

## RESEARCH ARTICLE

# Functional traits and propagule pressure explain changes in the distribution and demography of non-native trees in Spain

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## Abstract

**Questions:** Non-native tree species (NNT) may bring about economic benefits, but also threats to ecosystems, mostly if they show expansive trends.

**Location:** A set of 12,000 permanent plots of the second (1986–1996), third (1997–2007) and fourth (2008–2017) Spanish Forest Inventory.

**Methods:** We quantified changes over time (1986–2017) of the NNT present in forests of peninsular Spain and we assessed how NNT's traits, propagule pressure and human perception of NNT explain changes in distribution and demography of NNT. We quantified changes in four demographic parameters of every NNT: changes in the occupancy of species (number of plots where the species are present), annual changes in tree density and basal area, and tree growth. To explain the observed species trends, we selected functional traits related to the resource acquisition strategy, and key human drivers.

**Results:** Most of the NNT expanded their occupancy in the study area and increased their density, basal area, and tree growth through time. Increases in tree density and growth were greater in NNT with greater tolerance for low water potentials, with low specific leaf area, and with high propagule pressure. Increases in basal area were greater with high height of the NNT.

**Conclusions:** The overall increase in occupancy suggests that there is room for expansion of NNT in Spain. This knowledge will help to predict the dynamics of NNT already present in Spain and identify risks for forest biodiversity.

## KEYWORDS

biological invasions, demography, distribution range, Iberian Peninsula, life-history traits, National Forest Inventory, non-native tree species, temporal trends

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## 1 | INTRODUCTION

The rate of non-native tree species (NNT) introductions has increased markedly over the last decades worldwide, due to the growing demand for tree-derived goods and services (Brundu & Richardson, 2016; Castro-Díez et al., 2019). However, NNT can naturalize in the recipient regions, and some show a high potential to expand and colonize new areas (i.e. invasive species, *sensu* Richardson et al., 2000). Biological invasions are currently considered as one of the key drivers of ecosystem change and biodiversity loss (Gaertner et al., 2009; Vilà et al., 2011). Moreover, some non-native species may have undesired effects on ecosystems and socio-economy, even before becoming invasive (e.g. species producing allergenic pollen, tree plantations with high flammability). Therefore, it is critical to further understand the characteristics and drivers of the success of NNT (Dodet & Collet, 2012).

The success of NNT in the recipient ecosystem may be driven by the intrinsic properties of the species, by abiotic and biotic characteristics of the receiving ecosystem, and/or by the introduction history (i.e. the frequency and intensity of the introduction, or time since introduction) (Catford et al., 2009; Pyšek et al., 2009). Intrinsic biological characteristics of species can make them inherently efficient colonizers or competitors, increasing their chances of spreading in the host community (Catford et al., 2009; Dodet & Collet, 2012). Therefore, understanding why some functional traits are key to species population expansions should help to further evaluate the demographic success of NNT species (Richardson & Rejmánek, 2011).

Besides species' functional traits, human actions may contribute to the success of NNT, especially by increasing propagule pressure (Degasperis & Motzkin, 2007; Wilson et al., 2007; Catford et al., 2009), which could be affected by the time since introduction (Pyšek et al., 2009). Propagule pressure depends on the rate of seed production, the extent of the species' occupancy and the density of the species (Wilson et al., 2007; Pyšek et al., 2009; Richardson & Rejmánek, 2011). Propagule pressure affects the genetic diversity and the probability of reaching a favourable environment (Catford et al., 2009). Longer residence times (i.e. time since introduction) may contribute to stronger and wider propagule spread (Degasperis & Motzkin, 2007; Pyšek et al., 2009; Kattge et al., 2020). Residence time can also reflect temporal changes in abiotic and biotic characteristics of host communities that benefit non-native species (Catford et al., 2009). Moreover, the social dimension of non-native species can be critical to effectively prevent invasions (Estévez et al., 2015). This is because species with a positive societal interest have greater chances for high propagule pressure, but also because decision-making regarding species management is influenced by the attractiveness of species (Binimelis et al., 2008). Despite its importance, the social dimension as predictor of NNT success has received less attention than other types of predictors (Estévez et al., 2015).

While the influence of species traits on non-native species' success has been explored frequently (Pyšek et al., 2009; van Kleunen et al., 2010; Castro-Díez et al., 2011), we still have a limited

understanding of how functional traits, human management and social perceptions explain changes in the structure, production and demography of NNT populations. Data obtained from national forest inventories (NFIs) are particularly relevant because they quantify forest structure and tree size in permanent plots every decade (Ruiz-Benito et al., 2014; Alberdi et al., 2020). Yet, information from NFIs has rarely been used to study demographic trends of NNT species (Hernández et al., 2014; Collins et al., 2020; Lázaro-Lobo et al., 2021; Oswald et al., 2021).

Our study aims to analyse temporal changes of NNT in permanent plots throughout about 30 years of the Spanish Forest Inventory (SFI, 1986–2017) and to identify factors associated with these changes. Specifically, we ask: (1) how NNT occupancy, abundance, and demographic variables have changed since the 1980s; and (2) how important species traits, propagule pressure, and societal interest are for explaining the demographic and distributional changes. We hypothesize that most NNT will be increasing their occupancy and will show high demographic success, due to human factors increasing propagule pressure. However, we also expect great differences across NNT, with greater success of species with traits associated with a conservative resource use strategy, with higher propagule pressure and with greater societal interest.

## 2 | METHODS

### 2.1 | National Forest Inventory data for the NNT

Our analyses were based on published information on the second (1986–1996), third (1997–2007) and fourth (2008–2017) Spanish Forest Inventory (2SFI, 3SFI and 4SFI respectively). The SFI is a monitoring and evaluation project that sampled circular plots systematically distributed on a 1-km<sup>2</sup> grid independently of its origin (i.e. natural or planted) across the forested area of Spain (i.e. forest cover over 5%) with at least one adult tree measured, i.e. diameter at breast height (d.b.h.) greater than or equal to 75 mm and height, to 130 cm (Villaescusa & Díaz, 1998). The 4SFI is currently ongoing, with available data for 16 out of the 50 Spanish provinces. We focused on permanent forest plots, that is those re-measured at least through 2SFI and 3SFI (5,770 plots across the full country, hereafter 23SFI) and/or through 3SFI and 4SFI (6,430 plots in the 16 provinces available, hereafter 34SFI). We checked the native or non-native status of all tree species sampled in the SFI according to Flora Iberica (Castroviejo, 2020). All species identified as non-native were considered as candidates to be included in the study. Based on this list, we selected the 17 NNT present in at least 20 plots in either comparison (23SFI or 34SFI).

The SFI plots have a variable radius where trees with d.b.h. greater than or equal to 7.5, 12.5, 22.5, and 42.5 cm are measured in a radius of 5, 10, 15 and 25 m. In each SFI plot, we calculated proxies of stand successional stage and aridity conditions to control for the effects of site conditions in the statistical models (see below). We selected mean d.b.h. for each SFI plot as a proxy for stand successional stage,



because it was significantly correlated with tree density ( $r = -0.33$ ,  $p < 0.001$ ) and total basal area ( $r = 0.44$ ,  $p < 0.001$ ). To estimate the climatic conditions experienced by the NNT, we calculated the De Martonne aridity index ( $I_{DM}$ ) as  $I_{DM} = P/(T + 10)$ , where  $P$  is the annual mean precipitation,  $T$  is the annual mean temperature, and 10 is a constant to avoid negative values. Climatic data were downloaded 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).

## 2.2 | Quantification of temporal trends of NNT species

For each NNT species we quantified its area of occupancy (*sensu* Gaston, 1991) in continental Spain as the number of SFI plots occupied by adult trees, that is those with d.b.h. > 7.5 cm and height > 130 cm (number of plots).

Forest structure was characterized by stand density (Dens, number of trees ha<sup>-1</sup>) and total stand basal area (BA, m<sup>2</sup> ha<sup>-1</sup>). Both parameters refer to adult trees. For each species and period (23SFI and 34SFI) we calculated changes in the area of occupancy of species (i.e. total change in the number of plots where the species was present in adult stage) and annual changes in tree density ( $\Delta$ Dens, number of trees ha<sup>-1</sup> year<sup>-1</sup>), basal area ( $\Delta$ BA, m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) and tree growth (m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>). The annual changes were calculated as the changes between consecutive inventories divided by the number of years between them. The change in plot basal area is a composite measure of three processes: the growth of living trees, the transition of juvenile to adult trees, and the loss of BA due to death of trees (see e.g. Ruiz-Benito et al., 2014). The annual tree growth was calculated as the increase of d.b.h. of the trees present in selected plots in consecutive inventories (see e.g. Gómez-Aparicio et al., 2011). We used the SFI information on land use type, which includes categories named 'forest' and 'forest plantation', to separate plots between plantations and forests of natural origin.

## 2.3 | Characterization of species-specific traits

We selected functional traits extensively documented as key traits for plant resource use strategy: water potential causing 50% loss of hydraulic conductivity (P50, MPa), specific leaf area (SLA, m<sup>2</sup> kg<sup>-1</sup>), wood density (WD, g cm<sup>-3</sup>), maximum tree height (MTH, m), leaf habit (LP, evergreen and deciduous), seed mass (SM, mg) and dispersal syndrome [DS, grouped as assisted (zoochory, anemochory) and non-assisted (autochory) dispersal]. These traits are relevant to growth, survival and reproduction of the species (Díaz et al., 2016; Kunstler et al., 2016; Greenwood et al., 2017) (see Table 1). Trait information was compiled from the open-access TRY database version 5 (<http://www.try-db.org>). We found a non-significant correlation between the selected traits, except for P50 and SLA, which showed a significant positive correlation ( $r = 0.69$ ,  $p < 0.01$ , Appendix S1).

None of the traits showed significant phylogenetic correlation (see Appendix S2 for further information).

## 2.4 | Characterization of propagule pressure and societal interest

Total number of adult trees recorded in the 2SFI plots (NT) and residence time (RT) were used as a proxy for the propagule pressure of each tree species at the beginning of the study period. To estimate the minimum RT we searched the year of the first record of each species in Spain (Rejmánek, 2000) by exploring the Spanish Forestry literature (see Table 2 and Appendix S3). Given the unequal precision of minimum RT found across species and sources, we grouped all values in two categories, namely, before or after 1900.

We used the Google Trends tool (<http://trends.google.es>) which measures societal interest on a topic (in this case, each species) based on searches using a particular keyword (Burivalova et al., 2018). Google Trends provides monthly values of trends for five keywords at a time, for a selected temporal and geographical range. These values were normalized relative to the highest value, which is set to 100. In our case we use the scientific names of the NNT as keywords (we avoided common names because sometimes the same name represents more than one species), we restricted the search to the geographical region of Spain, and the search period from 2005 (the first year covered by Google Trends) to 2019. To obtain a comparable index across species (GT index), we followed Bayón and Vilà (2019): we first formed an initial group of five species and retained the species with the highest trend value; then, we compared the species which obtained the highest rank in the first search with the next four species. We repeated the same procedure until ending the full list of species. In this way, we identified the species with the highest trend value (*Cupressus sempervirens*), which received a score of 100. Then we compared each of the remaining species with *Cupressus sempervirens* to get a value relative to 100. The PP and GT indices were neither correlated with each other nor with the other selected traits (all correlations:  $p > 0.18$ ).

## 2.5 | Statistical analysis

Pearson's chi-squared test was used to determine whether the occupancy of new plots was significantly different from a random distribution with respect to land use type (plantation versus natural forest) considering the distribution of both types of land use in the overall data set.

To analyse demographic changes since the 1980s we fitted linear models with changes in tree density ( $\Delta$ Dens), total tree basal area ( $\Delta$ BA) and tree growth in each plot as response variables, and SFI period (23SFI and 34SFI), species identity and the period  $\times$  species identity interaction as predictors. In this way we assessed whether changes in  $\Delta$ Dens,  $\Delta$ BA and growth were constant across SFI periods and species or not. Mean tree size and De

**TABLE 1** Functional traits used in this study, including their units, interpretation for ecosystem functioning and hypotheses that may explain potential changes in species performance

Trait	Mechanisms leading to changes in range, density, basal area	References
Specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$ )	Leaves with lower SLA have a higher return on investment. Plants with low SLA are considered more conservative in terms of resource use	Kunstler et al., 2016; Reich et al., 1998; Westoby et al., 2000; Wright et al., 2004
Wood density (WD, $\text{g cm}^{-3}$ )	Trees with higher wood density invest a higher proportion of carbon in plant support but obtain a higher resistance to physical damage, which contributes to increased longevity	Castro-Diez et al., 1998; Chave et al., 2009; Greenwood et al., 2017; Kunstler et al., 2016
Seed mass (SM, mg)	Trees with smaller seeds usually produce larger numbers of seeds with lower chances of seedling survival. Seed size correlates positively with competition ability and negatively with colonization success	Westoby, 1998
Maximum tree height (MTH, m)	Competition ability (larger trees have greater competitive abilities and successional progress)	Moles et al., 2009; Westoby, 1998
Water potential causing 50% loss of hydraulic conductivity (P50, kMpa)	Trees with high embolism resistance that operate with a more negative pressure (lower P50) limit loss of xylem conductivity during drought stress, thereby reducing the risk of hydraulic failure	Choat et al., 2012; Reich, 2014
Leaf habitat (LH, evergreen, deciduous)	Long-lived leaves (evergreen) require a higher investment in support, thus having a lower return on investment. In turn, they take longer to be amortized	Wright et al., 2004
Dispersal syndrome (DS, autochory, anemochory, barochory, zoochory)	Seed dispersal assisted by wind or animals may have a wider range than non-assisted dispersal	Arjona et al., 2018; Nathan, 2006

Martonne aridity index of each plot were also included in the models as predictors to control for the effect of stand successional stage and aridity conditions on the response variables. Given the normal distribution of the response variables, we used an identity link function with a normal distribution of residuals. Moran spatial correlograms and permutation tests were computed to check for autocorrelation in model residuals using geolocations of each plot (x-y coordinates) for constructing a correlation matrix. The *p*-values were obtained using Monte-Carlo simulations based on 1000 permutations of the data.

We assessed the contribution of functional traits, propagule pressure and societal interest to explain changes of occupancy and demography of the NNT using linear models (one model for each predictor, see Table 2). In these models, each species in each SFI period was an observation. Occupancy,  $\Delta$ Dens,  $\Delta$ BA and growth over consecutive SFIs were the response variables, and each predictor of Table 2, the SFI period and their interaction were the explicative variables using one model for each predictor. The interaction term allowed us to evaluate whether the effect of factors varied across SFI periods. We removed influential points using Cook's distance

with a cut-off of  $4/n$ , where *n* is the number of permanent plots censused (Chatterjee & Hadi, 2012), which filtered approximately 3% of the data points.

For all the linear models fitted, we performed analysis of variance (ANOVA type III) to test the null hypothesis that the response means are identical across combinations of predictors. We estimated  $R^2$  as the proportion of the variance of a dependent variable explained by predictors in linear models. SM and NT were log-transformed and all continuous predictors were mean-centred and scaled by 1 standard deviation before analysis to facilitate direct comparisons of the effect sizes of each predictor. Model residuals were checked graphically for normality and homogeneity of variances using diagnostic plots. Residuals for models fitted to RT, dispersal syndrome and life habit deviated from a normal distribution and were heteroscedastic. Thus, we performed non-parametric Kruskal-Wallis rank sum tests to analyse their effect on occupancy,  $\Delta$ Dens,  $\Delta$ BA and growth. In models fitted to RT, species with missing data were removed prior to analysis. Statistical analyses were performed using R 4.0.1 (R Core Team, 2020) and the packages 'stats' (R Core Team, 2020) and 'car' (Fox & Weisberg, 2019).



TABLE 2 List of 17 non-native tree species and their functional traits and human factors used in this work

Species	Family	Acronyms	GO	LP	DS	P50 (MPa)	SLA (m <sup>2</sup> kg <sup>-1</sup> )	SM (mg)	WD (g cm <sup>-3</sup> )	MTH (m)	NT (no trees)	GT (STV)	RT (yr)
<i>Acacia dealbata</i>	Fabaceae	AcDe	Aus	Evergreen	Zoochory	-0.90	15.69	11.84	0.59	17.95	14	84.13	1824
<i>Acacia melanoxylon</i>	Fabaceae	AcMe	Aus	Evergreen	Zoochory	-0.90	14.70	12.89	0.55	27.38	83	23.28	1801
<i>Castanea sativa</i>	Fagaceae	CaSa	Eur	Deciduous	Zoochory	-3.00	14.12	2384.16	0.57	28.00	8,773	91.93	0
<i>Chamaecyparis lawsoniana</i>	Cupressaceae	ChLa	NAm	Evergreen	Anemochory	-5.17	5.82	2.39	0.49	23.84	1,177	45.12	na
<i>Cupressus sempervirens</i>	Cupressaceae	CuSe	Eur	Evergreen	Autochory	-4.46	5.82	7.61	0.56	26.00	162	100.00	1500–1900
<i>Eucalyptus camaldulensis</i>	Myrtaceae	EuCa	Aus	Evergreen	Anemochory	-2.22	4.68	1.89	0.73	32.06	2,872	29.02	1850
<i>Eucalyptus globulus</i>	Myrtaceae	EuGl	Aus	Evergreen	Anemochory	-2.22	12.57	8.82	0.72	48.00	9,588	66.38	1846
<i>Eucalyptus gomphocephala</i>	Myrtaceae	EuGo	Aus	Evergreen	Anemochory	-2.22	7.87	8.88	0.87	47.46	81	0.00	na
<i>Eucalyptus nitens</i>	Myrtaceae	EuNi	Aus	Evergreen	Anemochory	-2.22	7.87	2.92	0.54	47.26	171	0.00	na
<i>Larix</i> spp.	Pinaceae	LaSp	Eur	Deciduous	Anemochory	-3.55	10.66	6.41	0.51	32.00	1,362	27.65	1900–1970
<i>Picea abies</i>	Pinaceae	PiAb	Eur	Evergreen	Anemochory	-3.98	5.71	6.51	0.53	33.50	153	76.83	1900–1970
<i>Pinus radiata</i>	Pinaceae	PiRa	NAm	Evergreen	Anemochory	-2.65	7.97	35.51	0.49	41.50	21,128	86.15	1850
<i>Platanus hispanica</i>	Platanaceae	PIHi	Art	Deciduous	Anemochory	-1.60	7.57	4.15	0.67	35.00	208	89.20	na
<i>Populus canadensis</i>	Salicaceae	PoCa	Art	Deciduous	Anemochory	-2.13	13.37	0.46	0.47	37.29	541	0.00	1700
<i>Pseudotsuga menziesii</i>	Fabaceae	PsMe	NAm	Evergreen	Zoochory	-3.60	8.49	12.38	0.46	36.18	857	38.10	1960
<i>Quercus rubra</i>	Fabaceae	QuRu	NAm	Deciduous	Autochory	-1.61	15.01	2959.19	0.66	40.35	359	56.59	1970
<i>Robinia pseudoacacia</i>	Fagaceae	RoPs	NAm	Deciduous	Autochory	-0.50	23.29	18.94	0.69	31.47	427	0.00	1800

Abbreviations: DS, dispersal syndrome; GO, region of origin (Art, Artificial; Aus, Australia; Eur, Europe; NAm, North America); GT, Google Trends; LP, leaf habit; MTH, maximum tree height; NT, total number of adult trees; P50, water potential causing 50% loss of hydraulic conductivity; RT, residence time; SLA, specific leaf area; SM, seed mass; STV, species trend value; WD, wood density.

As we found a significant effect of both P50 and SLA on changes in density and growth (see section 3 – Results), and because P50 and SLA were correlated (Appendix S1), we fitted two additional models including both predictors simultaneously to discern the relative importance of P50 and SLA on the response variables. In each of these models we used changes in density and growth as explanatory variables and included P50, SLA and SFI, as predictors. We fitted an ANOVA type II sum of squares, which allows estimating the unshared variance explained by each predictor (Chatterjee & Hadi, 2012).

### 3 | RESULTS

#### 3.1 | Temporal changes in occupancy and abundance of non-native tree species

NNT in Spain showed large variation in the number of permanent plots occupied by each species. *Pinus radiata*, *Castanea sativa* and *Eucalyptus globulus* were the most frequent NNT (present in more than 1000 permanent plots in each SFI period), while the remaining species occupied between seven and 481 plots (Figure 1b). Thirteen out of the 17 species analysed expanded their occupancy across SFI periods (Figure 1b). The total number of plots colonized by all NNT was 697 (increase of 14.7%, from 4716 to 5413) and 750 (increase of 14.09%, from 5281 to 6025) for 23SFI and 34SFI, respectively (Figure 1b). *Acacia melanoxylon* and *A. dealbata* were particularly noteworthy, with increases above 50% in the number of permanent plots occupied during both SFI periods. By contrast, *E. globulus*, *E. camaldulensis*, *Picea abies* and *Larix* spp. showed a small reduction in the occupancy in at least one of the studied periods. On average, 57% of the new plots occupied by NNT were in natural forest, while the remaining 43% were in forest plantations. The Pearson's chi-squared test indicated that this distribution did not differ significantly from the 58.93% of natural forest distributed over all analysed plots of 23SFI and 34SFI (23SFI:  $\chi^2$  test = 1.20,  $p = 0.27$ ; 34SFI:  $\chi^2$  test = 2.93,  $p = 0.09$ ; see Appendix S4 for detailed information on each species).

#### 3.2 | Temporal changes in the demography of non-native tree species

Fitted linear models at plot level indicated a consistent and generalized increase in tree density, basal area and growth for all NNT in the two SFI periods (see positive values in Figure 2 and Appendix S5). The magnitude of this increase differed between species (all  $F$ -tests  $p < 0.05$ ; Appendix S6, Figure 2). Regarding tree density and growth, the species with more intense increases across both SFI periods were *Chamaecyparis lawsoniana*, *Eucalyptus gomphocephalus*, *Larix* spp, *Picea abies*, *Pinus radiata* and *Pseudotsuga menziesii*. *Populus x canadensis* was also one of the best-performing species in terms of basal area changes (Figure 2). For most species, the increase in

density and growth was greater in the 34SFI than in the 23SFI period (Appendix S5 and S6), although there was a significant SFI period  $\times$  species interaction (all  $F$ -tests  $p < 0.05$ ; Appendix S6) indicating that the change through time was species-dependent (Figure 2). In relation to the variables introduced in the models to control for site effects, the aridity index had a significant effect on changes in tree density (the higher the aridity the lower the increases in density), while plots with big trees experienced a higher increase in BA and growth (Appendix S5 and S6). The magnitude of Moran's  $I$  was low in all distance classes (maximum absolute value  $< 0.05$ ) and Moran correlograms did not show significant autocorrelation in model residuals after Holm-Bonferroni correction (Appendix S7).

#### 3.3 | Effects of the functional traits propagule pressure and societal interest on demography success of non-native trees

Among the explored predictors of changes in basal area, tree density and tree growth, we found significant effects for four of them: P50, SLA, MTH and NT (a proxy for propagule pressure) (Appendix S8 and S9 and Kruskal–Wallis tests,  $p > 0.05$ ). Species with a higher NT and lower P50 showed higher increases of tree density and growth through the studied periods (Figure 3, Appendix S10 and S11). Species with a higher SLA showed lower increases of tree density (Figure 3, Appendix S10 and S11). The interactions of total number of adult trees, P50 and SLA with SFI interval were not significant (all  $F$ -tests  $p > 0.05$ ; Appendix S11) indicating that these effects were consistent over the two studied periods. Species with larger MTH showed larger increases in basal area consistently over the two studied periods (Figure 4, Appendix S10 and S11). Leaf type, dispersal syndrome, RT and GT index had no significant effect on the changes in basal area, tree density and growth (Appendix S8 and S9). Regarding the models fitted to evaluate the joint effect of P50 and SLA on changes in density and growth, only P50 had a significant effect on the response variables (Appendix S12 and S13).

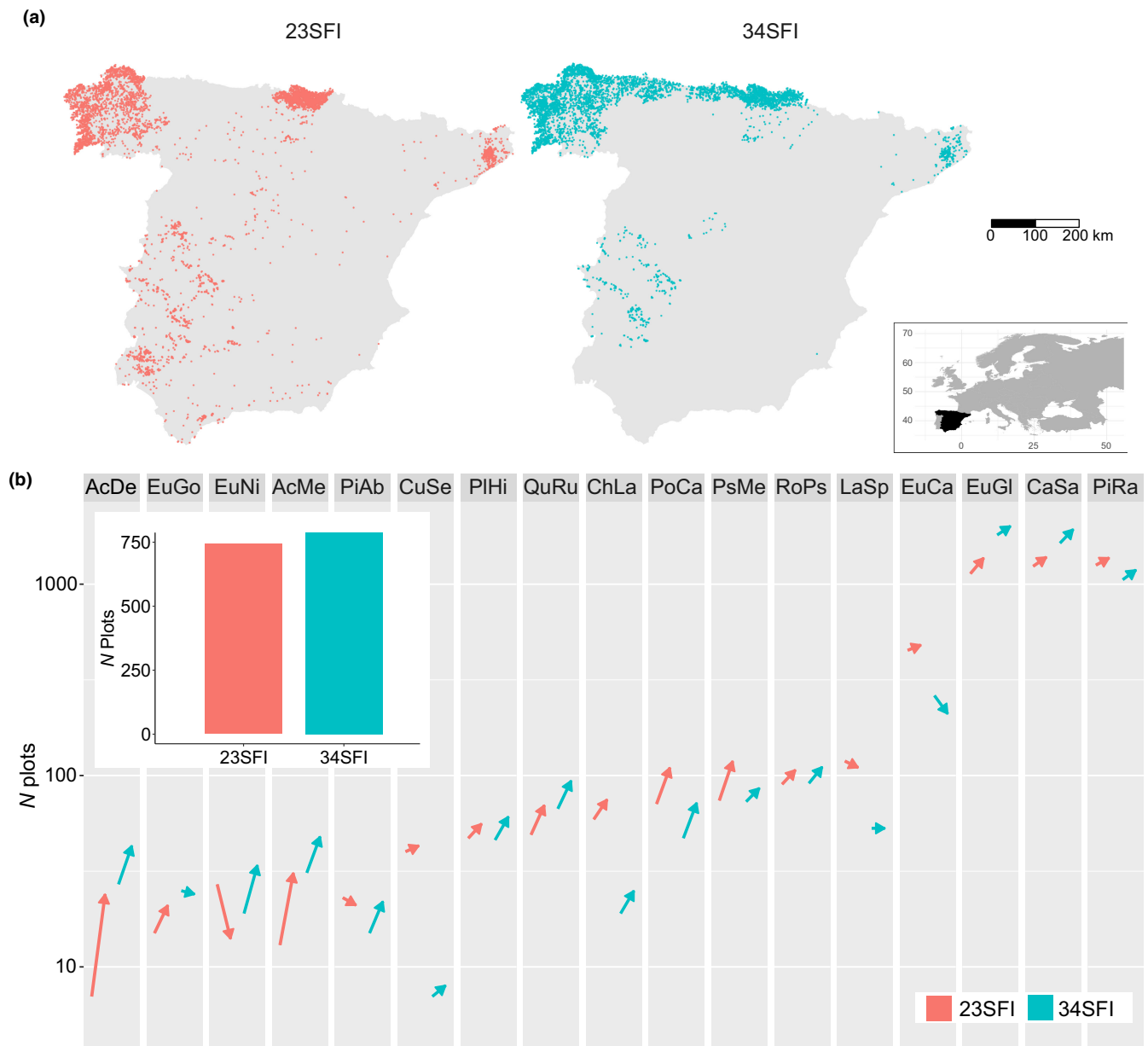
### 4 | DISCUSSION

After exploring what demographic changes occur in NNT in peninsular Spain across consecutive SFIs, we found a consistent expansion of occupancy for most NNT, accompanied by an increase of tree density, basal area, and growth for all NNT. These changes were correlated to functional traits involved in species resistance to drought, and with one of the indicators of propagule pressure.

#### 4.1 | Changes in non-native tree species' distribution and demography across time

In our study, most NNT increased their areas of occupancy in continental Spain, with an average increase of 37% and 28% in 23SFI





**FIGURE 1** Spatial distribution of permanent plots and temporal trends in occurrence of non-native tree species (NNT) across Spanish Forest Inventory (SFI) periods: 23SFI (red) and 34SFI (blue). (a) Location of permanent plots in the Iberian Peninsula. Each coloured point denotes a permanent plot with at least the occurrence of one NNT. The bottom right map indicates the location of the Iberian Peninsula in Europe. (b) Temporal changes in the number of plots where the target species occurred between consecutive inventories. Bar plots show the increase in the number of plots occupied by NNT in each SFI period. Note that total number of plots for 3SFI in 23SFI and 34SFI is not the same because permanent plots used in each SFI period varied. Acronyms used for each species can be found in [Table 2](#)

and 34SFI respectively. We highlight that this analysis is restricted to the forest area of Spain, so these values might change if we account for non-forest areas not covered by SFIs. A substantial proportion of NNT increases occurred in forests of natural origin with no apparent signs of human planting, suggesting that they were most likely natural colonizations. The expansion in occupancy can be used as a proxy of species spreading in existing forests (Gassó et al., 2009), which is one of the components of their impact (Sapsford et al., 2020). The increase in occupancy of NNT in Spain is consistent with trends previously reported worldwide (Hernández et al., 2014; Essl

et al., 2019), which may be related to the benefits provided by NNT and their use as extensive plantations (Brundu & Richardson, 2016; Castro-Díez et al., 2019). This expansion can be also explained by the fact that some Spanish forests are in developing stages (Ruiz-Benito et al., 2014; Astigarraga et al., 2020). Succession following agricultural abandonment is widespread (Cruz-Alonso et al., 2019), and likely opens opportunities for tree expansion of pioneer species, including several NNT (pines, acacias and eucalyptus) (Richardson, 1998).

The increase in occupancy of most NNT in the study area was accompanied by a general increase in tree density, basal area and

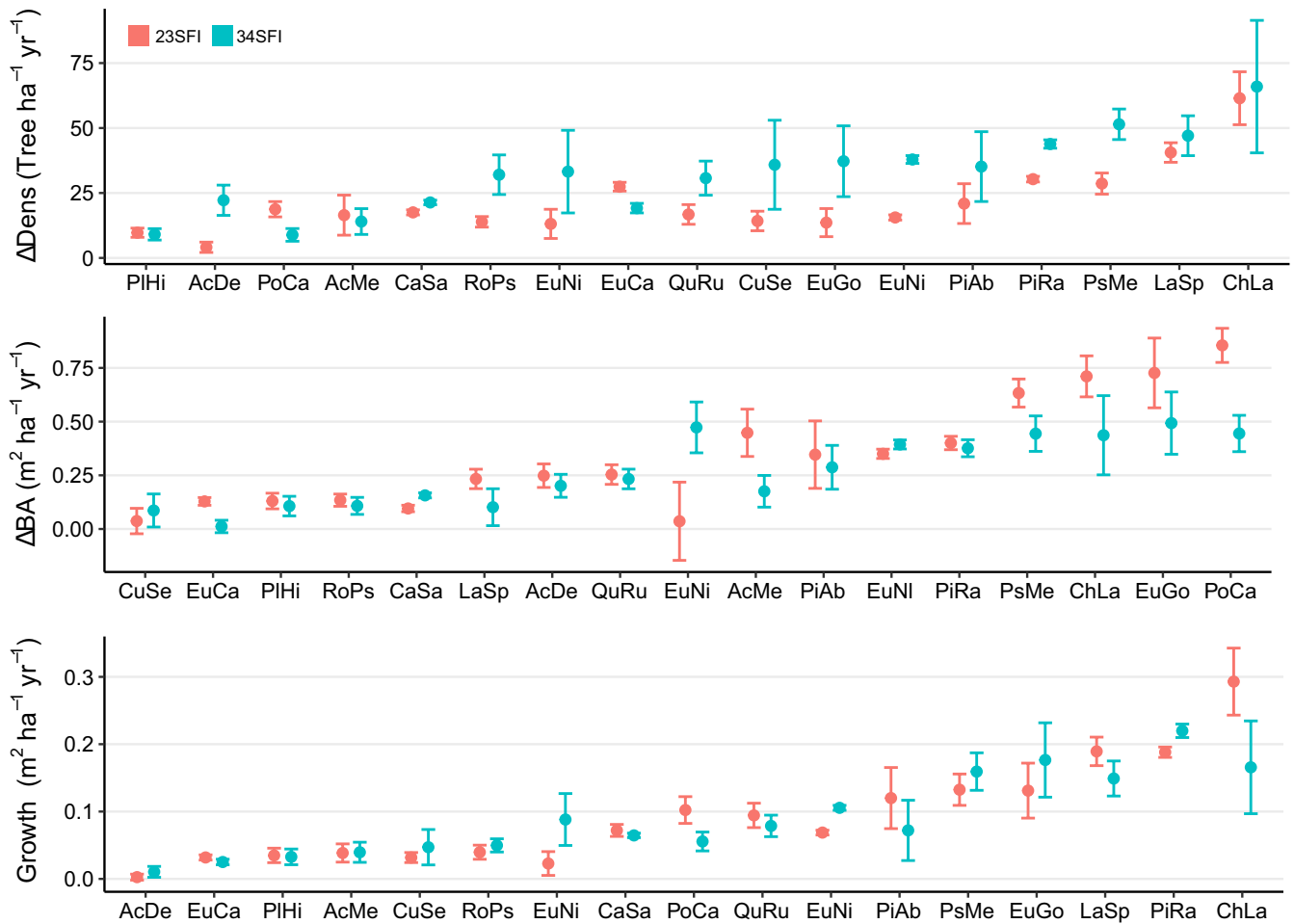


FIGURE 2 Changes in tree density, growth, and basal area (BA) of each non-native tree species (NNT) between consecutive Spanish Forest Inventory (SFI) surveys (23SFI and 34SFI). Bar plots show mean values for each species and SFI period. Error bars represent standard errors of the mean. Species acronyms are given in Table 2. Positive values denote an increase in tree density, basal area or tree growth

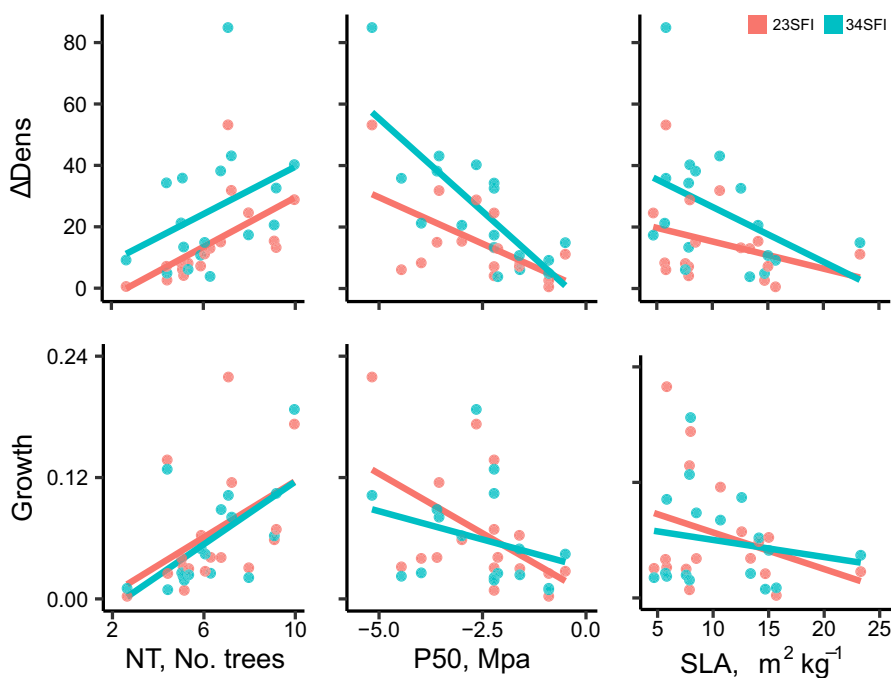
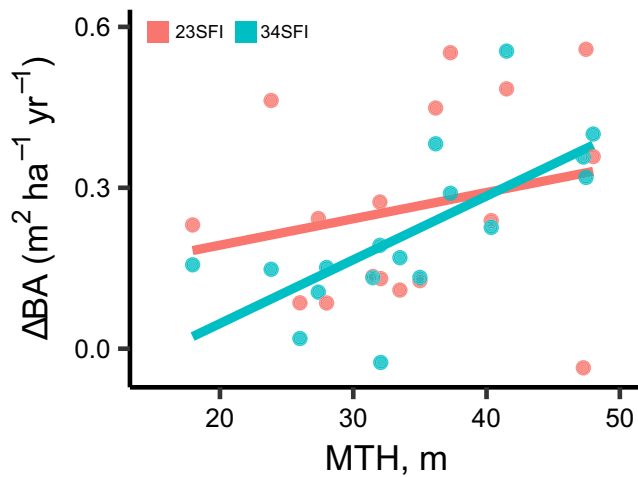


FIGURE 3 Relationship between number of trees (NT), water potential causing 50% loss of hydraulic conductivity (P50) and specific leaf area (SLA) and changes in tree density (number of trees  $\text{ha}^{-1} \text{year}^{-1}$ ) and growth ( $\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$ ), in Spanish Forest Inventory (SFI) plots between consecutive inventories. Each point represents the mean value for a species. Solid and dashed lines denote significant and non-significant regression respectively for each SFI period: from 2SFI to 3SFI (23SFI, red) and from 3SFI to 4SFI (34SFI, blue). Non-significant fits between the response variables and the other traits studied can be seen in Figure S4





**FIGURE 4** Relationship between maximum tree height (MTH) and above-ground forest productivity. Each point represents the mean value for a species. Solid lines show significant regression lines for each SFI period: from 2SFI to 3SFI (23SFI, red) and from 3SFI to 4SFI (34SFI, blue). Figure S4 shows the non-significant fits between the variable response and the other traits studied. BA, basal area

tree growth in SFI plots. This increase was consistent for most species even after controlling for site conditions (i.e. including the aridity index and tree size in the models). Previous research based on the same surveys also reported overall increases in these variables over the same period for most Iberian native tree species, which could be due to the developing successional stage of many Iberian forests (Ruiz-Benito et al., 2014; Astigarraga et al., 2020). We also found that the mean growth of NNT increased across SFI periods, which contrasts with previous results for Iberian native tree species, whose mean growth rate decreased over time (Astigarraga et al., 2020). The slow-down in growth of native species is a common pattern in European (Senf et al., 2018) and North American forests (Zhang et al., 2015) and it has been linked to forest ageing (Astigarraga et al., 2020). Therefore, our finding shows a contrasting trend between NNT and native tree species, which may be attributed to a preponderance of a pioneer strategy among NNT. This may explain their success in the Spanish forest area dominated by early succession forests (Richardson, 1998; Hernández et al., 2014; Pötzelberger et al., 2020).

#### 4.2 | Functional traits as drivers of non-native tree species trends

The higher increases in density and growth shown by the NNT which lose hydraulic conductivity at lower water potentials (low P50) suggests that hydraulic safety is a key factor for tree success in continental Spain. Xylem hydraulics represents a direct limit to the drought tolerance of vascular plants (Brodribb & Cochard, 2009) and hydraulic failure is a major global cause of productivity loss and plant mortality during droughts (Choat et al., 2012; Greenwood

et al., 2017). P50 is considered a key trait in predicting hydraulic efficiency during drought stress (Choat et al., 2012; Greenwood et al., 2017) and it has been successfully related to changes in composition in European forests (Ruiz-Benito et al., 2017; García-Valdés et al., 2021) and responses to climate change (García-Valdés et al., 2021).

Species with high hydraulic safety (low P50) tend to have a conservative strategy in relation to leaf carbon investment, that is, low SLA, which implies a slow return on investment (Wright et al., 2004). Indeed, along with other authors (Greenwood et al., 2017; Trueba et al., 2017; Zhang et al., 2017), we found a positive correlation between P50 and SLA ( $r = 0.69$ ,  $p < 0.001$ , see section 2 – Methods). SLA is a key trait in plant growth and water use strategy (Poorter et al., 2009) and low SLA is often associated with a higher drought resistance (Westoby et al., 2004). When we repeated the analyses by including P50 and SLA in a joint model to discern the relative importance of both variables, we found that the additional percentage of variance explained by SLA dropped from 13.3% to only 1.47%, while the variance explained by P50 reached 35.30% (Appendix S13). A similar pattern was found using growth as dependent variable (Appendix S12 and S13). Hence, although increases in tree density and growth occurred at low SLA, the amount of variance explained by SLA was shared with P50. This advocates for the use of physiological 'hard' traits, such as P50, which are mechanistically linked to carbon or water economy and might be better predictors of species performance than morpho-anatomical 'soft' traits such as SLA which, although simpler to measure, cannot always be suitable surrogates (Blackman et al., 2010; Wright et al., 2010; Trueba et al., 2017; Belluau & Shipley, 2018).

Taller NNT had greater increases in basal area, which can reflect both growth increases and mortality decreases (Poorter et al., 2008; Moles et al., 2009). Maximum tree height is a major determinant of a species' ability to compete for light (Poorter & Rose, 2005; Díaz et al., 2016) which may reduce their mortality rates in comparison with shorter species (Poorter et al., 2008; Moles et al., 2009).

#### 4.3 | Effects of propagule pressure on trends of non-native tree species

Changes in tree density and growth of NNT were positively related to our proxies for propagule pressure. Propagule pressure has been identified as a key driver of non-native species' success (Lockwood et al., 2005; Simberloff, 2009), because a constant flow of propagules increases the chance of NNT reaching favourable locations for establishment (Lockwood et al., 2005). Besides, increasing the number of propagules may help to overcome problems associated with small population sizes, such as demographic and environment stochasticity, or genetic drift and inbreeding depression (Colautti et al., 2006; Simberloff, 2009).

Although we expected a higher increase in the area of occupancy in species with higher propagule pressure (Degasperis & Motzkin, 2007; Wilson et al., 2007; Catford et al., 2009), the effect of this predictor on NNT occupancy was not significant. The importance of

propagule pressure on species spread can be context- and species-dependent, which may make it difficult to identify general patterns. For instance, the number of propagules necessary to colonize a location may depend on the habitat type, vegetation cover and degree of disturbance (Lake & Leishman, 2004; Fernandes et al., 2018), as well as on management practices, dispersal syndrome and planting history of the species (Křivánek et al., 2006; Fernandes et al., 2018). Finally, we cannot rule out that our proxy for propagule pressure failed to fully capture the number of propagules available for each NNT, as this is also determined by the age and vitality of the populations.

Residence time was not related to NNT demographic performance. However, species with longer RT showed higher values of propagule pressure (mean  $\pm$  SD number of trees:  $4843 \pm 7185$  vs  $683 \pm 541$  for species with introductions before and after 1900, respectively), which suggests that species with longer RT have become more abundant. The positive relationship supports the idea that RT represents a dimension of propagule pressure i.e., a longer time since introduction is likely to result in higher cumulative numbers of individual propagules released (Wilson et al., 2007). The poor quality and quantity of information on NNT RT in Spain may have obscured any potential pattern. The lack of effect of the GT index, as a measure of societal interest in each NNT, agrees with previous similar attempts to relate it to success of non-native species (Bayón & Vilà, 2019). This may be partly because the GT index cannot discern whether searches are due to the commercial/ornamental value of the species or for other reasons not related to a positive perception of the species.

Propagule pressure estimates did not correlate with functional traits and factors from both groups had a similar importance in terms of amount of variance explained (i.e., total number of trees versus P50 and MTH). This stresses the need to implement integrative approaches, using different types of predictors, to explain NNT success (Catford et al., 2009). Our models left a large amount of variation unexplained, which indicates that other factors, or the improvement of the indicators already used, may be required to explain changes in distribution and demography of NNT in Spain. Among potential additional factors, we suggest detailed information on the management and previous history (see discussion in Ruiz-Benito et al., 2020), the origin of the forests (i.e. natural or planted character, Ruiz-Benito et al., 2012) and a better understanding on how biotic interactions between natural and non-native species (Wilson et al., 2007; Catford et al., 2009) determine the overall demographic success of NNT.

#### 4.4 | Concluding remarks and future avenues

We found that most of the studied NNT expanded into natural forests and increased their density, basal area, and tree growth through time. The increases in tree density and growth were greater in NNT with high resistance to xylem embolism and low SLA, indicating that conservative strategies in carbon and water use are beneficial for

tree performance of NNT in continental Spain. Taller species had greater increases in basal area, indicating the key role of the competitive ability for tree growth and survival. Propagule pressure, estimated as the total number of adult trees, contributed to enhance the demographic performance of NNT. The acceleration of the expansion of the species between the two studied periods suggests that most NNT will expand faster in the future. Our results suggests that monitoring NNT with conservative strategies should be a priority. The observed trends in the colonization and demographic success of NNT need to be further studied to understand their impact on the native community and, therefore, promoting systematic monitoring programmes such as NFIs are key to identify areas where native biodiversity is at high risk.

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#### AUTHOR CONTRIBUTIONS

Carlos Lara-Romero: conceptualization, methodology, data curation, formal analysis, visualization, writing – original draft. Paloma Ruiz-Benito: data curation, methodology, formal analysis, writing – review and editing. Pilar Castro-Díez: funding acquisition, project administration, conceptualization, methodology, writing – review and editing.

#### DATA AVAILABILITY STATEMENT

Spanish Forest Inventory data were provided by the Spanish Ministry of Agriculture, Fisheries and Food (MAPA) and are accessible via the following link [https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/cartografia\\_informacion\\_disp.aspx](https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/cartografia_informacion_disp.aspx). The Spanish Forest Inventory plots used in this study are identified in Appendix S14.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**Appendix S1.** Correlation tests performed on selected functional traits.

**Appendix S2.** Phylogenetic dot plot for the functional traits studied.

**Appendix S3.** Sources and references used to estimate intrinsic and human factors of each non-native tree species.

**Appendix S4.** Number of new permanent plots occupied by each NNT species and their discretization between natural forest and human plantations.

**Appendix S5.** Parameter estimates, and standard errors fitted by LMs performed for testing the effect of SFI period (23SFI and 34SFI), species identity (N=17), Diameter at Breast Height (DBH) and Aridity Index of Martonne on temporal changes in density ( $\Delta$ Dens), tree growth (Growth) and basal area ( $\Delta$ BA).

**Appendix S6.** Fixed-Effects ANOVA to test the effect of SFI period (23SFI and 34SFI), species identity (N=17), Diameter at Breast Height (DBH) and Aridity Index of Martonne on temporal changes in density ( $\Delta$ Dens), tree growth (Growth) and basal area ( $\Delta$ BA).

**Appendix S7.** Moran I correlogram of residuals from linear models fitted to test the effect of SFI period and species identity on temporal changes in density ( $\Delta$ Dens), tree growth (Growth) and basal area ( $\Delta$ BA).

**Appendix S8.** Relationship between intrinsic and human factors and changes in occupancy, density, growth and basal area of 17 NNT species in Spain.

**Appendix S9.** Effect of leaf type (LT), dispersal syndrome (DS) and residence time (RT) on changes in occupancy, density, growth and basal area of 17 NNT species in Spain.

**Appendix S10.** Parameter estimates and standard errors (in brackets) fitted by LMs performed for testing the effect of NT, P50, MTH and SFI comparison on temporal changes in density ( $\Delta$ Dens), tree growth (Growth) and basal area ( $\Delta$ BA).

**Appendix S11.** Fixed-Effects ANOVA to test the effect of NT, P50, SLA, MTH and SFI comparison on  $\Delta$ Dens, growth and  $\Delta$ BA.

**Appendix S12.** Parameters of the regression models fitted to assess the joint effect of P50 and SLA on changes in density and growth.

**Appendix S13.** Fixed-Effects ANOVA to test the joint effect of P50 and SLA on  $\Delta$ Dens and growth.

**Appendix S14.** Identifier code of the plots of the Spanish Forest Inventory used in this study.

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