in regional climate patterns and extreme events for populations and species. Extreme climate events, such as droughts and heat waves, have the potential to severely impact populations that are already close to the limits of their physiological tolerance. These factors can be further exacerbated in tree populations when coupled with detrimental biotic interactions, such as pathogen and insect infestations. We analysed a monitoring network dataset of tree defoliation from 2005 to 2013 including 560 plots situated in the Iberian Peninsula. We utilized a climatic suitability index obtained from Ecological Niche Models (ENMs), to investigate whether changes in the climatic suitability for seven forest species and the presence of biotic agents correlated with tree defoliation. Our results emphasized that higher levels of tree defoliation were significantly associated with lower climatic suitability. Likewise, these levels increased significantly with high pest intensity. Interestingly, climatic suitability interacted with pests to explain defoliation patterns. *Pinus sylvestris* and *Quercus pyrenaica* were particularly susceptible to defoliation in areas with lower climatic suitability and with increasing pest intensity. This suggests that pests play an important role in understanding species performance under less climatic suitable conditions, at least in the forests of the Spanish Iberian Peninsula. Our findings can serve as a valuable tool for identifying forest populations and species especially susceptible to the impacts of changing climatic conditions on a regional scale. This contribution aids in the incorporation of innovative conceptual tools and processes into the decision-making and management of forest ecosystems in the current context of climate change.

1. Introduction

Accumulating evidence suggests that forest die-off is a phenomenon widely reported in forest ecosystems around the globe (Allen et al., 2010; Hammond et al., 2022). This phenomenon, characterized by loss of green coverage, leaf browning, growth reduction, partial dieback and even tree mortality (Ostry et al., 2010), has a negative impact on forest ecosystem functions and services (Anderegg et al., 2013; Thom and Seidl, 2016). Quantifying the factors that trigger this phenomenon remains a major challenge given the complexity of the interactions among multiple threats, such as climate change and pest attacks (Anderegg et al., 2015a). While climate change has been linked to in-

creased die-off processes due to extreme climatic conditions such as acute drought and temperature stress (Greenwood et al., 2017; Senf et al., 2020), forest pests have contributed to the loss of foundational tree species (Simler-Williamson et al., 2019), creating substantial ecological and economic challenges. Understanding the interactions between these abiotic and biotic factors will be essential to predicting die-off processes for a sustainable forestry management in the current changing world (Anderegg et al., 2015a).

Global biogeographic assessments of forest die-off suggest that extreme climatic events have a differential effect on local tree populations due to the spatial variation in environmental conditions and species physiology (Allen et al., 2010). In the last years, the interest in demon-

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strating these predictions has gained importance due to the current context of climate change (Hampe and Petit, 2005; Vilà-Cabrera et al., 2019). Several authors have pointed that species perform less robustly when populations experience environmental conditions close to their tolerance limits (Thuiller et al., 2014), although empirical evidence remains rare (Dallas et al., 2017; Pironon et al., 2017; Sagarin and Gaines, 2002). However, these harsh conditions could explain forest die-off events along of the species distribution ranges.

Ecological Niche Models (ENMs) have become a popular approach to estimate environmental conditions under which species can maintain viable populations and the associated potential geographic distribution, particularly when the presence of species is the only information available (Franklin, 2010; Peterson et al., 2011). Presence data, represented as a set of localities where the species has been detected, are related with a set of environmental variables via various computational algorithms, to predict presence probability or relative presence probability (Merow et al., 2013). Model outputs, interpreted as a suitability index, synthesizes the degree to which such conditions are adequate for the species, according to the environmental gradients that the species encounter through their entire distribution range (Soberón and Peterson, 2005). Accordingly, ENMs have been widely used under average climatic conditions to predict changes in distributional patterns of the forest species (i.e., climatic suitability) (Hirzel and Le Lay, 2008; Pecchi et al., 2019). Based in this approach, it would be expected that lower climatic suitability represents less suitable conditions and thus lower capacity to respond to additional sources of stress such as disease, nutrient deficiencies, or extreme climatic events. Indeed, several studies have used estimates of this index to explain the impact of extreme climatic episodes, such as acute drought and temperature stress, on co-occurring species (Pérez Navarro et al., 2019; Sapes et al., 2017), on populations of dominant tree species across regions (Lloret and Kitzberger, 2018; Margalef-Marrase et al., 2020) and on tree populations affected by insect pests (Jaime et al., 2019). These empirical evidences demonstrate that this index could become an attractive tool to standardize the magnitude of climate variability on tree population performances, improving our ability to predict the vulnerability of populations or species to ongoing climate change (Lloret and Kitzberger, 2018; Margalef-Marrase et al., 2022).

On the other hand, assuming that less suitable conditions can be identified using abiotic factors, other factors may impose additional constraints on population performances. Although several studies have demonstrated the compounding effects of climatic variables along with biotic agents (i.e., pathogens and pest insects) on tree die-off (Chapman et al., 2012; Creeden et al., 2014; Hart et al., 2014), we still do not have full understanding on how forest performance responds to the interaction between changes in suitable conditions and biotic agents (e.g., pests). In this regard, conducting an analysis that evaluates such interactions would significantly enhance our comprehension of forest die-off events across species' distribution ranges. Moreover, such an analysis would provide informative results pertaining to the conservation efforts aimed at addressing these issues.

In Europe, patterns of forest die-off are particularly relevant in the Iberian Peninsula (de la Cruz et al., 2014). For example, episodes of die-off, marked by severe defoliation, impacted approximately 14,000 ha of Spanish pine forests (Voltas et al., 2013). Extreme climatic conditions, coupled with the presence of pathogens and outbreaks of pest insects, were likely the primary drivers (Jaime et al., 2019). Given the increasing drought and temperature expected in the Mediterranean areas due to climate change, the Iberian Peninsula represents a suitable place to evaluate how these less suitable climatic conditions, along with biotic agents, could affect the performance of forest species in the future. We used four Spanish *Quercus* species and three *Pinus* species as a case study to understand the critical factors affecting forest health in Mediterranean forests. These forests have been monitored from 1985 to the present through an intensive monitoring forest health network us-

ing harmonized ICP methods (Eichhorn et al., 2016). This network provides a unique framework for comprehending the intricate mechanisms driving species decline across their entire geographical distribution (Axelson et al., 2019). Specifically, we investigate whether changes in suitable climates for forests and the presence of pests correlate with species responses (e.g., tree defoliation), aiming to increase our understanding of forest die-off events and discuss potential management implications. Our method entails the following steps: a) evaluate the potential of ENMs to predict the geographical distribution of climatic suitability for forest species, and b) assess how climatic suitability, the presence of damaging biotic agents, and their interplay may explain patterns of tree defoliation in the Iberian Peninsula. We hypothesize that tree defoliation is dependent on i) the climatic requirements of each tree species (tree defoliation should be higher in marginal climates in relation to the species' climate niche), and ii) pest availability (tree defoliation should be higher at sites where several pests are present).

2. Materials and methods

2.1. Study area and forest species

The study area covers the Spanish Iberian Peninsula (Fig. 1), an area geographically isolated from the rest of Europe by the Pyrenees, and from Africa by the Strait of Gibraltar. This zone represents a transitional area between temperate and Mediterranean climates with lower temperatures towards the northern regions and a decrease in elevation and precipitation towards the south and east due to the contrasting influences of the Atlantic Ocean and the Mediterranean Sea (Gazol et al., 2022). Given the increasing drought and temperature expected in the Spanish Iberian Peninsula due to climate change (Davi et al., 2020), this area represents suitable place for studying how these less suitable climatic conditions and induced disturbances by pests may affect the performance of forest species.

We studied seven common European tree species (three Pinaceae and four Fagaceae) widely distributed in Spanish Iberian Peninsula namely: *Pinus halepensis*, *P. pinaster*, *P. sylvestris*, *Quercus faginea*, *Q. ilex*, *Q. suber* and *Q. pyrenaica*. Aleppo pine (*P. halepensis*) is a species whose current distribution is confined to the thermo- and meso-Mediterranean biogeographic belts (Ducrey et al., 1996). Maritime pine (*P. pinaster*) is a specie widely distributed in the western Mediterranean Basin and along the Atlantic coast of Portugal, Spain, and France (Tapias et al., 2004). Scots pine (*P. sylvestris*) is a one of the most widespread conifers in Europe with rear-edge populations in the northern Spain (Carlisle and Brown, 1968), where drought-induced dieback has recently been observed (Galiano et al., 2010). Lusitanian oak (*Q. faginea*) is a widespread tree in the Iberian Peninsula, extending through Morocco, Algeria, Portugal and Spain (Gonzalez-Benito and Perez-Ruiz, 1992). Holm oak (*Q. ilex*) is widely considered a circum-Mediterranean tree species that covers a large geographic range in the Mediterranean Basin, from the Iberian Peninsula and northwestern Africa to Greece and northern Anatolian Peninsula (Martín-Sánchez et al., 2022). Cork oak (*Q. suber*) is a species distributed throughout the western Mediterranean region, where it holds both high economic importance and a vast ecological significance (Benito Garzón et al., 2008). Finally, Pyrenean oak (*Q. pyrenaica*) is a widely distributed species in the western Mediterranean region, extending through southwest France, the Iberian Peninsula and northern Morocco (Camisón et al., 2015).

2.2. Distribution and climatic data

To represent the distribution of the species studied, we obtained occurrence data at a 1 × 1 km resolution from the EU-Forest dataset (Mauri et al., 2017) (Appendix 1). This database is based on almost 250,000 plots in the National Forest Inventories of most European countries and includes a total of 588,983 occurrence records for 242

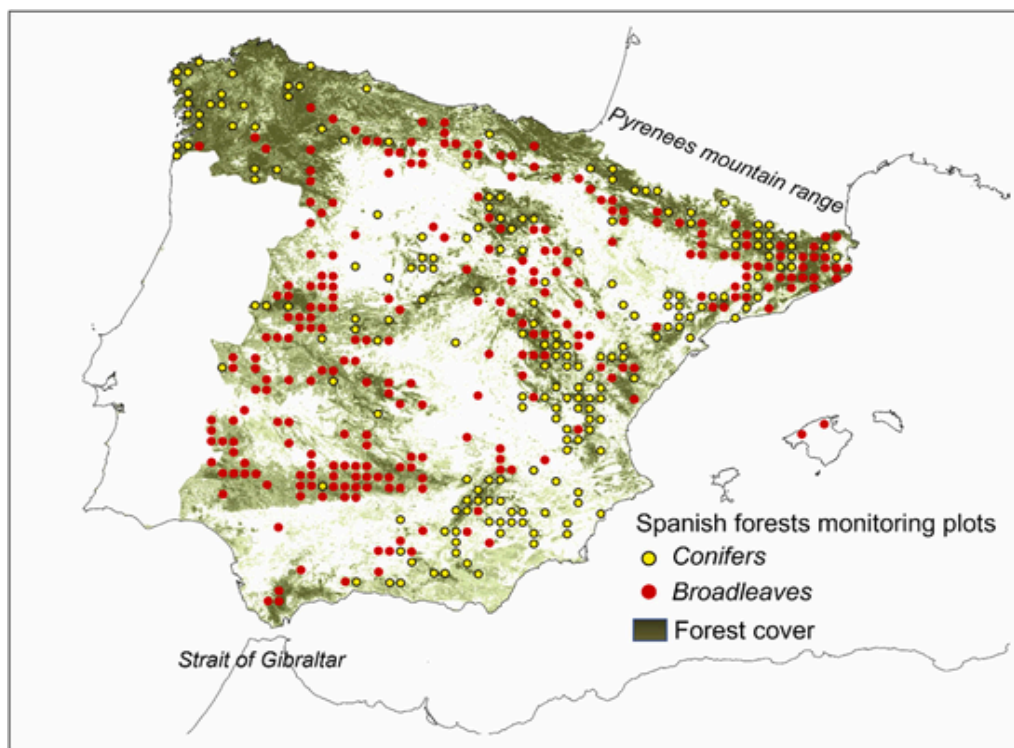


Fig. 1. Spatial distribution of Level I Forests monitoring plots of the Spanish network. Yellow dots represent plots for the *Pinus* species analysed and red dots represent plots for the *Quercus* species.

tree species. For each analysed species, we reduced effects of spatial autocorrelation and overfitting in the ENMs (Veloz, 2009), by thinning records within a distance of 5 km using the `ntbox` package (Osorio-Olvera et al., 2020) in R version 3.6.1 (R Core Team, 2019). We set aside one data subset for independent model testing (5 % of the occurrences) and split the remaining occurrences randomly into 50–50 % subsets for model calibration and internal testing, respectively.

We used climatic data to predict the geographical distribution of climatic suitability for forest species across their distribution range. Climatic data (average conditions representative of 1973–2013) were downloaded from the CHELSA database at a 30 arc-second resolution (~900 m) (<http://chelsa-climate.org/>). This dataset offers enhanced climatic estimates in regions with complex terrain (Karger et al., 2017). We selected four bioclimatic variables to capture a wide spectrum of seasonal and annual climatic patterns across the study area while minimizing redundancy ($|r| \leq 0.66$; see Appendix 2): mean annual temperature and precipitation (`bio1` and `bio12`, respectively), along with temperature and precipitation seasonality (`bio4` and `bio15`, respectively). These variables were selected due to their significant association with crucial ecological processes in forest such as distribution, reproduction, and phenology (Zuckerberg et al., 2020), as well as their impact on the cumulative effects of drought on forests (Gazol et al., 2022). Climate data were aggregated by averaging to 1×1 km to match the species data grid. All spatial information processing was handled using ArcGIS 10.3.1 (ESRI, 2015).

2.3. Tree crown condition and biotic agent data

Defoliation is one of the main factors used to study the impact of environmental drivers on forest die-off (Carnicer et al., 2011). In forest die-off studies, defoliation refers to the reduction of overall crown volume. This variable is a good proxy indicator of future mortality and forest health, and it integrates the effects of other factors such as water and

nutrient availability (Sánchez-Salguero et al., 2012). Tree defoliation rates in the Spanish Iberian Peninsula was investigated using data from the Spanish Level I monitoring forest health network (Fig. 1), which conducts annual assessments at a 16×16 km grid across Spain (Eichhorn et al., 2016). In brief, at least 24 dominant trees per plot with a height of >0.6 m are surveyed annually, and defoliation status is assessed. Defoliation is assessed visually on all the selected trees into one of twenty percentage classes (intervals of 5 units between 0 and 100) in comparison to a local “reference tree” by the same independent team (see (Eichhorn et al., 2016)). To match the defoliation data and biotic agents with climatic baseline data we used tree plot data from 2005 until 2013. We analysed 560 plots to assess spatial patterns of tree defoliation for each species. The percentage of tree defoliation was computed at the plot level, representing the average defoliation across the entire 9-year study period (Table 1). Pests (i.e., pathogen and insects) were recorded by field crews when possible. Pathogen and insect pests are described using standard symptoms, apparent severity (level of damage and number of affected trees), and the inferred cause (when known)

Table 1

Description of the analysed plots per species. In each case the description includes: number of analysed plots, ranges of tree defoliation, pest severity and climatic suitability.

Species	<i>n</i> plot	% Tree defoliation (range)	Climatic suitability (range)	Pest severity (range)
Conifers				
<i>Pinus halepensis</i>	95	14.76–33.01	0.258–0.863	0–139
<i>Pinus pinaster</i>	80	5.000–40.83	0.385–0.938	0–168
<i>Pinus sylvestris</i>	76	9.310–57.50	0.397–0.783	0–143
Broadleaves				
<i>Quercus ilex</i>	182	11.72–51.74	0.321–0.818	0–160
<i>Quercus suber</i>	35	8.701–48.33	0.257–0.892	0–155
<i>Quercus faginea</i>	45	10.00–53.01	0.314–0.964	0–115
<i>Quercus pyrenaica</i>	46	7.220–33.84	0.362–0.952	0–218

(see (Eichhorn et al., 2016)). Pest severity was expressed as number of trees-integrating multiple species- affected during our 9-year study period. Additionally, we categorized pests into distinct groups, including defoliators, borers, gall-maker, and fungi, to evaluate the effects of different agent groups on tree defoliation (Appendix 3). By including these variables in our models, we aim to provide a comprehensive understanding of the multifaceted factors influencing tree defoliation, thereby informing more targeted and effective forest management strategies.

2.4. Climatic suitability modelling

We used ENMs to assess relationships between each forest tree species distribution and climatic variables, and to obtain measures of broad-scale climatic suitability, under the averaged climatic conditions that characterize our study sites (1973–2013 period). The assumption behind ENMs is that species' distribution in the geographical space (occurrences record) represent the range of environmental conditions that under which species are able to reproduce and survive (Soberon and Peterson, 2005). Model outputs can thus be interpreted as an index of the climatic suitability experienced by populations in a given site (Franklin, 2010) and can be used to assess the relationship between suitable conditions and forest die-off events.

We used Maxent version 3.4.4 (Phillips et al., 2017) to model and map the geographic distribution of suitable climate for forest species within the study area. To select the area with which to calibrate the model, we used a minimum convex polygon produced by the full set of sampling points for each species (Appendix 1). For all species, we used the KUENM R package (Cobos et al., 2019), in R (R Core Team, 2019), to select the best model provided by Maxent from a series of candidates arranged by different combinations of parameter settings (Merow et al., 2014). Herein, we created 119 candidate models by combining the whole set of independent variables, 17 regularization multiplier values (0.1–1.0 at intervals of 0.1, 2–6 at intervals of 1, and 8 and 10), and the 7 possible combinations among the following feature classes: linear, quadratic, and product. Candidate models were selected by considering significance (partial ROC, with 500 iterations and 50 % of data for bootstrapping), omission rates ($E < 5\%$), and model complexity (models within 2 AICc units of the minimum value among the candidate models). We then created the best fitted final models using the full set of occurrences and the selected parameterization (Appendix 4). Finally, we carried out an additional external validation of the best fitted models with partial ROC and similar omission rates using an independent dataset. We used the raw output of Maxent models in further analyses because this is the output with the most straightforward interpretation (Merow et al., 2013).

2.5. Statistical analyses

2.5.1. Geographical distribution of climatic suitability

We randomly selected 1000 sampling points within the distribution range of each species in Iberian Peninsula (Fig. 1) and sampled climatic suitability values and elevation using a Digital Terrain Model at a 30 arc-second resolution (~900 m) (<http://chelsa-climate.org/>). Subsequently, we employed three sequential approaches to illustrate the geographical patterns of forest climatic suitability. Firstly, we conducted generalized least squares (GLS) models, regressing climatic suitability values against elevation, latitude, and longitude coordinates. This approach allowed us to investigate changes in climatic suitability for forest species across their distribution ranges in Iberian Peninsula. Secondly, we evaluated the spatial autocorrelation of climatic suitability using Moran's index. Given the extensive spatial scale of our study area (Fig. 1), this index was used in identifying spatial clustering of climatic suitability, shedding light on potential spatial autocorrelation effects for further analyses (Tellería et al., 2021). Lastly, to address potential

spatial autocorrelation effects in the GLS models, we considered five alternative spatial correlation structures (exponential, Gaussian, spherical, linear, and rational quadratic) and employed AICc to select the optimal model (Dormann et al., 2007). These analyses were conducted using the "nlme" package (Pinheiro et al., 2020) in R.

2.5.2. Tree defoliation modelling

To assess the effects of climatic suitability and pests on the distribution patterns of tree defoliation, we conducted GLS models with tree defoliation as the dependent variable and climatic suitability and pest severity as explanatory variables. The interactions between climatic suitability and pest severity were also introduced. The effect of spatial autocorrelation was controlled considering five spatial correlation structures (exponential, Gaussian, spherical, linear, and rational quadratic) and we used AICc to select the best model. Previous to analysis, we standardized all explanatory variables (mean = 0, standard deviation = 1; (Gelman, 2008)).

3. Results

3.1. Climatic suitability via ENMs

For each of our seven species, we found at least one model that met all our performance criteria: statistically significant partial ROC tests (mean AUC ratio of 1.43; $P < 0.001$; Appendix 4), and low omission error values (mean of 0.04 %). Based on these performance estimates, our models were better than random and had good discrimination capacity in recovering the climatic niches for each forest species. There was a single model within the candidates for each species that had an AIC value that exceeded 2 units from all other candidates. The most important variables on average contributing to models of forest trees were mean annual temperature (bio1; 57.1 %) followed by precipitation seasonality (bio15; 28.6 %) and annual precipitation (bio12; 14.3 %; Table 2). Mean annual temperature had a unimodal effect on climatic suitability for most species analysed except for *Q. suber* that reported a positive linear effect. On the other hand, precipitation seasonality had a negative or unimodal effect on climatic suitability for most species except for *Q. suber* and *P. pinaster*, which exhibited a preference for high precipitation seasonality. Finally, annual precipitation had a unimodal effect on climatic suitability for *Quercus* species, while for *Pinus* species, climatic suitability of *P. sylvestris* increased with precipitation, decreased with precipitation for *P. halepensis*, and had a unimodal effect for *P. pinaster*.

Geographical distributions of climatic suitability for each species are showed in Fig. 2. In the Iberian Peninsula, climatic suitability in-

Table 2

Estimates of the relative contribution of bioclimatic variables to predict climatic suitability for the forest species. The values represent the percent contribution importance of each variable in the best selected models. Percent contribution indicates the change in regularized gain by adding the corresponding variable.

Species	Bioclimatic variables			
	bio1	bio4	bio12	bio15
Conifers				
<i>Pinus halepensis</i>	11.9 (Ω)	23.7 (-)	26.6 (-)	37.7 (-)
<i>Pinus pinaster</i>	39.9 (Ω)	17.8 (+)	28.9 (Ω)	15.5 (+)
<i>Pinus sylvestris</i>	74.2 (Ω)	13.9 (-)	0.50 (+)	11.4 (-)
Broadleaves				
<i>Quercus ilex</i>	29.2 (Ω)	11.0 (-)	31.2 (Ω)	28.6 (Ω)
<i>Quercus suber</i>	9.10 (+)	3.70 (-)	41.7 (Ω)	45.5 (+)
<i>Quercus faginea</i>	44.4 (Ω)	15.3 (Ω)	21.0 (Ω)	19.3 (-)
<i>Quercus pyrenaica</i>	54.6 (Ω)	4.10 (-)	26.8 (Ω)	14.5 (Ω)

Symbols in parentheses show the trend of the response curves for the variables: + increase, - decrease, Ω hump-shaped, = no trend.

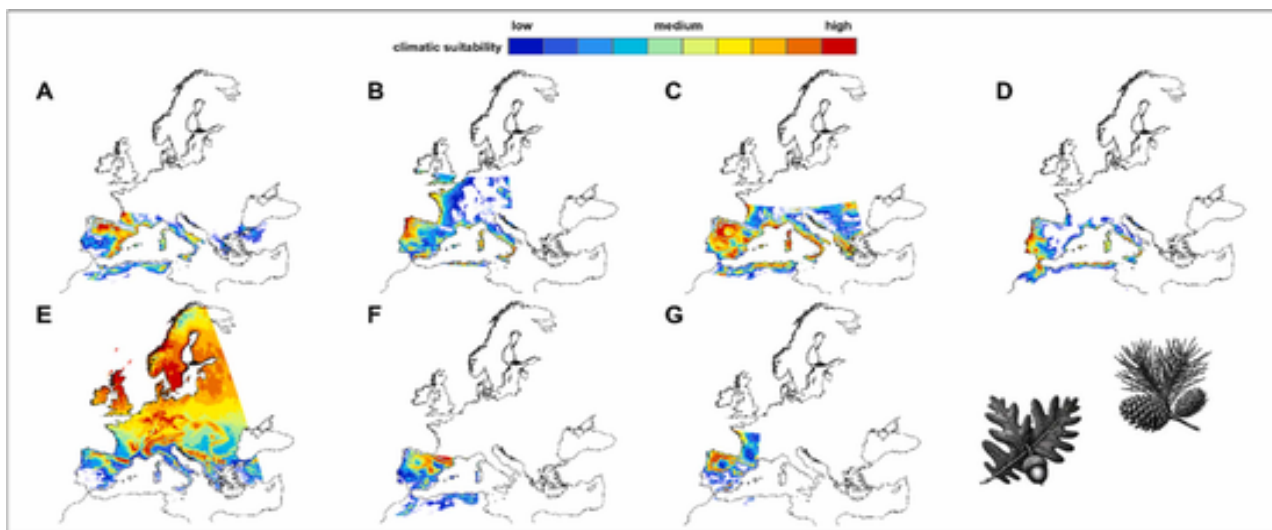


Fig. 2. Climatic suitability distribution per analysed species. A, *Pinus halepensis*; B, *P. pinaster*; C, *Quercus ilex*; D, *Q. suber*; E, *P. sylvestris*; F, *Q. faginea* and G, *Q. pyrenaica*.

creased significantly with elevation for most forest species except for *P. halepensis* and *Q. suber* where the highest suitability values were distributed in the lowest elevation areas (Table 3). In relation to longitudinal patterns, higher suitable climates for most species were significantly lo-

Table 3
Distribution patterns of climatic suitability for each species within the study area.

Species	Intercept	Elevation	Longitude	Latitude
Conifers				
<i>Pinus halepensis</i>	-0.21 [*]	-0.32 ^{***}	0.43 ^{***}	0.11
<i>Pinus pinaster</i>	-0.02	0.08 [^]	-0.82 ^{***}	0.36 ^{***}
<i>Pinus sylvestris</i>	-0.01	0.70 ^{***}	-0.11 [*]	0.48 ^{***}
Broadleaves				
<i>Quercus ilex</i>	-0.15	0.08	-0.11	-0.24 [*]
<i>Quercus suber</i>	0.03	-0.20 ^{***}	-0.66 ^{***}	-0.08
<i>Quercus faginea</i>	-0.04	0.39 ^{***}	0.21 [*]	0.32 ^{***}
<i>Quercus pyrenaica</i>	0.03	0.56 ^{***}	-0.35 ^{***}	0.42 ^{***}

Significance: [^] p < 0.10,

** p < 0.01,

* p < 0.05,

*** p < 0.001.

Table 4

Defoliation model of studied species. Results are for the coefficients of the best generalized least squares mixed models (GLS) selected according to AICc, in which the canopy forest defoliation have been regressed against climatic suitability index (HSI) and pest severity (INS_DEF = defoliator insects, INS_PER = borer insects, INS_AGA = insect gall-makers, HON_TIZ = bur oak blight) for 3 gymnosperm species and 4 angiosperm species. Interactions between variables are indicated with “:”.

species	Intercept	HSI	INS_DEF	HS:INS_DEF	INS_PER	HS:INS_PER	HON_TIZ	HS:HON_TIZ	INS_AGA	HS:INS_AGA
Conifers										
<i>Pinus halepensis</i>	20.8 ^{***}	-2.28 ^{***}	0.09	0.06						
<i>Pinus pinaster</i>	23.6	-1.94 [*]	0.73	-0.21						
<i>Pinus sylvestris</i>	17.9 ^{***}	-2.81 ^{***}	1.7 [*]	-2.59 ^{***}						
Broadleaves										
<i>Quercus ilex</i>	22.0 ^{**}	-1.69 ^{**}			-0.16	-0.31	0.99 [*]	-0.24		
<i>Quercus suber</i>	22.7 ^{***}	-4.93 ^{***}			4.39 [*]	-1.18	-1.35	-0.59	0.03	-0.96
<i>Quercus faginea</i>	25.8 ^{***}	-1.46 [*]			0.55	2.83			0.08	0.6
<i>Quercus pyrenaica</i>	14.5 ^{***}	-2.16 ^{***}			2.31 ^{***}	-1.26 [*]				

Significance [^] p < 0.10,

* p < 0.05,

** p < 0.01,

*** p < 0.001.

cated in western areas except for *P. halepensis* and *Q. faginea* where climatic suitability exhibited a significant increasing pattern eastward. Finally, climatic suitability exhibited a significant increase northward except for *Q. ilex* and *Q. suber* where the highest suitability values were distributed in the south.

Within the surveyed plots (Table 1), the climatic suitability values ranged from 0.258 to 0.938 for *Pinus* species, while for *Quercus* species the values ranged from 0.257 to 0.964, thus indicating great variability in climatic suitability across sites.

3.2. Influence of climatic suitability and biotic agents on the patterns of forest defoliation

In all cases, the highest effect on tree defoliation was explained by lower climatic suitability followed by pest severity, mainly defoliator insects for *Pinus* species and borer insects for *Quercus* species. Higher levels of tree defoliation were associated with lower climatic suitability and mostly greater intensity of pest severity (Table 4, Fig. 3). For *P. sylvestris* the interaction between climatic suitability and the defoliator insects revealed that the combined effect of these two factors (low climatic suitability and high pest severity) leads to a higher tree defolia-

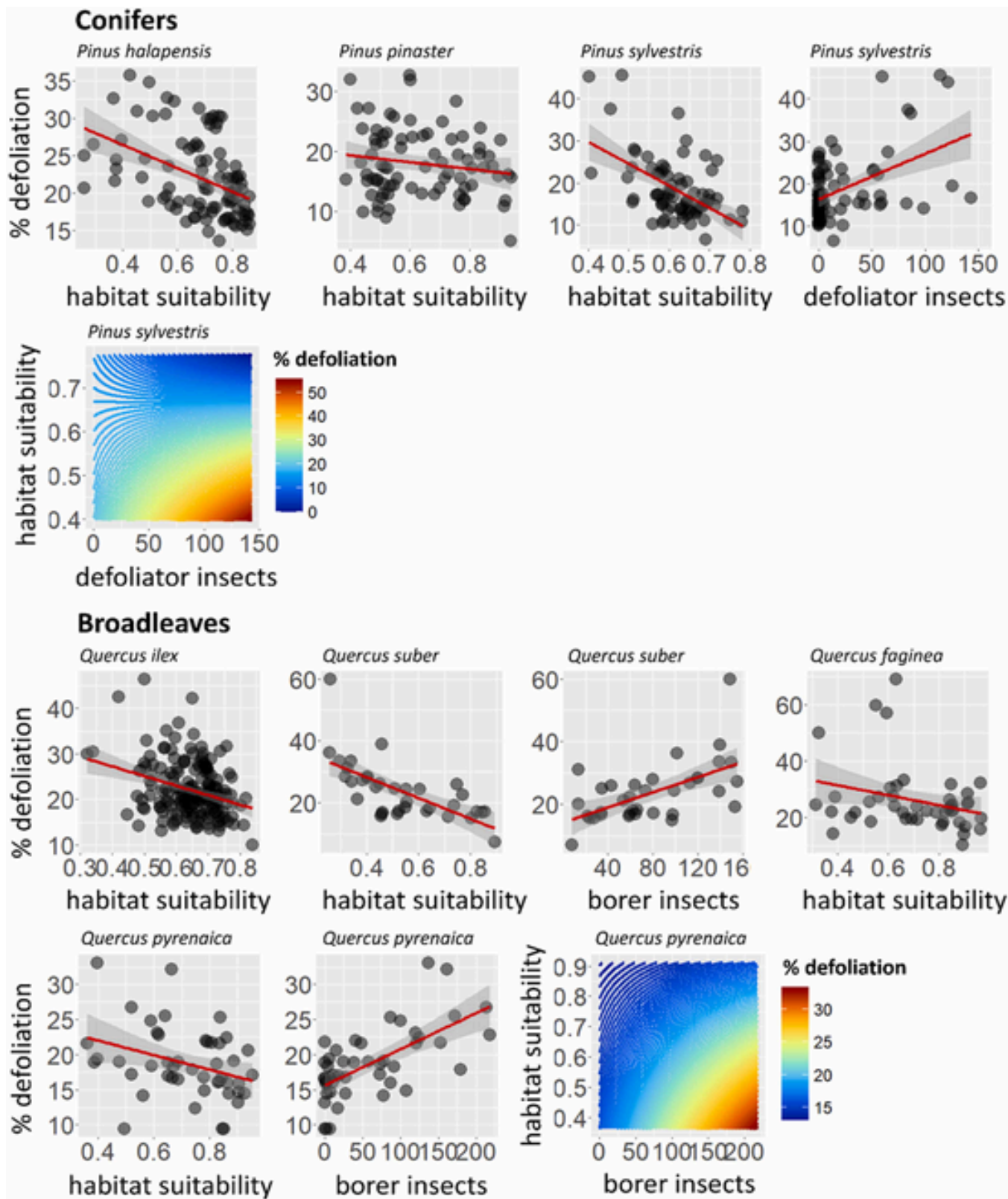


Fig. 3. Plots depicting the significant relationships obtained within the GLS with tree defoliation as the dependent variable and climatic suitability and pest severity as explanatory variables. The significant interactions between climatic suitability and pest severity were also included. Figures should be read from left to right.

tion than the effect of either alone (Table 4, Fig. 3). This was also evident in *Q. pyrenaica*.

4. Discussion

We present a comprehensive spatial assessment of tree defoliation based on a systematic health monitoring network. Forest health networks focused on specific species not only capture the spatial and temporal patterns of tree defoliation and mortality across large areas (Carnicer et al., 2011; de la Cruz et al., 2014; Neumann et al., 2017) but also highlight characteristic health patterns of forest ecosystems of regional concern (Duque-Lazo et al., 2018). This information is particularly crucial for vulnerable populations located at the geographical edges of their distribution range or in xeric areas susceptible to severe and prolonged droughts (Navarro-Cerrillo et al., 2022). Our findings suggest that a combination of stress factors is likely the main cause of defoliation across the distribution areas of the analysed species in Spain. This aligns with previous studies indicating that elevated tree defoliation rates are a significant symptom of climate change impact on drought-prone forests in southern Europe (Carnicer et al., 2011).

4.1. Climatic suitability via ENMs

ENM approaches have arisen as a widely used modelling technique to map the current species distributions based on climate preferences (Franklin, 2010). The ENMs obtained adequate results according to evaluation metrics and can thus be considered to effectively model current distributions of climatic suitability (Peterson et al., 2008). Our study supports the view that annual temperature and precipitation seasonality are important drivers of patterns of tree distribution at large scales, particularly within this biogeographic region in Europe (Ashcroft et al., 2011). As it was expected, in the Iberian Peninsula the regions with the highest climatic suitability values for most forest species were located in wet mountain areas except for *P. halepensis* and *Q. suber* where the most suitable climates were distributed in dry coastal environments. *Q. ilex* is located in areas with mesic conditions, especially in the centre and some coastal areas of the north-east. These patterns are consistent with those reported by (Serra-Diaz et al., 2013) and (Tapias et al., 2004).

Caution should be taken when interpreting ENM predictions, given the assumptions that these types of models implicitly include. ENMs assume that species respond homogeneously to climate variability across their distribution range, disregarding intra-specific genetic variability and phenotypic plasticity, which may also favour species' local adaptation under less suitable conditions (Vanhove et al., 2021). Furthermore, the use of broad spatial scale climate databases (~1 km²) may ignore the potential effects of other abiotic factors, such as microclimatic landscape features (Franklin et al., 2013). Despite these shortcomings, ENMs enable the identification of various climatic conditions unfavourable for forest species, such as drier and warmer seasonal climates. This information could be utilized to pinpoint climate conditions that exacerbate tree defoliation.

4.2. Driver of defoliation trees

We found that the combination of climatic suitability and pests was able to explain regional forest defoliation patterns in Spanish Iberian Peninsula during the period of 2005–2013. This agrees with other studies that have used ENMs to explain the effect of historical climatic suitability (Lloret and Kitzberger, 2018; Pérez Navarro et al., 2019; Sapes et al., 2017) and the pest severity (Jaime et al., 2019) on forest die-off vulnerability at local and regional scales.

Our results emphasize that, at regional scale, higher levels of tree defoliation were associated with lower climatic suitability. Biogeographic predictions establish that populations inhabiting areas with

low climatic suitability exhibit lower survivorship and recruitment (Center-Periphery hypothesis; (Weber et al., 2016)), and thus, higher extinction risk due to less favourable environmental conditions. Precisely, in these areas closest to the physiological tolerance limits of the species, the effect of extreme climatic conditions (i.e., acute drought and temperature stress) is probably more severe (Senf et al., 2020; Zimmermann et al., 2009), promoting species' die-off and imposing high levels of local selection (Bigler et al., 2006). Contrary to our results, (Jaime et al., 2019) found that high levels of *P. sylvestris* mortality by bark beetle infestation in Catalonia (Spain), were associated with higher climatic suitability. The contrasting patterns observed may reflect complex interactions between tree growth, resource allocation, and climatic conditions at a local scale. As suggested by (Jaime et al., 2019), trade-offs between tree growth and resource allocation to defence mechanisms, such as resin production, may play a role in shaping these patterns. In areas with higher climatic suitability for host trees, faster growth rates may lead to reduced investment in defence mechanisms against pests (Ferrenberg et al., 2015). These findings underscore the importance of considering both local and regional-scale factors when developing forest management strategies (Lindner et al., 2010). While local-scale studies may highlight specific mechanisms driving pest infestation, regional-scale assessments can provide valuable insights into broader patterns and potential implications for forest management.

On the other hand, it is worth highlighting that the correlation between species fitness and climatic suitability can be subject to considerable uncertainty (Dallas et al., 2017; Dallas and Hastings, 2018; Santini et al., 2019). It is likely that species interactions, local variables, human influence, dispersal limitation, or local adaptations can substantially interfere with the expected modelled relationship (Dallas et al., 2017; Osorio-Olvera et al., 2019; Sexton et al., 2009). Our results shed some light in this sense as they support the relationship between low species performance and less favourable conditions. They also support the hypothesis that climatic suitability index could be used as a tool for standardizing the response of vegetation to climatic variability across time and space (Lloret and Kitzberger, 2018; Margalef-Marrase et al., 2020).

In addition to climatic suitability, pests were also significant in explaining the observed defoliation of tree species. Our results show that *P. sylvestris* tree defoliation increased significantly with high values of pest severity specially *Thaumetopoea pityocampa*, commonly known as the pine processionary. Larvae of this insect form long processions and cause great economic damage in coniferous forests (Campôa et al., 2021; Hódar et al., 2003). This insect pest is extremely relevant in the dynamic of relict Mediterranean *P. sylvestris* forests (Hódar et al., 2003), by drastically reducing the growth and the reproductive capacity of trees by reducing its photosynthetic tissues or generating greater susceptibility to other pathogens or drought events. On the other hand, tree defoliation in *Q. suber* and *Q. pyrenaica* increased with high levels of borer insects specially the black-banded oak borer, *Coraeus florentinus*. This biotic agent is mainly distributed in the Mediterranean forests where it bores the branches of different species of *Quercus* (Gallardo et al., 2018). Frequent outbreaks of black-banded oak borer cause great damage due to the feeding activity of the larvae (Fürstenau et al., 2012). The larvae make longitudinal and annular galleries under the bark of terminal branches, interrupting the sap flow and causing the branches to dry (Jurc et al., 2009). The reduction in the number of healthy branches results in loss of tree vigour and a progressive tree die-off (Cárdenas and Gallardo, 2018).

We also found that climatic suitability interacts with pests, indicating that the simultaneous effect of both conditions (low climatic suitability and high pest severity) leads to a higher tree defoliation intensity than expected by each factor alone. In our case, *P. sylvestris* and *Q. pyrenaica* were particularly susceptible to defoliation in areas with lower climatic suitability and with increasing intensity of pests. In other words, extreme climatic conditions (drought and warming) and pest in-

festations produce synergistic effects that mutually reinforce each other (Anderegg et al., 2015a; Gea-Izquierdo et al., 2019; Jactel et al., 2012). For example, severe drought and temperature increases not only have negative effects on tree growth or survival but can also directly enhance insect fitness (e.g., reproduction, development, dispersal) (Hartmann et al., 2018). On the other hand, insect infestation may interact with carbon deficiency or hydraulic failure to promote mortality under drought stress conditions (McDowell et al., 2008). Climate change can then put forest ecosystems in a vicious circle where increasing drought would intensify insect infestation that lead to growth loss and mortality, which in turn leads to carbon deficiencies and higher atmospheric carbon concentrations, amplifying global warming (Jactel et al., 2012).

4.3. Management implications

By establishing a clear relationship between tree defoliation, climatic suitability, and pests, we expect a substantial impact of low climatic conditions to forest vulnerability related to global warming. This impact is attributable not only to the direct consequences of extreme climatic conditions (Anderegg et al., 2015b), but also to the prevalence of pest infestations (Gea-Izquierdo et al., 2019). In this sense, forest managers should prioritize monitoring and management efforts in areas with lower climatic suitability, where trees may be more vulnerable to pest infestation and defoliation. Early detection of pest outbreaks in these areas can facilitate timely intervention and mitigation measures to prevent further damage (Finley and Chhin, 2016; Rullan-Silva et al., 2013). Considering the differential effects observed among various pest types on tree defoliation, it becomes imperative to adapt management strategies accordingly. For instance, given the significant positive impact of defoliator insects on tree defoliation, particularly evident in certain species like *P. halepensis* and borer insects in *Quercus* species, targeted control measures aimed at reducing these pest populations could prove beneficial in mitigating defoliation levels. Silvicultural practices may need to be adapted to account for varying levels of pest pressure across different climatic zones (Liebhold, 2012). In areas with lower climatic suitability, forest managers may consider implementing measures to enhance tree resilience, such as selective breeding for pest-resistant varieties (Lieutier, 2002), or promoting diverse stand structures that support natural pest control mechanisms. Additionally, further research is required to identify common thresholds of climatic suitability, below which species consistently experience drought-induced die-off (Mitchell et al., 2014). Determining such thresholds would enable more accurate predictions of the consequences of drought events in species-rich forests under different forecasted climate scenarios. Overall, our study underscores the importance of integrating knowledge of pest ecology, climatic factors, and species-specific responses into forest management strategies to effectively mitigate the impacts of tree defoliation and promote forest health and resilience in the face of changing environmental conditions.

5. Conclusions

This study provides valuable insights into the relationship between climatic suitability, biotic agents, and regional patterns of tree defoliation. ENMs have proved useful for this purpose by providing indexes of climatic suitability that explain population-level processes such as forest die-off. Significantly, our findings highlight a heightened vulnerability to defoliation in tree populations established in less climatically suitable sites, particularly when these sites also experience an increase in pest severity. While it is important to acknowledge that the correlation between demographic variables and outputs from ENMs can be uncertain, our study provides evidence supporting its validity, particularly when examining poor climatic conditions and demographic processes like tree defoliation. Importantly, our study underscores the uncertainty surrounding forest die-off and pest infestation processes

within the framework of climate change. As Mediterranean regions are expected to experience higher drought frequencies and warming temperatures, altering insect-host dynamics, it becomes imperative to conduct further research examining the climatic niche of both insect pests and host species. Such investigations are crucial for better anticipating the potential effects of these interactions on future forest dynamics.

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CRediT authorship contribution statement

Jhony Fernando Mendez Cruz: Writing – original draft, Validation, Software, Methodology. **José Ángel Sánchez Agudo:** Writing – review & editing, Validation, Supervision, Investigation, Conceptualization. **Ricardo Enrique Hernández-Lambrano:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Juan Luis Parra:** Writing – review & editing, Validation, Supervision, Investigation, Formal analysis.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to create an image of the main species analysed. After using this tool, the author(s) reviewed the image content as needed and take(s) full responsibility for the content of the publication.

Uncited reference

ESRI 2015; Margalef-Marrase et al., 2020; Osorio-Olvera et al., 2019; Serra-Diaz et al., 2013; Vilà-Cabrera et al., 2019.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122048](https://doi.org/10.1016/j.foreco.2024.122048).

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