

Biotic, abiotic, and anthropogenic drivers of demographic performance of non-native *Eucalyptus* and *Pinus* species in forested areas of Spain

Adrián Lázaro-Lobo^{a,*}, Paloma Ruiz-Benito^{a,b}, Carlos Lara-Romero^c, Pilar Castro-Díez^a

^a Ecology and Forest Restoration Group, Life Science Department, University of Alcalá, Ctra. Madrid-Barcelona, Km. 33,600, 28805 Alcalá de Henares, Spain

^b Remote Sensing Research Group, Department of Geology, Geography and Environment, University of Alcalá, Calle Colegios 2, 28801 Alcalá de Henares, Spain

^c Evolutionary Ecology Research Group, Superior School of Experimental Science and Technology (ESCET), Rey Juan Carlos University, C/ Tulipán S/N, Mostoles, Madrid, Spain

ARTICLE INFO

Keywords:

Climate
National Forest Inventory
Propagule pressure
Soil properties
Temporal trends
Tree demography

ABSTRACT

Non-native trees enhance services that are fundamental for human well-being. Yet, the extensive use of non-native trees has the potential of causing environmental and socio-economic harm. *Eucalyptus* and *Pinus* are the most widely distributed and extensively planted tree genera worldwide, because their rapid growth allows profitable production of timber and pulp. Their naturalization is causing severe effects on the environment, but the relative importance of underlying factors determining their demographic performance is not well known. Thus, our aim was to evaluate the relative importance of biotic, abiotic, and anthropogenic factors driving demographic changes of *Eucalyptus* and *Pinus* at the regional scale. We compiled environmental variables and demographic data for *Eucalyptus globulus*, *Eucalyptus camaldulensis*, and *Pinus radiata* across 6388 permanent forestland plots surveyed in the Spanish Forest Inventory (SFI). We used the second (1986–1996), third (1997–2007), and fourth (2008–2017) SFI datasets to quantify annual changes in basal area per plot between consecutive inventories (Δ BA; $\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$). We also quantified the components of Δ BA: tree ingrowth (transitions from juvenile to adult trees), growth, and mortality. We evaluated juvenile recruitment with in-situ regeneration (No. juvenile trees ha^{-1}) within plots already occupied by the focal species in the previous inventory, and with natural colonization of plots where the focal species was absent at the beginning of the time interval. We found that the structure of the biotic community was especially important to explain demographic performance of non-native trees growing in benign environments (*E. globulus* and *P. radiata*), whereas abiotic factors were particularly important regulating basal area increments of *E. camaldulensis*, which occurs in harsher environments. Basal area increments decreased with species and functional richness, heterospecific density, mean annual temperature, and increased with soil capacity to retain nutrients and water. Colonization of new plots increased with propagule availability in the surrounding landscape. Tree cutting was beneficial for *P. radiata*. Collectively, our results suggest that non-native trees perform better in forests with high propagule pressure, low biotic resistance, favourable abiotic conditions, and human management.

1. Introduction

Non-native tree species have been deliberately introduced globally to satisfy increasing demands for tree-derived ecosystem services (e.g., resource provision, erosion control, and climate regulation; MacDicken et al., 2015; Castro-Díez et al., 2019). Yet, non-native trees can negatively affect native biodiversity and ecosystem functioning through biotic interactions (e.g., competition) and changes in abiotic conditions (Castro-Díez et al., 2014, 2019; Dickie et al., 2014; Lázaro-Lobo et al., 2021a). Negative effects of non-native trees mostly occur when they

naturalize and become invasive (Richardson and Rejmánek, 2011; Brundu and Richardson, 2016). Therefore, understanding the underlying factors driving demographic changes of non-native trees (e.g., tree growth, mortality, juvenile-to-adult transition, and regeneration) is critical for continued progress in managing and preventing invasion events.

Eucalyptus and *Pinus* are the most widely distributed and extensively planted tree genera worldwide, given that their rapid growth allows profitable production of timber and pulp, even in climatically or edaphically harsh regions, where native trees are lacking or have low

* Corresponding author.

E-mail address: adrianlalobo@gmail.com (A. Lázaro-Lobo).

<https://doi.org/10.1016/j.foreco.2022.120111>

Received 16 December 2021; Received in revised form 14 February 2022; Accepted 16 February 2022

Available online 22 February 2022

0378-1127/© 2022 The Authors.

Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

productivity (Simberloff et al., 2010; Stanturf et al., 2013; Calviño-Cancela and van Etten, 2018). The fate of planted stands can range from continued intensive production to abandonment, where populations can naturalize and intermix with regenerated native vegetation or decline (Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008; Reyes et al., 2015; Fernandes et al., 2018; Queirós et al., 2020). *Eucalyptus* is a highly diverse genus with over 600 species that are native to Australia and adjacent Indonesia and New Guinea, but it has been widely introduced beyond its native range (Badalamenti et al., 2018; Calviño-Cancela and van Etten, 2018). The genus *Pinus* encompasses more than 120 species, which are almost exclusively native to the Northern Hemisphere (cf. *P. merkusii*), but have been introduced widely throughout the Southern Hemisphere (Simberloff et al., 2010; Calviño-Cancela and van Etten, 2018). Introduction and naturalization of *Eucalyptus* and *Pinus* has continued to cause severe effects on the environment, such as depletion of soil water and nutrients, changes in biological communities, and alteration of soil properties (e.g., soil acidification; Williams and Wardle, 2007; Soumare et al., 2016; Deus et al., 2018). Moreover, fire risk tends to increase in areas that have been planted with *Eucalyptus* and *Pinus* (Calviño-Cancela et al., 2016). Thus, their widespread introduction has created multiple social conflicts among scientists, stakeholders, and the general public due to their high economic value and adverse environmental effects (Veiras and Soto, 2011; Dickie et al., 2014). These impacts could be further intensified through climate and land-use change. Therefore, identifying the drivers of demographic changes (e.g., tree growth, mortality, juvenile-to-adult transition, and regeneration) in *Eucalyptus* and *Pinus* species at the regional scale is crucial for minimizing ecological risks while maintaining economic productivity.

The demographic performance of non-native trees is affected by multiple biotic (e.g., resident community structure), abiotic (e.g., climate, topography, and soil), and anthropogenic factors (e.g., management and land use; Theoharides and Dukes, 2007; Catford et al., 2009; Lázaro-Lobo and Ervin, 2021). Propagule availability strongly contributes to the successful spread of introduced trees (Lockwood et al., 2009; Simberloff, 2009), although its relative importance can vary depending upon local conditions (i.e., characteristics of resident communities; Fernandes et al., 2018). The structure of the resident community (e.g., taxonomic and functional diversity, plant density) influences the long-term population dynamics of non-native trees, both directly through biotic interactions, and indirectly through effects on the physical environment (Knops et al., 1999; Naeem et al., 2000; Garau et al., 2009; Beaury et al., 2019). Among abiotic factors, climate affects tree species distribution at large scales, given that plants are constrained to certain temperature and precipitation ranges (Sakai et al., 2001; Milbau et al., 2009; Lázaro-Lobo et al., 2020), while soil attributes (e.g., texture, organic matter content, pH) and topographic relief regulate water and nutrient availability at local scales (Gurevitch et al., 2002; Milbau et al., 2009; Catry et al., 2015). Likewise, natural and anthropogenic disturbances may alter biotic and abiotic conditions, as well as propagule pressure, which can ultimately affect tree demography. For example, fire can increase seedling recruitment of fire-adapted non-native trees (Richardson and Brown, 1986; Williams and Wardle, 2007; Larcombe et al., 2013; Calviño-Cancela et al., 2018), whereas silviculture practices can reduce competition, thereby enhancing survival, growth, and recruitment of target species (Ruiz et al., 2008; Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008; Nereu et al., 2019). Given that many biotic, abiotic, and anthropogenic factors can affect different demographic stages of non-native trees, understanding the relative importance of these multiple drivers of demographic performance is critical for managing non-native species.

In Spain, *Eucalyptus globulus*, *E. camaldulensis* and *Pinus radiata* are tree species with high economic value, accounting for the largest proportion of forest land cover and harvested wood among non-native tree plantations (Castro-Díez et al., 2016). These species may also alter the structure and functioning of ecosystems. To minimize ecological risks while maintaining economic productivity, we aimed to determine the

relative importance of biotic, abiotic, and anthropogenic factors driving demographic changes in these non-native tree species. Demographic performance of the focal species was assessed through changes in plot basal area between successive Spanish Forest Inventories (SFI), together with their components (i.e., juvenile-to-adult transition, growth, and mortality), as well as through regeneration trends (i.e., in-situ regeneration and colonization of new plots). Given that the focal species have been originally planted for forestry (Montero, 1997; Ruiz et al., 2008; Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008), they are expected to occupy areas where the abiotic conditions (e.g., climate and soil) are already favorable. Thus, we expected abiotic factors to be less relevant than biotic and anthropogenic factors for the focal species performance. We predicted that non-native tree demographic performance would be: 1) lower in communities with higher functional and taxonomic diversity because of a more efficient use of resources, and thus, a stronger biotic resistance through competition (Levine et al., 2004; Beaury et al., 2019); 2) lower in areas with harsh abiotic conditions, such as high mean annual temperature, low annual precipitation, and low soil capacity to retain nutrients and water; and 3) higher in forests with high human interventions which were aimed at increasing timber or pulp yield of our focal non-native tree species.

2. Materials and methods

2.1. Focal species and study region

Southern blue gum (*Eucalyptus globulus* Labill.) is native to southeastern Australia and is the most frequently grown species in the genus, reported as naturalized in southern Europe, North America, India, Western Australia, New Zealand, and islands in the Pacific and Indian Oceans (Potts et al., 2008; Rejmánek and Richardson, 2013; Calviño-Cancela and van Etten, 2018). Red river gum (*Eucalyptus camaldulensis* Dehnh.) is native to all mainland states of Australia. It is probably the most widely planted tree in arid and semi-arid regions, and reported as naturalized in California, Central and South America, South Africa, the Mediterranean Basin and southern Asia (Stanturf et al., 2013; Badalamenti et al., 2018; Hirsch et al., 2020). Both *Eucalyptus* species have been introduced for pulp and paper production (Sanz-Elorza et al., 2004). Monterey pine (*Pinus radiata* D. Don), a very localized endemic that is native to coastal California, is one of the most widely used conifers in global forestry due to its multiple applications in industry, such as timber, pulp and engineered wood products. It has become naturalized in Europe, South Africa, South America, Atlantic and Pacific islands, Australia, and New Zealand (Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008; Mead, 2013; Rejmánek and Richardson, 2013).

Our study was conducted in forested areas of Spain (i.e., forest cover > 10%; Tomppo et al., 2010), which have high ecological, economic, and social value (Alberdi et al., 2017). Spanish forests range from productive monospecific plantations to highly diverse natural communities, and occur across a wide variety of climatic, edaphic, and topographic situations (Castro et al., 1997). *Eucalyptus globulus*, *E. camaldulensis*, and *P. radiata* were introduced into Spain in mid-19th C. and have been widely planted since mid-20th C (Ruiz et al., 2008; Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008). *Eucalyptus globulus* extends over 325,000 ha in Spain, especially close to the Cantabric and Atlantic coasts of North Spain, while *E. camaldulensis* covers 105,000 ha and is mainly present in central and southwestern Spain (Ruiz et al., 2008; Fig. 1). *Pinus radiata* mostly occurs in northern Spain, particularly in the Basque Autonomous Community, covering 280,000 ha (Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008). Many plantations are still active, growing in even-aged monospecific stands. However, some plantations have been abandoned. Currently, these co-occur with naturally regenerated temperate or Mediterranean native trees (e.g., *Quercus* spp., *Pinus* spp., *Betula* spp., and *Fagus sylvatica*; Castro et al., 1997). Spontaneous in situ regeneration and colonization of nearby sites have been documented for our three focal species (Reyes et al., 2015; Fernandes et al., 2018;

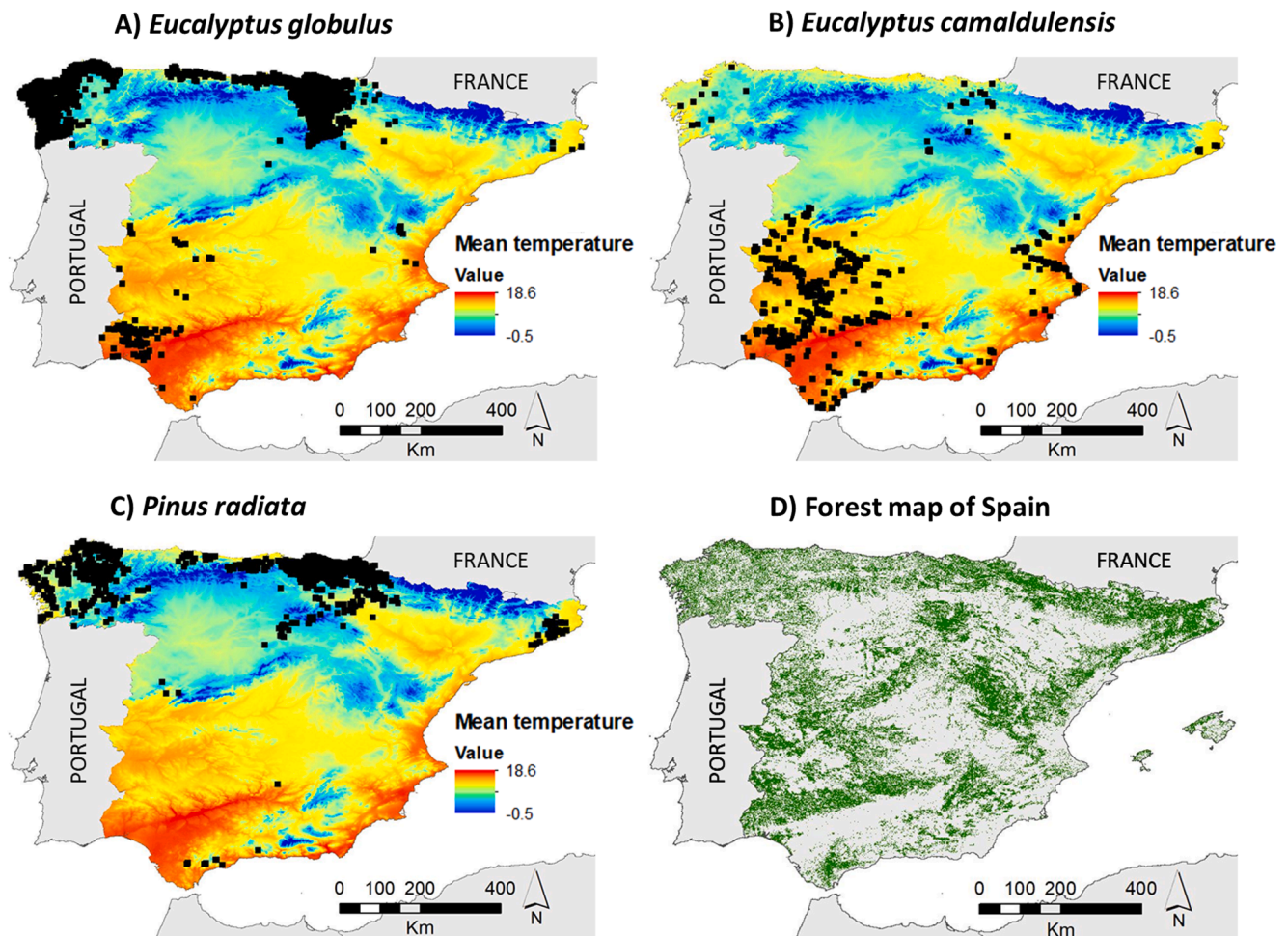


Fig. 1. Distribution maps of the focal species that were constructed from the third Spanish Forest Inventory, including (A) *Eucalyptus globulus*, (B) *Eucalyptus camaldulensis*, and (C) *Pinus radiata*. Locations of the focal species in the Spanish Forest Inventory are indicated with black squares. The heat layer covering Spain represents the mean annual temperature between 1981 and 2010 and ranges from -0.5 to 18.6 °C (red and blue colours, respectively; CHELSA database; Karger et al., 2017). (D) Forested areas of Spain (from Spanish Forest Map,). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

available at <https://www.miteco.gob.es/>

Queirós et al., 2020). Nowadays, *E. globulus*, *E. camaldulensis*, and *P. radiata* can be found in Spain along a gradient of stand conditions, from monospecific plantations to mixed stands with native trees.

2.2. Data collection

2.2.1. National forest inventory data for the focal species

We extracted information that was related to our focal species from the second (1986–1996), third (1997–2007), and fourth (2008–2017) SFI datasets (2SFI, 3SFI, and 4SFI, respectively). The SFI is a monitoring and evaluation project that, approximately every 10 years, systematically samples permanent plots that are located on a 1 km^2 grid-cell network across the forested land surface of Spain (Villaescusa and Díaz, 1998). Each SFI plot consists of four circular concentric subplots of 5, 10, 15 and 25 m radius where adult trees with a diameter at breast height (DBH) ≥ 7.5 , 12.5, 22.5, and 42.5 cm respectively are measured. Adult tree measurements include DBH, tree height, species identity, and tree status (alive or dead). Basal area (BA, $\text{m}^2 \text{ ha}^{-1}$) of individual trees is calculated from DBH, considering the radius of the sampling plot to which the individual tree belongs. Juvenile trees ($2.5 \leq \text{DBH} < 7.5$ cm and height > 1.3 m) are counted in the 5-m radius subplot (Alberdi et al., 2017).

We identified 6388 permanent plots between consecutive

inventories where any of the focal species were present as adults (Fig. 1): 3129 plots from 2-3SFI and 3259 plots from 3-4SFI. For each focal species, we quantified changes in basal area per plot between consecutive inventories (ΔBA , $\text{m}^2 \text{ ha}^{-1} \text{ year}^{-1}$; i.e., annual changes in the basal area of the species per ha), considering adult trees (i.e., DBH ≥ 7.5 cm and height 130 cm). We also quantified the components of ΔBA : (1) tree ingrowth, i.e., the increase in BA due to the transition from juveniles to adults in the 5-m radius subplot ($\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$); (2) tree growth, i.e., the increase in BA due to the growth of living trees ($\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$); and (3) tree mortality, i.e., the loss of BA due to dead trees ($\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$) (see Ruiz-Benito et al., 2014; Astigarraga et al., 2020).

Juvenile recruitment of the focal species was evaluated using two complementary variables: 1) in-situ regeneration of SFI plots already occupied by the focal species at the beginning of the time interval, and 2) colonization of plots where the focal species was absent at the beginning of the time interval. In-situ regeneration corresponded to the density of juvenile trees (No. trees ha^{-1}) in the last consecutive inventory (3SFI for 2-3SFI and 4SFI for 3-4SFI) within the 5-m radius subplot of SFI plots already occupied by the focal species in the previous inventory. For colonization, we first identified all SFI plots where the corresponding species was present in the initial consecutive inventory (2SFI for 2-3SFI and 3SFI for 3-4SFI); and we then we selected all SFI plots within a 1-, 2-, 5-, and 10-km radius circle where the corresponding focal species was

absent (candidate plots to be colonized). We used the last consecutive inventory (3SFI for 2-3SFI and 4SFI for 3-4SFI) to identify which of these candidate SFI plots were colonized by the corresponding focal species (i. e., not present in the initial inventory and present in the final inventory). We selected the 2-km radius buffer around the plots because we obtained a high proportion of colonized SFI plots among the candidates using this radius (see Table S1). In focusing only on natural colonization, we excluded planted plots, which were identified using SFI data that recorded the origin of the regeneration of our focal species (see details in Table S2). The percentage of plots in the 3SFI dataset that were naturally colonized by *E. globulus*, *E. camaldulensis*, and *P. radiata* was 22.46%, 17.56%, and 0.01%, respectively, and close to 0% for all species in the 4SFI, probably because the 4SFI is currently ongoing and data is not available for a high proportion of plots yet. Therefore, we only considered the 3SFI dataset for colonization.

2.2.2. Biotic properties underlying demographic success of non-native trees

We obtained information regarding the biotic community from the initial consecutive inventory (2SFI for 2-3SFI and 3SFI for 3-4SFI; Table 1). For each SFI plot, we extracted conspecific density (density of the focal species; No. adult trees ha⁻¹), heterospecific density (density of the remaining adult tree species rooted within the plot; No. adult trees ha⁻¹), species richness (No. tree species in the plot), functional richness, and functional dispersion. Trait information that was used to estimate functional richness and functional dispersion of the SFI plots was compiled from the open-access TRY database version 5 (<http://www.try-db.org>; Kattge et al., 2020). The selected traits were relevant to growth, survival, and reproduction of the species, and have available values in the database that was consulted: water potential causing 50% loss of hydraulic conductivity (kPa); specific leaf area (m² kg⁻¹); wood density (g cm⁻³); maximum tree height (m); and seed mass (mg) (Swenson et al., 2012; Díaz et al., 2016; Kunstler et al., 2016). All traits were standardized to have zero mean and unit variance prior to the estimation of functional richness and dispersion. Functional richness and functional dispersion were calculated for each SFI plot using the FD package (Laliberté and Legendre, 2010) in R 3.6.1 (R Core Team, 2021). Functional richness was calculated as the minimal convex-hull volume containing all the tree species of the plot in a multidimensional principal coordinates analysis (PCoA) trait-space ordination (Villéger et al., 2008). Functional dispersion was calculated as the mean distance of each tree species of the plot to the PCoA trait-space centroid, weighted by its relative abundance (Laliberté and Legendre, 2010). Functional dispersion increases as the most abundant trait values get farther from the centroid of the trait space (Laliberté et al., 2014). The number of trees of each species present in each SFI plot was used as an indicator of species relative abundance.

Propagule pressure was only used as predictor for the analyses regarding colonization and it was assessed as the mean density of the focal species within a 2-km radius circle around each candidate plot to be colonized in the initial consecutive inventory (2SFI for 2-3SFI and 3SFI for 3-4SFI). As indicated above, candidate plots refer to those plots lying within a 2-km radius circle around occupied plots, where the corresponding focal species was absent in the initial consecutive inventory.

2.2.3. Abiotic factors underlying demographic success of non-native trees

We compiled a broad range of geospatially explicit environmental variables that were related to climate, topography and soil, which, based on the literature, could potentially affect the demography of our focal species across Spain (Table 1; Catry et al., 2015; Fernandes et al., 2018; Queirós et al., 2020). We downloaded climatic data from the Climatologies at High resolution for the Earth's Land Surface Areas (CHELSA) database at 30 arcsec (~1 km) resolution for the period 1981–2010 (Karger et al., 2017). We selected mean and extreme values of climatic variables, together with those indicating intra-annual variability: mean annual temperature; mean maximum temperature of the warmest

Table 1

Potential predictors of non-native tree demography, which are classified as biotic, abiotic (climatic, topographic, and edaphic) and anthropogenic variables.

Variable	Description	Source
Biotic properties		
Conspecific density ^a	Number of individuals of focal species	Spanish Forest Inventory
Heterospecific density ^a	Number of individuals of other species	TRY database version 5
Species richness ^a	Number of species	
Functional richness ^a	Amount of niche space filled by species in the community	
Functional dispersion	Mean distance of individual species to the centroid of all species in multidimensional trait space	
Propagule pressure ^a	Availability of propagules (focal tree density) within a 2-km radius circle around the plot	
Climate		
Mean annual temperature ^a	Annual average daily air temperatures	CHELSA
Temperature seasonality	Standard deviation of the monthly mean temperatures	
Maximum temp. of warmest month	The highest temperature of any daily mean maximum temperature	
Minimum temp. of coldest month	The lowest temperature of any daily mean minimum temperature	
Annual precipitation ^a	Accumulated precipitation amount over 1 year	
Precipitation seasonality	Standard deviation of the monthly mean precipitation	
Precipitation of the driest quarter	Accumulated precipitation amount during the driest quarter of the year (June-August)	
Topography		
Elevation	Height above sea level	NASA (SRTM)
Slope gradient ^a	Steepness (slope inclination in degrees)	
Soil properties		
Sand (%) ^a	50 µm – 2 mm mass fraction of the < 2 mm soil material	ISRIC (Soil grids)
Silt (%)	2–50 µm mass fraction of the < 2 mm soil material	
Clay (%)	< 2 µm mass fraction of the < 2 mm soil material	
Coarse fragments (soil stoniness) ^a	Mass fraction of the soil material > 2 mm	
Cation exchange capacity ^a	Number of exchange sites on soil colloids and clay minerals	
Organic carbon	Mass fraction of carbon by weight in the < 2 mm soil material (g C/kg soil)	
pH	Measure of the acidity or alkalinity of the soil solution in a ratio of 1:5 soil to water	
Anthropogenic influence		
Tree cutting ^a	Binary	Spanish Forest Inventory

^a Variables finally included in the GLMMs after variable selection, including the assessment of collinearity among all predictors.

month; mean minimum temperature of the coldest month; temperature seasonality (i.e., variation in temperature throughout the year); precipitation seasonality; annual precipitation; and mean precipitation of driest quarter (June-August). For topography, we obtained digital elevation data at 90 m spatial resolution from the Shuttle Radar Topography Mission (SRTM) database, which was originally produced by NASA (CGIAR, 2021), and calculated slope gradient (slope inclination in degrees) using ArcGIS 10.8.1 (ESRI, Redlands, CA, USA). Lastly, we extracted raster layers with data from multiple soil properties related to nutrient and water-holding capacity at 250 m resolution from the

SoilGrids database (ISRIC, 2021). Soil properties were extracted for the uppermost 15-cm of soil (fertile layer) and included percent of sand, silt and clay, coarse fragments, cation exchange capacity (CEC), organic carbon, and pH.

2.2.4. Anthropogenic influence on the demographic success of non-native trees

We used the last of the consecutive inventories (3SFI for 2-3SFI and 4SFI for 3-4SFI) to extract information regarding the occurrence of recent tree cutting (thinning and pruning) in the plots.

2.3. Statistical analysis

We first conducted a variation partitioning analysis for each response variable and SFI comparison (2-3SFI and 3-4SFI) using the *vegan* package (Oksanen et al., 2019) in R 3.6.1 (R Core Team, 2021). Response variables included changes in basal area (total and separated into tree ingrowth, growth, and mortality), in-situ regeneration, and colonization. This statistical method decomposes the variation of the response variables (adjusted R-squared values) into independent fractions, which reflect the relative importance of groups of predictors (biotic properties, abiotic factors, and anthropogenic influence) and their joint effects (Heikkinen et al., 2004; Legendre and Legendre, 2012; Llana et al., 2012; Lázaro-Lobo and Ervin, 2021). We included all the evaluated predictor variables in these analyses because collinear variables do not have to be removed prior to partitioning (Oksanen et al., 2019).

We then used Generalized Linear Mixed Models (GLMMs) to evaluate the effects of the selected predictors (Table 1) on demographic changes for our focal species between consecutive inventories (2-3SFI and 3-4SFI), with the *glmmTMB* package (Magnusson et al., 2017) in R 3.6.1 (R Core Team 2021). Before conducting the GLMMs, we tested linearity between each response and explanatory variable. We also tested collinearity among the potential environmental predictors with Pearson's correlations. We ensured that the retained variables were not strongly correlated with one another (Pearson's $r < 0.5$, sensu Dormann et al., 2013; Table S3). If two variables were correlated, we retained the variable that had the lowest Akaike information criterion (AIC) value (Akaike, 1974). We standardized the numerical variables to make the interpretation of their effect sizes comparable (i.e., GLMM coefficient estimates as defined in Schielzeth, 2010; Magnusson et al., 2017).

Separate GLMMs were performed for each response variable and focal species. We selected the appropriate error distribution and link function for each response variable (Zuur et al., 2009). Changes in basal area of adult trees (total and due to growth) were analyzed with Gamma errors using a log-link because, given the skewness of their data distributions, model residuals were not normally distributed, and we obtained lower AIC values when compared to the models with Gaussian error distribution. In contrast, changes in basal area due to ingrowth and mortality were evaluated with zero-inflated gamma models due to the large number of zeros that were present in the data. In-situ regeneration (No. Juvenile trees ha^{-1}) was modelled as a negative binomial response due to overdispersion of our data. The presence of colonizing individuals in candidate plots was analyzed with a binomial distribution. For the analyses regarding changes in basal area and in situ regeneration, we used Spanish Forest Inventory period (2-3SFI and 3-4SFI) as a fixed factor and SFI plot as a random factor to account for observations of our response variables over multiple periods of time. For the analyses regarding colonization, we only used the 2-3SFI comparison because the percentage of naturally colonized SFI plots was close to 0% for all species in the 3-4SFI comparison.

3. Results

3.1. Relative importance of biotic, abiotic, and anthropogenic predictors on demographic changes of non-native *Pinus* and *Eucalyptus* species

Among our three groups of predictors, those accounting for the biotic properties generally explained a larger fraction of variation than did abiotic and anthropogenic factors for *E. globulus* and *P. radiata* (Table 2). Yet, abiotic factors accounted for the highest proportion of the variation in *E. globulus* and *P. radiata* colonization, as well as *E. camaldulensis* basal area increments. Anthropogenic predictors usually explained the lowest percentage of variance, except for in-situ regeneration of our focal species and basal area change of *P. radiata*. In the latter two cases, tree cutting explained a larger proportion of the variance than did abiotic factors (Table 2). Overall, our analysis revealed that a large proportion of the variance was unexplained in our response variables (60–99.9%; Table 2).

3.2. Effects of biotic properties on demographic performance

Changes in basal area of adult trees were strongly affected by both conspecific and heterospecific tree density, as well as by species and functional richness (Fig. 2). In *E. globulus* and *P. radiata*, plots with higher initial conspecific density exhibited higher basal area increments due to the growth of the standing trees, despite *P. radiata* also having higher mortality ($p < 0.001$; Fig. 2; Fig. S1). *Eucalyptus camaldulensis* plot-level growth and mortality also increased with initial conspecific density ($p < 0.001$). By contrast, ingrowth (i.e., the increase in basal area due to the transition of juveniles to adults) of our three focal species decreased with conspecific density ($p < 0.006$). Basal area increments of *E. globulus* and *P. radiata* were lower in plots with higher heterospecific density, species richness, and functional richness ($p < 0.002$) due to slower growth, higher mortality, or lower ingrowth. Basal area increments of *E. camaldulensis* also decreased with species richness due to higher mortality ($p < 0.03$).

In situ regeneration of *E. globulus* was positively associated with both increasing conspecific and heterospecific tree density ($p < 0.001$), and negatively related to species and functional richness ($p \leq 0.02$). For *E. camaldulensis*, in situ regeneration decreased with conspecific density and increased with heterospecific density ($p < 0.004$; Fig. 2). Colonization of nearby plots by our focal species increased with increasing propagule pressure ($p \leq 0.01$). Moreover, *E. globulus* colonization was positively related with the heterospecific density of the candidate plots ($p < 0.005$; Fig. 2).

3.3. Effects of abiotic factors on demographic performance

Mean annual temperature negatively affected the basal area increments of our focal species ($p \leq 0.02$; Fig. 2). In *E. globulus*, this effect was mainly due to lower growth ($p < 0.001$), whereas in *E. camaldulensis* and *P. radiata*, it was due to lower ingrowth and higher mortality, respectively ($p < 0.009$; Fig. S1). Basal area increments of *E. camaldulensis* were greater in areas with high annual precipitation ($p < 0.001$; Fig. 2); however, precipitation did not affect *E. globulus* and *P. radiata*, which occurred in more benign environments than did *E. camaldulensis* (e.g., lower temperatures, higher precipitation, and lower climate seasonality; Fig. S2). Plots that were located on steeper slopes had greater increases in basal area of *E. globulus* ($p < 0.001$; Fig. 2), as a result of higher ingrowth ($p < 0.002$), and despite higher tree mortality ($p \leq 0.02$; Fig. S1). In contrast, basal area increments of our focal species decreased with sand content of the rooting substrate ($p < 0.004$; Fig. 2). Coarse fragment content (soil stoniness) was negatively related with basal area increments of *Eucalyptus* species ($p < 0.001$; Fig. 2), due to lower growth or ingrowth ($p < 0.05$; Fig. S1). Lastly, *E. globulus* growth increased with soil cation exchange capacity ($p < 0.05$; Fig. 2).

Table 2

Variation partitioning analyses for each of the demographic response variables. Variance is explained by three groups of predictors: biotic, abiotic, and anthropogenic. The numbers correspond to adjusted R^2 values as percentages and range from 0 to 100%. The results that are shown represent the average of two independent Spanish Forest Inventory comparisons (2-3SFI and 3-4SFI; see Table S4), except for colonization where we only used the 2-3SFI. Bold values indicate the group of predictors that explained the largest percentage of variation for each response variable and species.

	Response variable	Predictors			Unexplained variance
		Biotic	Abiotic	Anthropogenic	
<i>Eucalyptus globulus</i>	Basal area change	19.0	6.5	1.8	72.7
	– Ingrowth	7.0	3.0	0.1	89.9
	– Growth	26.0	2.5	2.0	69.5
	– Mortality	3.0	0.0	0.0	97.0
	In situ regeneration	5.5	1.4	1.8	91.3
	Colonization	3.0	5.0	0.0	92.0
<i>Eucalyptus camaldulensis</i>	Basal area change	7.5	25.5	0.0	67.0
	– Ingrowth	5.5	4.5	1.0	89.0
	– Growth	11.5	9.5	2.1	76.9
	– Mortality	5.5	2.5	0.2	91.8
	In situ regeneration	10.0	0.2	3.5	86.3
	Colonization	0.2	0.0	0.0	99.8
<i>Pinus radiata</i>	Basal area change	28.5	5.5	6.0	60.0
	– Ingrowth	3.5	0.2	0.0	96.3
	– Growth	19.5	4.5	0.7	75.3
	– Mortality	22.0	2.0	0.4	75.6
	In situ regeneration	5.0	0.0	1.5	93.5
	Colonization	0.0	0.1	0.0	99.9

In situ regeneration of our focal species was not significantly affected by the abiotic factors that were evaluated ($p > 0.05$; Fig. 2). However, colonization of nearby plots by *E. globulus* was positively related to increasing sand content ($p < 0.007$; Fig. 2), whereas *E. camaldulensis* colonization decreased with increasing annual precipitation and slope ($p \leq 0.01$; Fig. 2).

3.4. Effects of anthropogenic influence on demographic performance

Plots with signs of recent tree cutting exhibited greater increases in basal area of *P. radiata* ($p < 0.001$; Fig. 2) due to lower tree mortality ($p < 0.03$; Fig. S1). In contrast, tree cutting was negatively related with basal area increments of *E. globulus* at the plot level due to lower growth ($p < 0.001$; Fig. 2; Fig. S1). In-situ regeneration and colonization of *P. radiata* were enhanced by tree cutting ($p < 0.05$; Fig. 2).

4. Discussion

Our results show that demographic changes of non-native *Eucalyptus* and *Pinus* in Spain are influenced by a combination of biotic, abiotic, and anthropogenic factors. As we had initially hypothesized, biotic community structure had a greater importance than did abiotic and anthropogenic factors in explaining demographic changes in *E. globulus* and *P. radiata*. One possible explanation for this finding is that such species had been initially planted for forestry and currently occupy areas with favourable climatic, topographic, and edaphic conditions (Montero, 1997; Ruiz et al., 2008; Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008). However, abiotic factors had greater importance in explaining colonization of *E. globulus* and *P. radiata*. Moreover, abiotic factors were especially important in explaining basal area increments of *E. camaldulensis*. In Spain, this non-native tree occurs in environments that are harsher than those of *E. globulus* and *P. radiata*, i.e., higher temperatures, lower precipitation, and more pronounced climate seasonality (Fig. S2). Thus, our results suggest that abiotic factors play a greater role than biotic and anthropogenic factors in regulating demographic changes of non-native trees occurring in harsh environments.

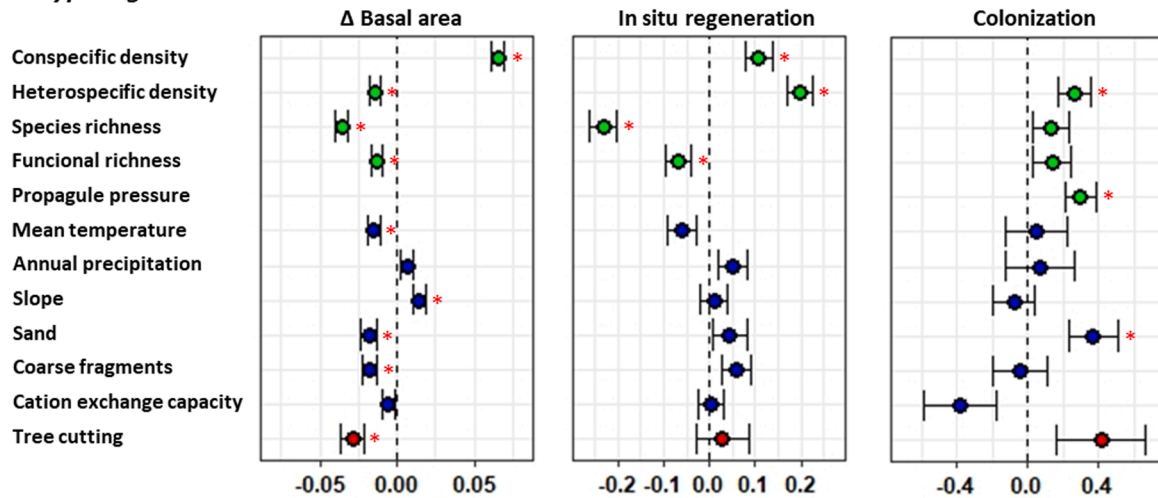
4.1. Effects of biotic properties on demographic performance

The structure of the community had a great effect on the demography of the non-native trees under evaluation (Fig. 2; Fig. S1; Table S5). Our results suggest that intraspecific competition for resources (e.g., light, water, and nutrients) has negative consequences for tree survival and ingrowth, as found by Adler et al., 2018. Yet, plots with more conspecific trees had stronger increases in absolute basal area due to higher plot-level tree growth. This is probably due to a greater number of trees within the plot, rather than being attributable to individual tree growth, which tends to decline with increasing densities (Serrada et al., 2008).

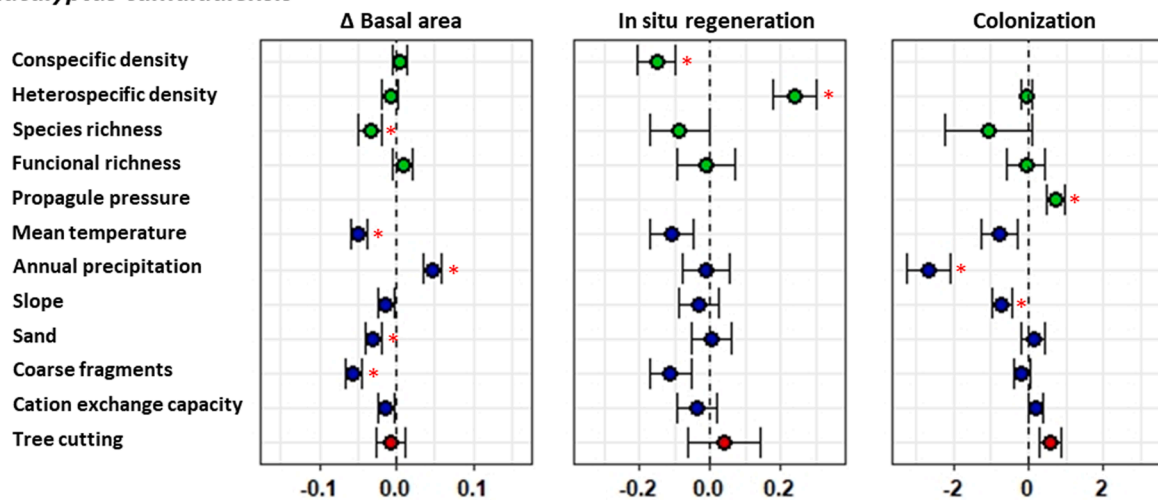
Heterospecific density had opposite effects on adult trees and juveniles. The lower increases in basal area of adult *E. globulus* and *P. radiata* trees with higher heterospecific density is probably due to competition for limiting resources (Holmgren et al., 1997). Previous research has found that tree growth and establishment of our focal species are reduced with higher native forest and vegetation cover due to competition and effects on the physical environment (Garau et al., 2009; Becerra and Bustamante, 2011; Fernandes et al., 2018). Our results also indicate that in situ regeneration of *Eucalyptus* species and *E. globulus* colonization are favoured by high heterospecific density, probably through a facilitation effect that improves microenvironmental conditions, such as lower water stress, thermal fluctuations, and radiation, as well as higher organic matter content and greater soil stability (Callaway and Walker, 1997). Nevertheless, this facilitation effect of heterospecific density on juveniles becomes an inhibitory effect as trees grow, as shown by the negative effect of heterospecific density on tree basal area.

Taxonomic and functional richness generally had a negative effect on basal area increments and in situ regeneration, which is partially consistent with the biotic resistance hypothesis (Levine et al., 2004; Beaury et al., 2019). This hypothesis postulates that areas with high diversity can be more resistant to non-native species establishment, probably because of a lower proportion of ecological niches that are available for non-native species to occupy (Funk et al., 2008; MacDougall et al., 2009; Lázaro-Lobo and Ervin, 2021). Our study demonstrates that once non-native *Eucalyptus* and *Pinus* have established, high tree diversity negatively affects their basal area increments and regeneration. High tree diversity in plots containing non-native species could be

A) *Eucalyptus globulus*



B) *Eucalyptus camaldulensis*



C) *Pinus radiata*

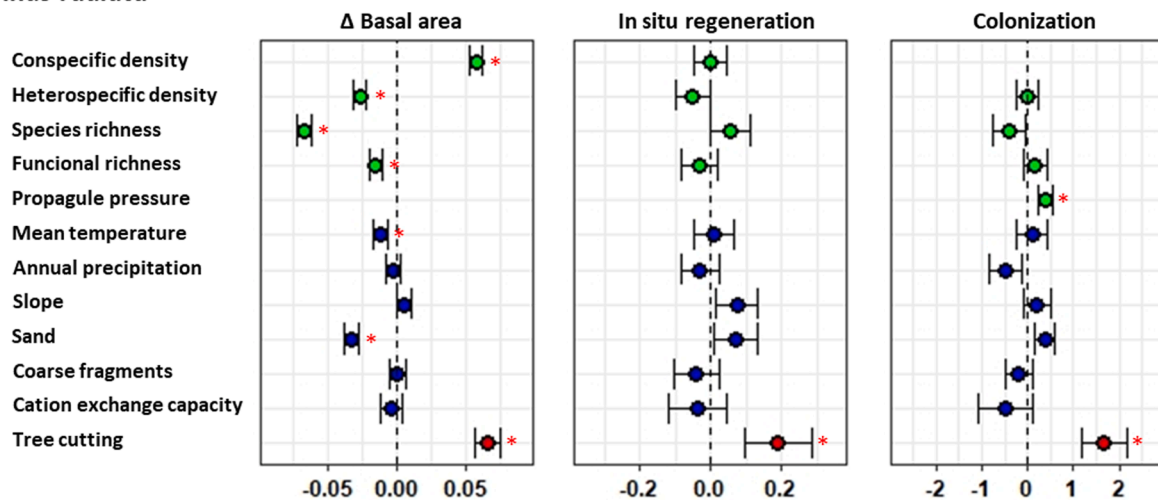


Fig. 2. Relative contribution of biotic (green), abiotic (blue), and anthropogenic (red) predictors explaining changes in basal area of adult trees and juvenile recruitment (in situ regeneration and colonization of nearby plots) of our focal species through time. Dots represent the GLMM coefficient estimates, and bars indicate 95% standard errors. The distance of the dots to the vertical dashed line indicates the magnitude of the influence that the predictor variable has on the corresponding demographic variable. Values higher and lower than 0 indicate positive and negative effects on the corresponding variable, respectively. Statistically significant relationships (p-value < 0.05) are indicated with a red asterisk. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

due to strong regeneration and growth of native vegetation, which could compete with the exotic species.

Colonization of new plots increased with propagule availability in the surrounding landscape. Our result is consistent with previous studies pointing to propagule pressure as one of the most important factors contributing to the establishment of non-native species (Lockwood et al., 2009; Simberloff, 2009). Thus, managers should monitor areas near mature stands of our focal species to avoid further expansion and establishment. We also found that *Eucalyptus* species colonized a greater proportion of plots than did *P. radiata*, which suggests that *Eucalyptus* is more likely to expand readily into nearby areas than would *P. radiata* in Spain.

4.2. Effects of abiotic factors on demographic performance

Climatic variables greatly contributed to demographic changes in our focal species. Basal area increment at the plot-level decreased with mean annual temperatures. Previous research also suggests that the performance of our focal species decreases with increasing temperatures, but their regeneration and occurrence are adversely affected by very low temperatures and high number of frost days (Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008; Larcombe et al., 2013; Catry et al., 2015; Hirsch et al., 2020). Annual precipitation had a strong positive effect on *E. camaldulensis* basal area increment, but it had no effect on *E. globulus* and *P. radiata*, probably because *E. camaldulensis* occurs in areas that are more prone to water stress (Fig. 1; Fig. S2). Previous research also found that temperature and rainfall are important factors for *E. camaldulensis* performance, even though *E. camaldulensis* has a higher drought tolerance than *E. globulus* and is adapted to a wide range of rainfall regimes (i.e., from 250 to 1500 mm annual precipitation; Hirsch et al., 2020).

Topography was important for both *Eucalyptus* species. Slope gradient was positively related to basal area increments of *E. globulus* at the plot-level, possibly due to reduced plant competition, waterlogging, and management intensity (Catry et al., 2015; Deus et al., 2019). Yet, *E. camaldulensis* colonization was hampered by high slope gradient, which could be related to lower soil stability. Among edaphic variables, soil texture had the greatest influence on demographic changes of our focal species. Our results show that a high content of large soil particles (sand and coarse fragments) reduces basal area increments. In sandy soils, which can drain rapidly, the limiting factors are often nitrogen, minerals, and water, which are necessary for plant functioning and growth (Gurevitch et al., 2002; Lázaro-Lobo et al., 2021b). Thus, nutrient and moisture deficiency could reduce the performance of our focal species in forested areas (Merino et al., 2003). Lastly, increasing cation exchange capacity of the soil increased *E. globulus* plot-level growth, possibly because there were more nutrients that were available for plant growth (Gurevitch et al., 2002).

4.3. Effects of anthropogenic influence on demographic performance

Tree cutting within the plots had a negative effect on *E. globulus* plot-level growth, but *P. radiata* survival, in situ regeneration, and colonization increased with tree cutting. The effects on *E. globulus* are probably due to tree thinning, which decreased basal area increments at the plot-level. However, the positive effect on *P. radiata* suggests that the reduction of basal area by thinning is being compensated by enhanced growth of the remaining trees, which could be related to higher resource availability resulting from human interventions (Ruiz et al., 2008; Sanchez-Rodriguez and Rodríguez-Soalleiro, 2008).

We compiled a broad range of environmental variables to explain demographic changes of our focal species, but much of the variance was left unexplained. Therefore, future studies should consider other factors beyond those that were obtained from the Spanish Forest Inventory datasets. For instance, abundance or structure of herbaceous and shrub vegetation could be used for further evaluating the influence of biotic

interactions, together with fire history to assess fire effects on our focal species. This additional information would increase our understanding of mechanisms underlying demographic changes of non-native trees.

5. Conclusions

Understanding the relative importance of biotic, abiotic, and anthropic drivers on demographic performance is critical for managing non-native trees and conserving native forests. We found that environmental variables differentially affect demographic changes in non-native trees within forested areas across Spain. The structure of the biotic community is key explaining demographic changes of non-native trees growing in more benign environments (*E. globulus* and *P. radiata*), whereas abiotic factors gained importance to regulate colonization of nearby areas by such tree species, as well as basal area increments of *E. camaldulensis*, which occurs in harsher environments. Altogether, our results suggest that non-native trees perform better in forests with low biotic resistance, favorable abiotic conditions, and human management (i.e., tree cutting). We provide evidence that an adequate conservation of structurally and species diverse native vegetation is key to decrease demographic performance of non-native trees.

CRedit authorship contribution statement

Adrián Lázaro-Lobo: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Paloma Ruiz-Benito:** Conceptualization, Methodology, Software, Validation, Investigation, Resources, Writing – review & editing, Visualization. **Carlos Lara-Romero:** Conceptualization, Methodology, Software, Validation, Investigation, Data curation, Writing – review & editing, Visualization. **Pilar Castro-Díez:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – review & editing, Visualization, Supervision, Funding acquisition.

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.

Acknowledgements

This research was supported by the Ministry of Science and Innovation of Spain, the Spanish Research Agency, the European Regional Development Fund [EXARBIN (RTI2018-093504-B-I00) and InvaNET (RED2018-102571-T) projects], and by the REMEDINAL project of the Community of Madrid (TE-CM S2018/EMT-4338). PRB was supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010) and the University of Alcalá “Ayudas para la realización de Proyectos para potenciar la Creación y Consolidación de Grupos de Investigación (Grants for carrying out Projects to promote the Creation and Consolidation of Research Groups)”. CLR was supported by a Juan de la Cierva Incorporación post-doctoral fellowship (Spanish Ministry of Science: IJC2019-041342-I). The authors are grateful for the helpful suggestions provided by two anonymous reviewers.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120111>.

References

- Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M., Tredennick, A.T., Veblen, K.E., Comita, L., 2018. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecol. Lett.* 21 (9), 1319–1329.
- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19 (6), 716–723.
- Alberdi, I., Cañellas, I., Vallejo Bombín, R., 2017. The Spanish National Forest Inventory: history, development, challenges and perspectives. *Pesqui. Florest. Bras.* 37 (91), 361. <https://doi.org/10.4336/2017.pfb.37.91.1337>.
- Astigarraga, J., Andivia, E., Zavala, M.A., Gazol, A., Cruz-Alonso, V., Vicente-Serrano, S. M., Ruiz-Benito, P., 2020. Evidence of non-stationary relationships between climate and forest responses: Increased sensitivity to climate change in Iberian forests. *Glob. Change Biol.* 26 (9), 5063–5076.
- Badalamenti, E., Cusimano, D., La Mantia, T., Pasta, S., Romano, S., Troia, A., Iardi, V., 2018. The ongoing naturalisation of *Eucalyptus* spp. in the Mediterranean Basin: new threats to native species and habitats. *Aust. For.* 81 (4), 239–249.
- Beaury, E.M., Finn, J.T., Corbin, J.D., Barr, V., Bradley, B.A., Rejmanek, M., 2019. Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecol. Lett.* 23 (3), 476–482.
- Becerra, P.I., Bustamante, R.O., 2011. Effect of a native tree on seedling establishment of two exotic invasive species in a semiarid ecosystem. *Biol. Invasions* 13 (12), 2763–2773.
- Brundu, G., Richardson, D.M., 2016. Planted forests and invasive alien trees in Europe: a code for managing existing and future plantings to mitigate the risk of negative impacts from invasions. *NeoBiota* 30, 5–47.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78 (7), 1958–1965.
- Calviño-Cancela, M., van Etten, E.J.B., 2018. Invasive potential of *Eucalyptus globulus* and *Pinus radiata* into native eucalypt forests in Western Australia. *For. Ecol. Manag.* 424, 246–258.
- Calviño-Cancela, M., Chas-Amil, M.L., García-Martínez, E.D., Touza, J., 2016. Wildfire risk associated with different vegetation types within and outside wildland-urban interfaces. *For. Ecol. Manag.* 372, 1–9.
- Calviño-Cancela, M., Lorenzo, P., González, L., 2018. Fire increases *Eucalyptus globulus* seedling recruitment in forested habitats: Effects of litter, shade and burnt soil on seedling emergence and survival. *For. Ecol. Manag.* 409, 826–834.
- Castro, E.B., González, M.C., Tenorio, M.C., Bombín, R.E., Antón, M.G., Fuster, M.G., Manzanque, A.G., Manzanque, F.G., Saiz, J.C.M., Juaristi, C.M., Pajares, P.R., Ollero, H.S., 1997. Los bosques ibéricos: una interpretación geobotánica. *Planeta*, Barcelona, Spain.
- Castro-Díez, P., Godoy, O., Alonso, A., Gallardo, A., Saldaña, A., Vila, M., 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecol. Lett.* 17 (1), 1–12.
- Castro-Díez P., Fernández M., Godoy O., 2016. Spain, in: Hasenauer H, Gazda A, Konner M, Lapin, K., Mohren, G.M.J., Spiecker, H., et al. (Eds.), Non-native tree species for European forests: experiences, risks and opportunities. COST Action FP1403 NNEXT Country Reports, Joint Volume. 2nd Edition. University of Natural Resources and Life Sciences, Vienna, Austria, pp. 420.
- Castro-Díez, P., Vaz, A.S., Silva, J.S., Loo, M., Alonso, Á., Aponte, C., Bayón, Á., Bellingham, P.J., Chiuffo, M.C., DiManno, N., Julian, K., Kandert, S., La Porta, N., Marchante, H., Maule, H.G., Mayfield, M.M., Metcalfe, D., Monteverdi, M.C., Núñez, M.A., Ostertag, R., Parker, I.M., Peltzer, D.A., Potgieter, L.J., Raymundo, M., Rayome, D., Reisman-Berman, O., Richardson, D.M., Roos, R.E., Saldaña, A., Shackleton, R.T., Torres, A., Trudgen, M., Urban, J., Vicente, J.R., Vilà, M., Ylloja, T., Zenni, R.D., Godoy, O., 2019. Global effects of non-native tree species on multiple ecosystem services. *Biol. Rev.* 94 (4), 1477–1501.
- Catford, J.A., Jansson, R., Nilsson, C., 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* 15, 22–40.
- Catry, F.X., Moreira, F., Deus, E., Silva, J.S., Águas, A., 2015. Assessing the extent and the environmental drivers of *Eucalyptus globulus* wildling establishment in Portugal: results from a countrywide survey. *Biol. Invasions* 17 (11), 3163–3181.
- CGIAR, 2021. SRTM 90m Digital Elevation Database v4.1. Consortium for Spatial Information (CGIAR-CSI. Available at <https://srtm.csi.cgiar.org/>).
- Deus, E., Silva, J.S., Castro-Díez, P., Lomba, A., Ortiz, M.L., Vicente, J., 2018. Current and future conflicts between eucalypt plantations and high biodiversity areas in the Iberian Peninsula. *J. Nat. Conserv.* 45, 107–117.
- Deus, E., Silva, J.S., Lacombe, M.J., Catry, F.X., Queirós, L., dos Santos, P., Matias, H., Águas, A., Rego, F.C., 2019. Investigating the invasiveness of *Eucalyptus globulus* in Portugal: site-scale drivers, reproductive capacity and dispersal potential. *Biol. Invasions* 21 (6), 2027–2044.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gormé, L.D., 2016. The global spectrum of plant form and function. *Nature* 529 (7585), 167–171.
- Dickie, I.A., Bennett, B.M., Burrows, L.E., Nuñez, M.A., Peltzer, D.A., Porté, A., Richardson, D.M., Rejmanek, M., Rundel, P.W., van Wilgen, B.W., 2014. Conflicting values: ecosystem services and invasive tree management. *Biol. Invasions* 16 (3), 705–719.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münckmüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36 (1), 27–46.
- Fernandes, P., Mágua, C., Correia, O., González-Moreno, P., 2018. What drives *Eucalyptus globulus* natural establishment outside plantations? The relative importance of climate, plantation and site characteristics. *Biol. Invasions* 20 (5), 1129–1146.
- Funk, J.L., Cleland, E.E., Suding, K.N., Zavaleta, E.S., 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol. Evol.* 23 (12), 695–703.
- Garau, A.M., Ghersa, C.M., Lemcoff, J.H., Baraño, J.J., 2009. Weeds in *Eucalyptus globulus* subsp. *maidenii* (F. Muell) establishment: effects of competition on sapling growth and survivorship. *New For.* 37 (3), 251–264.
- Gurevitch, J., Scheiner, S.M., Fox, G.A., 2002. *The ecology of plants*. Sinauer Associates, Massachusetts, USA, Sunderland.
- Heikkinen, R.K., Luoto, M., Virkkala, R., Rainio, K., 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *J. Appl. Ecol.* 41 (5), 824–835.
- Hirsch, H., Allsopp, M.H., Canavan, S., Cheek, M., Geerts, S., Geldenhuys, C.J., Harding, G., Hurley, B.P., Jones, W., Keet, J.-H., Klein, H., Ruwansa, S., van Wilgen, B.W., Wingfield, M.J., Richardson, D.M., 2020. *Eucalyptus camaldulensis* in South Africa—past, present, future. *Trans. R. Soc. South Africa* 75 (1), 1–22.
- Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78 (7), 1966–1975.
- ISRIC, 2021. SoilGrids - global gridded soil information. ISRIC World Soil Information. Available at <https://www.isric.org/explore/soilgrids>.
- Karger, D.N., Conrad, O., Böhrner, J., Kawohl, T., Keft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., Kessler, M., 2017. Climatologies at high resolution for the Earth land surface areas. *Sci. Data* 4, 170122.
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., et al., 2020. TRY plant trait database – enhanced coverage and open access. *Glob. Change Biol.* 26, 119–188.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J., 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* 2 (5), 286–293.
- Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.-F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529 (7585), 204–207.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91 (1), 299–305.
- Laliberté, E., Legendre, P., Shipley, B., Laliberté, M.E., 2014. Package ‘FD’. Measuring functional diversity from multiple traits, and other tools for functional ecology.
- Larcombe, M.J., Silva, J.S., Vaillancourt, R.E., Potts, B.M., 2013. Assessing the invasive potential of *Eucalyptus globulus* in Australia: quantification of wildling establishment from plantations. *Biol. Invasions* 15 (12), 2763–2781.
- Lázaro-Lobo, A., Ervin, G.N., 2021. Native and exotic plant species respond differently to ecosystem characteristics at both local and landscape scales. *Biol. Invasions* 23 (1), 143–156.
- Lázaro-Lobo, A., Evans, K.O., Ervin, G.N., 2020. Evaluating landscape characteristics of predicted hotspots for plant invasions. *Invasive Plant Sci. Manag.* 13 (3), 163–175.
- Lázaro-Lobo, A., Lucardi, R.D., Ramirez-Reyes, C., Ervin, G.N., 2021a. Region-wide assessment of fine-scale associations between invasive plants and forest regeneration. *For. Ecol. Manag.* 483, 118930. <https://doi.org/10.1016/j.foreco.2021.118930>.
- Lázaro-Lobo, A., Ramirez-Reyes, C., Lucardi, R.D., Ervin, G.N., 2021b. Multivariate analysis of invasive plant species distributions in southern US forests. *Landscape Ecol.* 36 (12), 3539–3555.
- Legendre, P., Legendre, L., 2012. *Numerical ecology*, 3rd ed. Elsevier Science, Amsterdam, The Netherlands.
- Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* 7 (10), 975–989.
- Llaneza, L., López-Bao, J.V., Sazatornil, V., 2012. Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Divers. Distrib.* 18 (5), 459–469.
- Lockwood, J.L., Cassey, P., Blackburn, T.M., 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers. Distrib.* 15 (5), 904–910.
- MacDicken, K., Jonsson, Ö., Piña, L., Maulo, S., Adikari, Y., Garzuglia, M., Lindquist, E., Reams, G., D’Annunzio, R., 2015. *Global Forest Resources Assessment 2015: How have the World’s Forests Changed?* FAO, Rome.
- MacDougall, A.S., Gilbert, B., Levine, J.M., 2009. Plant invasions and the niche. *J. Ecol.* 97 (4), 609–615.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O’Brien, J., Brooks, M.M., 2017. Package ‘glmmTMB’. R Package Version 1.0.1.
- Mead, D.J., 2013. Sustainable management of *Pinus radiata* plantations. FAO Forestry Paper No. 170. Rome, FAO.
- Merino, A., López, A.R., Branas, J., Rodríguez-Soalleiro, R., 2003. Nutrition and growth in newly established plantations of *Eucalyptus globulus* in northwestern Spain. *Ann. For. Sci.* 60, 509–517.

- Milbau, A., Stout, J.C., Graae, B.J., Nijs, I., 2009. A hierarchical framework for integrating invasibility experiments incorporating different factors and scales. *Biol. Invasions* 11, 941–950.
- Montero, G., 1997. Breve descripción del proceso repoblador en España (1940–1995). *Legno Celulosa Carta* 4, 35–42.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91, 97–108.
- Nereu, M., Silva, J.S., Deus, E., Nunes, M., Potts, B., 2019. The effect of management operations on the demography of *Eucalyptus globulus* seedlings. *For. Ecol. Manag.* 453, 117630.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. Package 'vegan'. Community ecology package, version 2.5-6.
- Potts, B.M., McGowen, M.H., Williams, D.R., Sutor, S., Jones, T.H., Gore, P.L., Vaillancourt, R.E., 2008. Advances in reproductive biology and seed production systems of *Eucalyptus*: the case of *Eucalyptus globulus*. *South For.* 70, 145–154.
- Queirós, L., Deus, E., Silva, J.S., Vicente, J., Ortiz, L., Fernandes, P.M., Castro-Díez, P., 2020. Assessing the drivers and the recruitment potential of *Eucalyptus globulus* in the Iberian Peninsula. *For. Ecol. Manag.* 466, 118147.
- R Core Team., 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.
- Rejmánek, M., Richardson, D.M., 2013. Trees and shrubs as invasive alien species—2013 update of the global database. *Divers. Distrib.* 19, 1093–1094.
- Reyes, O., García-Duro, J., Salgado, J., 2015. Fire affects soil organic matter and the emergence of *Pinus radiata* seedlings. *Ann. For. Sci.* 72, 267–275.
- Richardson, D.M., Brown, P.J., 1986. Invasion of mesic mountain fynbos by *Pinus radiata*. *S. Afr. J. Bot.* 52, 529–536.
- Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species – a global review. *Divers. Distrib.* 17, 788–809.
- Ruiz, F., Lopez, G.A., Toval, G., Alejano, R., 2008. La Selvicultura del *Eucalyptus globulus*. In: Serrada, R., Montero, G., Reque, J. (Eds.), *Compendio de selvicultura aplicada en España*. Instituto Nacional de Investigaciones Agrarias, Madrid, España.
- Ruiz-Benito, P., Madrigal-González, J., Ratcliffe, S., Coomes, D.A., Kändler, G., Lehtonen, A., 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. *Ecosyst.* 17, 1439–1454.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32, 305–332.
- Sanchez-Rodriguez, F., Rodríguez-Soalleiro, R., 2008. Selvicultura de *Pinus radiata* D. Don. In: Serrada, R., Montero, G., Reque, J. (Eds.), *Compendio de selvicultura aplicada en España*. Instituto Nacional de Investigaciones Agrarias, Madrid, España.
- Sanz-Elorza, M., Dana, E.D., Sobrino, E., 2004. Atlas de las plantas alóctonas invasoras de España. Dirección General para la Biodiversidad, Madrid, España.
- Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* 1, 103–113.
- Serrada, R., Montero, G., Reque, J.A., 2008. Compendio de selvicultura aplicada en España. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Ministerio de Educación y Ciencia, Madrid, España.
- Simberloff, D., 2009. The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 40, 81–102.
- Simberloff, D., Nunez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., et al., 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecol.* 35, 489–504.
- Soumare, A., Sall, S.N., Sanon, A., Cissoko, M., Hafidi, M., Ndoye, I., Duponnois, R., 2016. Changes in soil pH, polyphenol content and microbial community mediated by *Eucalyptus camaldulensis*. *Appl. Ecol. Environ. Res.* 14, 1–19.
- Stanturf, J.A., Vance, E.D., Fox, T.R., Kirst, M., 2013. *Eucalyptus* beyond its native range: Environmental issues in exotic bioenergy plantations. *Int. J. For. Res.* 2013, 463030.
- Swenson, N.G., Enquist, B.J., Pither, J., Kerkhoff, A.J., Boyle, B., Weiser, M.D., et al., 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Glob. Ecol. Biogeogr.* 21, 798–808.
- Theoharides, K.A., Dukes, J.S., 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* 176, 256–273.
- Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E., 2010. National forest inventories: pathways for common reporting. Springer, New York, USA.
- Veiras, X., Soto, M.A., 2011. La conflictividad de las plantaciones de pino y eucalipto en España y Portugal. Greenpeace, p. 98.
- Villaescusa, R., Díaz, R., 1998. Segundo Inventario Forestal Nacional (1986–1995). Ministerio de Medio Ambiente, ICONA, Madrid.
- Villéger, S., Mason, N.W., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
- Williams, M.C., Wardle, G.M., 2007. *Pinus radiata* invasion in Australia: identifying key knowledge gaps and research directions. *Austral Ecol.* 32, 721–739.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.