

Contributing to an evidence-based discourse regarding invasibility, stage of invasion and impacts of *Robinia pseudoacacia* L. in European forests

Hernández Mateo

hernandez.laura@inia.csic.es

Institute of Forest Sciences (INIA, CSIC)

Iciar Alberdi

Institute of Forest Sciences (INIA, CSIC)

Patricia Adame

Institute of Forest Sciences (INIA, CSIC)

Isabel Cañellas

Institute of Forest Sciences (INIA, CSIC)

Daniel Moreno-Fernández

Institute of Forest Sciences (INIA, CSIC)

Research Article

Keywords: black locust, forests, invasion stage, invasibility, impacts, filters, conservation policy

Posted Date: July 3rd, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4588783/v1>

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Additional Declarations: No competing interests reported.

Abstract

Robinia pseudoacacia L. (black locust) is a deciduous tree native to North America, widely introduced and naturalized in Europe. Despite being one of the world's most invasive woody angiosperms, its role in European forest policy remains contentious, with debates about its invasion potential, ecological impacts, and control measures and it is not formally classified as invasive in European regulation. This study uses data from three cycles of the Spanish National Forest Inventory (SFI) to examine the distribution, abundance, and dominance of black locust in Spanish forests over the past three decades. The study also assesses the invasibility and invasion stage across various forest types, identifying the biotic and abiotic factors influencing its distribution. Additionally, the impacts of black locust on forest ecosystem services, such as native tree species diversity and abundance, are evaluated. Black locust now occupies over 75,000 hectares of Spanish woodlands, with an average invasion degree of 1.55% at the forest type level. Its population has steadily increased, reaching an established invasion stage in most invaded native forests. The invasion affects forest attributes, including native species abundance and dominance, and overall plot richness. The impact varies with the degree of invasibility and invasion stage, being particularly significant in priority conservation habitats like depleted temperate and alluvial forests. These findings highlight the need for further research on black locust impacts in forest ecosystems to contribute to an evidence-based discourse regarding the reconsideration as an invasive species in European and national regulations.

1. Introduction

Robinia pseudoacacia L. (black locust, BL hereafter) has been extensively used as a forestry tree in central and Eastern Europe over the last two centuries due to its rapid growth rates (Vítková et al., 2017; Nicolescu et al., 2020). Its durable and rot-resistant wood is highly valued for fence posts, boatbuilding, and other purposes, while it is also suitable for fuelwood and pulp (Huntley, 1990). Additionally, it is considered a promising fast-growing species for biomass production (Oliveira et al., 2018; Straker et al., 2015). However, while BL brings positive economic benefits, its negative environmental impacts lead to conflicts of interest between different sectors. BL is listed among the 40 most invasive woody angiosperms globally (Rejmánek and Richardson, 2013), and in several European databases, it is classified as highly invasive (DAISIE (Roy et al., 2020); EPPO, 2023). Despite this, BL is not included in the list of Invasive Alien Species (IAS) of concern to the European Union via the European Union's IAS Regulation (EU1143/2014; Vítková et al., 2017), and it is officially considered to be invasive in a low number of European countries where the species is registered (approximately 37%) (Brus et al., 2016). Spain is no exception, and although BL has been declared an invasive species in some regional checklists and atlases (Sanz Elorza et al., 2004), it is merely considered an exotic species with invasion potential in national-level legislation (RD 630/2013). This ambiguous classification complicates the establishment of clear management priorities for the prevention and conservation strategies regarding BL. Therefore, it is essential to have the most reliable, comprehensive, and up-to-date information on the invasibility, invasion stage, and impacts of BL on native habitats to facilitate informed decision-making. While BL has been extensively studied for various purposes in central (Thurm et al., 2017; Vítková et al.,

2017; Nicolescu et al., 2020) and Eastern (Klisz et al., 2021) Europe, there is a lack of broad-scale research on this species in western European forests.

BL is a medium-sized deciduous tree native to North America, typically found in highly productive mixed mesophytic forests characterized by a large and variable number of species, as well as in pure stands (Huntley, 1990; Cierjacks et al., 2013). It is a light-demanding pioneer species that readily colonizes open sites within deciduous forests, often resulting from disturbances such as fire, floods, logging, or storms (Huntley, 1990). While it tolerates a wide range of soil conditions, it is limited by extreme frosts in winter and arid conditions (Stizia et al., 2016). These factors partly explain the distribution of BL in Europe, predominantly in sub-Mediterranean and Atlantic climatic conditions, ranging from Sicily to Norway and from sea level up to 1,640 m a.s.l in the Southern Alps (Stizia et al., 2016). Its rapid and vigorous asexual reproduction, along with its nitrogen-fixing capability, facilitates BL spread in urban habitats and along transportation corridors such as roads and rivers (Cierjacks et al., 2013). BL is capable of outcompeting a wide range of native trees in areas where agricultural or forestry practices have ceased (Bertacchi and Onnis, 2004). Its invasion has been reported in open dry forests and scrublands, alluvial habitats, agrarian landscapes, and disturbed sites such as urban and industrial environments or post-fire sites (Cierjacks et al., 2013; Stizia et al., 2016; Vítková et al., 2017; Cruz et al., 2021; Saulino et al., 2023), and climate warming is expected to further facilitate its expansion (Thurm et al., 2017; Puchalka et al., 2021). While the impact of BL on the function and structure of lichens (Nascimbene et al., 2010), grasslands (Matus et al., 2003), litter (Castro-Diez et al., 2019), and nutrient cycles (Castro-Diez et al., 2014) in native habitats has been reported, the long-term effects on tree species structure and assemblages are still under discussion.

In Spain, as in many other European countries, BL was one of the first North American trees to be introduced in the early 18th century, primarily for forestry purposes but also as an ornamental tree (Sanz Elorza et al., 2004; Vítková et al., 2017). It appears naturalized in scattered locations of Spain, particularly in northern Iberian Peninsula (Sanz Elorza et al., 2004). While BL is the subject of trials for biomass production (Oliveira et al., 2018), it is projected to cover 70% of its potential distribution in Spain based on climatic niche modelling (Gassó et al., 2012), and local studies have already reported impacts on nutrient cycles and soil properties in Mediterranean alluvial forests of Central Spain (Castro Diaz et al., 2012; 2019; Medina-Villar et al., 2016). However, there is a lack of detailed information on spread rates, determinants of spread, specific forest invasibility, and impacts on the diversity and structure of native forests on broader scales.

Although limited to forest ecosystems, previous studies have highlighted the suitability of using periodic National Forest Inventories (NFIs) to monitor the spread of invasive species in forests worldwide (Chirici et al., 2012; Hernández et al., 2014; Ostwald et al., 2015). Here, based on an analysis of sequential broad-scale databases from three cycles of the Spanish National Forest Inventory (SFI), we examine the current invasion stage of BL in Spanish forests, its evolution, and identify its invasibility in different forest types (Fig. 1). Additionally, we investigate the main biotic and abiotic variables driving the current invasion of

this species in Spanish woodlands, and we explore the impacts of BL on different forest ecosystem attributes, such as native species diversity, abundance, and dominance during the period studied (Fig. 1).

2. Material and methods

2.1. Study area

The study area covers the forest area of the entire climatic gradient of the Spanish Iberian Peninsula where BL was registered along the different SFI cycles, from the Atlantic and Alpine biogeoregions in northern Spain to more Mediterranean conditions in Central and Southern Spain, with ranging mean annual temperatures from 2°C to 18°C and annual precipitations from 290 mm to 1950 mm (Fig. 2).

2.2. National Forest Inventory data

For this study, we utilized data from the three most recent cycles of the SFI: the second cycle (SFI2; 1986–1996), the third cycle (SFI3; 1997–2007), and the fourth cycle (SFI4; 2008 to present). Unlike SFI2 and SFI3, SFI4 remains ongoing, and data for certain Spanish provinces are currently incomplete. Nevertheless, SFI4 has been conducted across most regions where black locust (BL) is present. In these SFI cycles, permanent plots were systematically established within the forest area at the intersections of a 1 km x 1 km grid, following a concentric plot design. Within each plot, measurements of diameter at breast height (DBH) and tree height were taken in four circular sub-plots with the same center and four radii (5, 10, 15, and 25 m), employing four minimum DBH thresholds for living trees (75, 125, 225, and 425 mm, respectively) (Alberdi et al., 2016). Additionally, recruitment (trees with DBH less than 7.5 cm) was assessed within the 5 m sub-plot, with recruits having DBH < 2.5 cm classified as seedlings and those with heights ≥ 1.3 m and $2.5 \leq \text{DBH} < 7.5$ cm classified as saplings. Finally, SFI3 and SFI4 documented the presence of every tree species within the 25-m radius, irrespective of the plant's development stage.

2.3. Data analysis

We utilized data from the most recent iteration of the SFI cycle to analyze the distribution of BL across Spain at a national scale, as well as its extent of spread within Spanish woodlands and its susceptibility to invasion across various forest types (see Fig. 2, Table 1). Given that the SFI is a map-based inventory, we calculated the area invaded by BL by taking into account the area and the equivalent number of plots of each forest type stratum with BL occurrence, as defined by the Spanish National Forest Map (SNFM) (MITECO, 2013). Framed in Chitrý et al (2008), then we estimated the habitat invisibility by BL (susceptibility to be invaded by the species) as the proportion of the total distribution of BL in SFI plots by each forest type/habitat, and we assessed the level of invasion of each forest type as the proportion of SFI plots at national level invaded by BL. For this, SFI plots were categorized into broad-spectrum forest types based on both national (MITECO, 2013) and European classifications such as Barbati et al., (2007). BL is found in non-native forest types such as conifer (ConPlant) and broadleaved (BroadPlant) plantations of *P. radiata* D. Don, *Eucalyptus* sp., *Quercus rubra* L., and intensively managed poplar

forests. Additionally, BL co-occurs in stands of non-native species with other IAS like *Acacia* spp. or *Ailanthus altissima* (Mill.), classified as exotic forests (Exotic). Among native forests, pure deciduous broadleaved forests (PureDeciduous) primarily comprise Atlantic species such as *Quercus robur* L., *Quercus petraea* (Matt.) Liebl, *Fagus sylvatica* L., *Corylus avellana* L., and *Castanea sativa* Mill., while pure evergreen broadleaved forests (PureEvergreen) are dominated by Mediterranean species like *Quercus ilex* L. and other sub-Mediterranean *Quercus* species. Pure pine forests (PureCone) consist mainly of Mediterranean species such as *Pinus nigra* Arnold. and *Pinus pinaster* Ait. Within mixed forests, both mixed broadleaved forests (MixedBroad) and mixed conifer and broadleaved forests (MixedConBroad) contain a blend of the aforementioned broadleaved and conifer species. Finally, alluvial or riparian (Alluvial) forests represent species-rich, often multi-layered communities characterized by diverse assemblages including *Alnus* spp., *Betula* spp., *Populus* spp., *Salix* spp., *Fraxinus* spp., *Ulmus* spp., etc.

According to Theoharides and Dukes (2007), and utilizing information from the SFI regarding both adult and regeneration of BL presence across repeated SFI plots over multiple cycles, we delineated two distinct stages of invasion. We classified plots exhibiting BL presence solely in the last SFI cycle but not in the preceding one, or plots displaying only BL regeneration beneath the canopy of other tree species, as being in the *colonization stage*. On the other hand, plots demonstrating the presence of BL at various developmental stages (across different diameter at breast height (dbh) classes) and where the species continues to regenerate in the last SFI cycle were categorized as being in the *established stage*.

Subsequently, we examined the invasion stage of BL across different biogeographical regions and forest types. In the subset of SFI plots where BL presence was recorded in two consecutive cycles (SFI2-SFI3 or SFI3-SFI4), we investigated shifts in BL abundance between cycles based on basal area (BAbl, m² ha⁻¹), adult and sapling density (Nbl, in trees ha⁻¹), as well as diameter distribution at both the national scale and within specific forest types. Additionally, we calculated the relative values of BL abundance (BAbl_rel and Nbl_rel, in %) to discern changes in dominance.

Furthermore, to explore potential impacts of BL presence on native species attributes, we categorized the species observed in each SFI plot as either native or non-native. Subsequently, we assessed shifts in native tree diversity (total native tree richness per plot, proportion of native tree species in the total richness of the plot, Shannon Weaver index, Simpson index), native tree abundance (BA_{nat}, N_{nat}), and dominance (BA_{nat_rel} and N_{nat_rel}, in %), as well as native sapling and seedling regeneration abundance and dominance. This evaluation was conducted by examining the impact of BL presence/absence (treated as a factor with two levels) in re-measured SFI plots both with and without BL, at the forest type level, using one-way analysis of variance (ANOVA).

To comprehensively evaluate the biotic and abiotic factors potentially influencing the current distribution and expansion of BL in Spanish woodlands, we leveraged the latest available SFI data (SFI3 and SFI4) from SFI units (provinces) where at least one BL presence was recorded, totalling 24,043 plots. Employing logistic regression, we established a binary response variable assigning a value of 1 to plots

where BL (adults or regeneration) was observed and 0 where it was absent. Drawing upon prior research on BL ecology and invasive behaviour (Huntley, 1990; Cierjacks et al., 2013; Vítková et al., 2017), we considered 16 predictors as independent variables.

Regarding abiotic drivers, we incorporated topographical variables (altitude) obtained from Spain's digital elevation model with a spatial resolution of 25 m. Additionally, we factored in the distance to the nearest river (D.rivers). Climatic data were derived from the WorldClim 2.0 database (Fick and Hijmans, 2017), comprising eight variables. For biotic drivers, we examined various forest attributes derived from SFI datasets, including tree richness, density, mean dbh, and basal area at the plot level. Moreover, to assess the significance of propagule pressure or distance from invasion loci, we computed the connectivity between BL-containing plots as the mean distance to the five closest plots with BL presence. Detailed information on variables, acronyms, units, and descriptive statistics is provided in Table 1. All predictors were standardized to facilitate comparison of their importance in the logistic regression (Schielzeth, 2010).

Table 1

Mean, minimum (Min), maximum (Max) and standard deviation (SD) of the predictors for the selected SFI plots without/with presence of black locust used to evaluate the biotic and abiotic factors potentially influencing the current distribution of black locust in Spanish forests.

Variable	SFI plots				SFI Plots with BL presence			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Altitude (m)	798	0	2594	424	320	0	1675	279
Tmean (°C)	11.7	0.4	18.6	2.4	13.3	7.9	17.4	1.3
Tseas (°C)	55.1	30.9	69.8	9.2	46.4	33.7	67.1	7.8
TDQ (°C)	16.6	-2.6	26.8	6.1	17.7	2.2	26.1	4.3
TWQ (°C)	19.1	7.6	26.8	2.6	19.4	15.0	26.1	1.4
Pannual (mm)	765	268	1603	283	1049	355	1592	275
Pseas (mm)	31	11	68	11	29	15	59	10
PDQ (mm)	115	13	325	54	164	20	256	52
PWQ (mm)	127	17	325	60	184	20	267	54
D.plotsRob (m)	28143	35	150122	21571	6883	36	125898	13479
D.rivers (m)	4054	0	26744	3255	2606	5	13674	2344
R.no-nat (#)	0	0	4	1	1	0	4	1
R.nat (#)	5	0	21	3	7	0	21	3
DBH (cm)	21.2	7.6	148.1	11.1	21.9	7.7	64.6	10.2
BA (m ² ha ⁻¹)	17.1	0.4	111.6	13.7	21.9	0.7	76.7	13.3
N (n° ha ⁻¹)	590	5	5744	600	639	5	3452	498
Tmean = mean annual temperature; Tseas = temperature seasonality; TDQ and PDQ = temperature and precipitation of the driest month, respectively; TWQ and PWQ = temperature and precipitation of the wettest month, respectively; Pannual = cumulative annual precipitation; Pseas = precipitation seasonality; D.plotsRob = distance to black locus plots; D.rivers = distance to the rivers; R.no-nat = richness of no-native trees different to black locust; R.nat = richness of tree native species, DBH = plot mean dbh, BA = plot total basal area, N = plot tree density								

We assessed linear multicollinearity among the 16 predictors using the variance inflation factor (VIF) and removed variables with values exceeding 5. Consequently, from the initial set of predictors, altitude, as well as the temperature and precipitation of the driest and warmest months, were excluded. Following

this elimination, the variance inflation factor remained below 3.6, indicating a low risk of multicollinearity (James et al., 2017). Subsequently, we employed a backward selection process based on the corrected Akaike Information Criterion (AICc), setting a threshold value of $\Delta AICc = 4$, to select the model terms. The regression analyses were conducted using R 4.2.2 (R Core Team, 2022).

3. Results

3.1. Spread degree, distribution, invasibility and stage of invasion of black locust in Spanish forests

The latest SFI cycles (SFI3 and SFI4) indicate that black locust (BL) currently occupies approximately 75,065.26 hectares (0.40%) of Spanish woodlands. Its distribution is primarily concentrated in the Atlantic biogeoregion, encompassing 71.4% of BL SFI records, with additional presence in the Mediterranean biogeoregion (27.4%). However, its occurrence is limited in the Alpine zone, accounting for only 0.9% of records (Fig. 2b). The climatic range associated with its spatial distribution in Spain exhibits temperate characteristics, characterized by mean temperatures of 13°C and an average total annual precipitation of 1,050 mm (Fig. 2a, Table 1), predominantly in low altitudes averaging 320 m a.s.l.

The species is typically found in other pure forests as a co-dominant species, recorded in 76.05% of the SFI plots. While it forms pure BL forests (where BL basal area exceeds 70% of the total basal area of the plot) in only 10.9% of the SFI plots with BL presence nationwide, it dominates (defined as the species with the highest basal area in the plot) in 19.39% of these plots. The spread of BL in forests appears to be independent of the naturalness of the stand, with 54.65% of its distribution occurring in native forests and 45.35% in non-native forests. The spread degree is 0.6% and 2.46% in each forest type, respectively, at the national level. Consequently, the forest types exhibiting the highest invasibility are diverse, spanning nine broad spectrum types of forest (see Fig. 3a). Within native forests, BL is most frequently found in alluvial, pure deciduous, and mixed broadleaved forests, while among non-native forests, it is commonly found in conifer and broadleaved plantations (see Fig. 3a). These five forest types collectively account for almost 80% of BL's distribution in Spain. The level of invasion is also notably higher in these forests where the species is predominantly found, ranging from 0.12% in pure Mediterranean conifer forests to 3.3% in alluvial forests (see Fig. 3b).

Although the stage of BL invasion can only be assessed in a limited set of SFI plots (N = 225), more than 73% of them exhibit an established invasion stage, contrasting with 27% of plots displaying a colonization stage. Remarkably, except for broadleaved and conifer plantations, as well as evergreen broadleaved forests, over 70% of SFI plots representing other native forest types where BL is present demonstrate an established stage of invasion (see Fig. 4). Consistent with the prevalence of the established invasion stage, the diameter at breast height (dbh) distribution of BL across SFI cycles indicates a tendency towards larger dbh classes (see Fig. 5a). Across forest types, and associated with the established stage of invasion, alluvial, exotic, and deciduous pure forests exhibit a more balanced distribution of dbh classes. In contrast, both conifer and broadleaved plantations, as well as mixed

broadleaved forests, display a significantly higher proportion of small-diameter trees, indicative of colonization stages of invasion (see Fig. 5b).

3.2. Impacts of black locust on the structure and diversity of native forests

Regarding the potential impacts of BL invasion on native tree species structure, a significant overall decrease in tree native abundance and dominance was observed in SFI plots with BL presence, as evidenced by a reduction in total native basal area per hectare and the proportion of native trees per hectare (see Fig. 6a, 6c). Similar trends were observed for other attributes, such as native regeneration, with a notable decrease in the proportion of native seedlings per hectare (see Fig. 7c).

However, we did not observe significant overall differences between SFI plots with and without BL presence for other related attributes. Nonetheless, significant impacts of BL presence on some of these attributes were identified at the forest type level. Forest types characterized by higher invasibility and a greater level of invasion establishment by BL, such as mixed broadleaved, alluvial, and pure deciduous forests, exhibited significant shifts in stand structure, regeneration, and even tree compositional diversity between SFI cycles in the presence of BL (see Fig. 6, 7, 8).

3.3. Biotic and abiotic factors involved in black locust current distribution

After performing the backward variable selection process using AICc, the following variables were selected in order of importance, based on their coefficient magnitude: Tmean, D.plotsRob, Pseas, Pannual, R.auto, D.rivers, Ralloc, and N (see Table 1). Conversely, BA, DBH, and Tseas were excluded from the model. The coefficients of the standardized variables are depicted in Fig. 9. Tmean and Pannual exhibited a positive association with the presence of BL, indicating that this species tends to occur in warm and humid environments. Furthermore, BL showed a positive correlation with the richness of both native and non-native tree species, suggesting a preference for mixed forests comprising both indigenous and exotic species. Additionally, D.plotsRob displayed a negative relationship with BL occurrence, implying that plots with BL tend to be clustered in close proximity. Similarly, Pseas exhibited a negative association with BL, indicating that this species thrives in areas with low precipitation variability. Moreover, the negative correlation between BL presence and D.rivers suggests that the likelihood of encountering BL increases in the vicinity of rivers. Lastly, BL was found to prefer open stands, as indicated by the negative coefficient of N, although N was identified as the least influential variable.

4. Discussion

The invasion potential and impacts of BL in native ecosystems in Europe is controversial, and it is not included as invasive species in the European IAS regulation. Likewise, although BL has been declared as

an invasive species in some regional checklists and atlases in Spain (Sanz Elorza et al. 2004), it is simply declared as an exotic species with invasion potential at the Spanish national level legislation.

Black locust spread and invasion stage in Spanish forests

After more than three centuries since its introduction in Europe, our findings confirm the enduring presence of BL in southern European forests. BL has now established itself across more than 75,000 hectares of Spanish woodlands, exhibiting an average invasion degree of 1.55% at the forest type level. Over recent decades, the species has demonstrated a gradual population increase, predominantly characterized by an established invasion stage in most invaded native forests. Notably, BL invasion has been shown to impact native forest attributes such as abundance, dominance, and species diversity, contingent upon the degree of invasibility and invasion stage.

The climatic niche of BL found in Spanish forests lends support to the niche conservatism hypothesis for invasive species, which has been a topic of debate (Liu et al., 2020). This hypothesis posits that species occupy similar environmental conditions in new geographical ranges or time periods (Petitpierre et al., 2012).

In its native range, BL thrives in a humid climate with an annual total precipitation ranging from 1,020 to 1,830 mm (Huntley, 1990), and average temperatures during the warmest period ranging from 18 to 27°C. In contrast, in its distribution in Spain, precipitation levels vary from 355 to 1,592 mm, with average temperatures during the warmest period ranging from 15 to 26.1°C. The average precipitation and temperature in Spain are recorded at 1,049 mm and 19.4°C, respectively. This comparison of ecological niche thresholds between the species' native and non-native ranges is crucial for the development of effective conservation strategies and for the assessment and prediction of invasion risks. As reported in other regions (Hutley, 1992; Nicolescu et al., 2000), temperature emerges as one of the most important factors filtering BL presence in southern European forests. BL also demonstrates sensitivity to frosts and precipitation seasonality (Huntley, 1992). Consequently, in Spain, BL is primarily distributed in more temperate climatic areas of northern Spain characterized by mild to warm summers and short, mild winters with moderate rainfall spread across the year. However, in north-eastern and central Spanish distributions, where Mediterranean conditions are more pronounced (characterized by higher climatic seasonality and drier conditions), BL is associated with alluvial ecosystems, which act as natural vegetation refuges. Despite being intolerant to drought, these trees are able to thrive amidst the semi-arid conditions of the Mediterranean region (Singer et al., 2014; Nadal-Sala et al., 2019) associated with continuous or intermittent streams, with available groundwater supply and higher air water vapor content, that create an optimal microclimate for deciduous tree species like BL. The association with rivers, supported by the negative relationship found with distance to rivers in the logistic regression, elucidates the ability of BL to persist in its Spanish distribution even in areas with a minimum annual precipitation as low as 355 mm.

Regarding its ecological role within forest communities, BL is typically found as a co-dominant species in pure or mixed native and non-native forests. Although it rarely forms pure stands, it emerges as the

dominant species in almost 20% of its distribution in Spain. Similarly, in its native range, while BL can occasionally form pure stands, it is more commonly encountered as a component of mature mesophytic mixed, mixed pine-oak, or pure pine forests (Huntley, 1990). This observation supports the notion that the invasiveness of an exotic species can be predicted by understanding its role in its native communities (Galán Díaz et al., 2023). Consequently, the native forest types most vulnerable to BL invasion in Spain are alluvial, broadleaved mixed, and deciduous mesophyllous pure forests, with invasion degrees of 3.3%, 2.5%, and 1.64%, respectively, at the national level. These findings indicate that BL is capable of colonizing, establishing self-sustaining populations, and expanding its presence (*sensu* Theoharides and Dukes, 2007) in these habitats. Moreover, the balanced diameter at breast height (dbh) to age distribution of BL observed in these forest types further supports these conclusions. Notably, mixed broadleaved and alluvial forests, which exhibit a higher percentage of plots with an established stage of BL invasion, are the native communities where significant impacts of BL presence have been detected. In these forest types, we observe a decline in the abundance and dominance of native tree and regeneration strata, as well as a reduction in the proportion of native species richness. These outcomes are concerning, particularly since these habitats represent the rare remnants of native deciduous forests preserved in the colline and montane belts of northern Spain, and the riparian forests, including alder forests, which are designated as priority conservation habitats for the Spanish Iberian Peninsula under the Habitat Directive 92/43.

Non-native forests such as conifer and broadleaved plantations are also among the communities with the highest degree of invasibility by BL. In northern Spain, where BL is predominantly distributed, forest plantations are subject to intensive management practices. Disturbance events, including clear-cuttings and other infrastructure associated with intensive forest plantations, can create niche opportunities for the spread of pioneer species like BL. Indeed, disturbances are considered one of the most significant factors contributing to the invasive spread of alien species. Ecosystems may become more susceptible to invasion when there is an increase in unused resources resulting from disturbance events (Davis et al., 2000). However, linked with the high degree of disturbances and rapid stand dynamics in intensive plantations, we observed an early stage of invasion in non-native forest types. This finding suggests that disturbances, in this case, can serve as both the trigger and the remedy to the persistent establishment of BL invasion in these communities.

Impacts of black locust in forest structure and diversity

Recent research on the ecological impacts of BL on ecosystems has elucidated its profound influence on litter dynamics as well as physical and chemical soil properties (Thomas et al., 2022). However, the effects of structural disparities between BL-infested forests and native communities remain understudied. Additionally, while Vitkova et al. (2017) conducted a review suggesting that BL's impact on the biodiversity of invaded communities is ambiguous, empirical evidence is scarce. In various woodland ecosystems, BL appears to exert negligible influence on native species richness or cover within secondary forests (Stizia et al., 2015). Conversely, in grasslands characterized by more rapid dynamics, BL demonstrates the capacity to homogenize processes at the plant community level (Trentanovi et al.,

2013). Our findings regarding the effects of BL on native forest structure and diversity echo these mixed results, as we observed significant impacts across half of the attributes studied, particularly at the forest level. Given the prolonged life cycle of trees and the gradual pace of forest dynamics, it is plausible to attribute the observed impacts to forest types exhibiting higher susceptibility to invasion and a greater prevalence of established invasion stages. In these forest types, specifically, our research documented a decline in the abundance and dominance of native tree and regeneration strata, accompanied by a reduction in the proportion of native tree species richness. Consequently, it is plausible to assert that over time, the invasive nature of BL could classify it as a transformative species altering forest structure and diversity (*sensu* Richardson et al., 2000; Marchante et al., 2011), defined as those species that substantially modify the character, condition, form, or nature of ecosystems, thereby becoming active agents in regional-forming processes.

Filters of black locust spread

Together with environmental variables, connectivity, or the proximity between BL populations, emerges as a primary determinant associated with the spread of BL in Spanish woodlands. This finding aligns with the predominant mode of non-long-distance vegetative propagation observed in BL (Hutley, 1990; Vitkova et al., 2017). Moreover, it resonates with the established premise that heightened availability of propagules among adjacent populations elevates the likelihood of establishment, persistence, naturalization, and invasion (Alston and Richardson, 2006). Regarding biotic variables influencing BL spread, our analysis reveals a positive correlation with both native and non-native total richness per plot, accompanied by an increase in total native richness and the Shannon-Weaver index at the plot level, consistent across various forest types. These findings align with the richness paradigm in biological invasions (Stohlgren et al., 2003), which posits that despite the hypothetical enhancement of ecosystem resilience to disturbances with increased species richness, evidence suggests the opposite pattern concerning forests' vulnerability to non-native plant invasions. It has been suggested that species richness might positively correlate with invasion due to shared promoting factors (Levine and D'Antonio, 1999). Accordingly, forest types characterized by higher richness, such as mixed and alluvial forests, exhibit elevated degrees of invasibility and levels of invasion. The analysis of both biotic and abiotic factors filtering BL's current distribution holds significance for invasion risk management and the formulation of strategies to control species spread across various scales. The climatic niche data presented herein, in conjunction with available land use information and the average connectivity (6 km) between populations, could facilitate the development of precise invasion risk maps. Furthermore, our findings indicate a negative relationship between BL and plot tree density. This underscores BL's pronounced intolerance to the shade of other species (Cruz et al., 2021), highlighting its status as a fast-growing opportunistic plant. Such insight underscores that promoting the development of native forest species in secondary forests (e.g., *Salix* spp., *Betula* spp.) is paramount in combatting BL colonization and spread. Nonetheless, chemical and/or mechanical treatments may sometimes be necessary to mitigate the initial cover of BL (see Vitkova et al., 2017 for a comprehensive review; Cruz et al., 2021).

Knowing NFIs to make good use of them

The spatially and temporally explicit information obtained from broad-scale periodic forest surveys such as NFIs constitutes essential empirical data supporting the evolving field of invasion ecology theory (Jeschke et al., 2012). This approach facilitated the quantification of BL occupancy in Spanish forests, the assessment of invasion levels in native ecosystems, the evaluation of forest community invasibility, the identification of invasion stages and impacts, and the examination of factors contributing to its invasive success and persistence. These insights are crucial for invasion monitoring, control, and risk assessment. However, NFI designs can pose some limitations when examining forest dynamics of non-dominant tree species, or, some particularly spatial-distributed communities such as alluvial forests. NFIs, including SFIs, often employ nested or concentric plot designs to streamline sampling efforts (Vidal et al., 2016). Although tree species presence is recorded comprehensively at the plot level, detailed individual tree variables like diameter and height are typically sampled only for trees meeting minimum size criteria, commonly based on diameter. Consequently, co-dominant species, typically with smaller diameters, may be underrepresented (Lin et al., 2020; Moreno-Fernandez et al., under review). Thus, while BL presence is documented in over 400 plots within the SFI, our analysis of its population dynamics has been restricted to only half of them, potentially compromising the robustness of our findings.

Moreover, due to the systematic grid-based establishment of SFI plots across Spanish woodlands, riparian forest communities characterized by linear spatial distributions along rivers might be inadequately represented. Although efforts are made to reinforce plot sampling in these habitats at the regional level, it is likely that the invasibility and level of BL invasion in Spanish alluvial forests are higher than the one reported in our study.

Conclusions

Our findings unequivocally affirm the establishment of BL in south-western European forests. Here, we provide insight into the extent of species spread in Spanish forests, where BL exhibits an average invasion level of 1.55% at the forest type level. Over recent decades, we observe a gradual increase in BL populations, with an established invasion stage prevailing in most invaded native forests. Furthermore, our study presents some of the initial evidence of impacts on native forest ecosystem services, including abundance, dominance, and tree species diversity, which vary depending on BL invasibility degree and invasion stage at the forest type level. Importantly, we note that the invasion and impacts of BL are particularly pronounced in priority conservation habitats, such as depleted temperate and alluvial Iberian forests. In light of these findings, there is an urgent need for further research to explore the broader impacts of BL on forest ecosystems. Such studies are essential to inform evidence-based discussions concerning the reconsideration of BL as an invasive species in European and national regulations, and, to the establishment of clear management priorities for the prevention and conservation strategies regarding BL in European forest.

Declarations

Author Contribution

L.H., conceptualization, data curation, formal analysis, writing – original draft; D.M.F., data curation, formal analysis, writing – review & editing; I.C., I.A. and P.A., writing – review & editing.

Acknowledgements

This work has been funded by the following research projects: I101/2022 (WHAT IF. Trayectorias selvícolas alternativas y su efecto en la vulnerabilidad y resiliencia de los bosques frente al cambio global), PID2019-110273RB-I00 (Dinámica forestal y vulnerabilidad ante el cambio global: factores y mecanismos a diferentes escalas espacio-temporales) and PIE-INIA-934340-FWCS. We thank the staff of the Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO) for the data accessibility.

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Figures

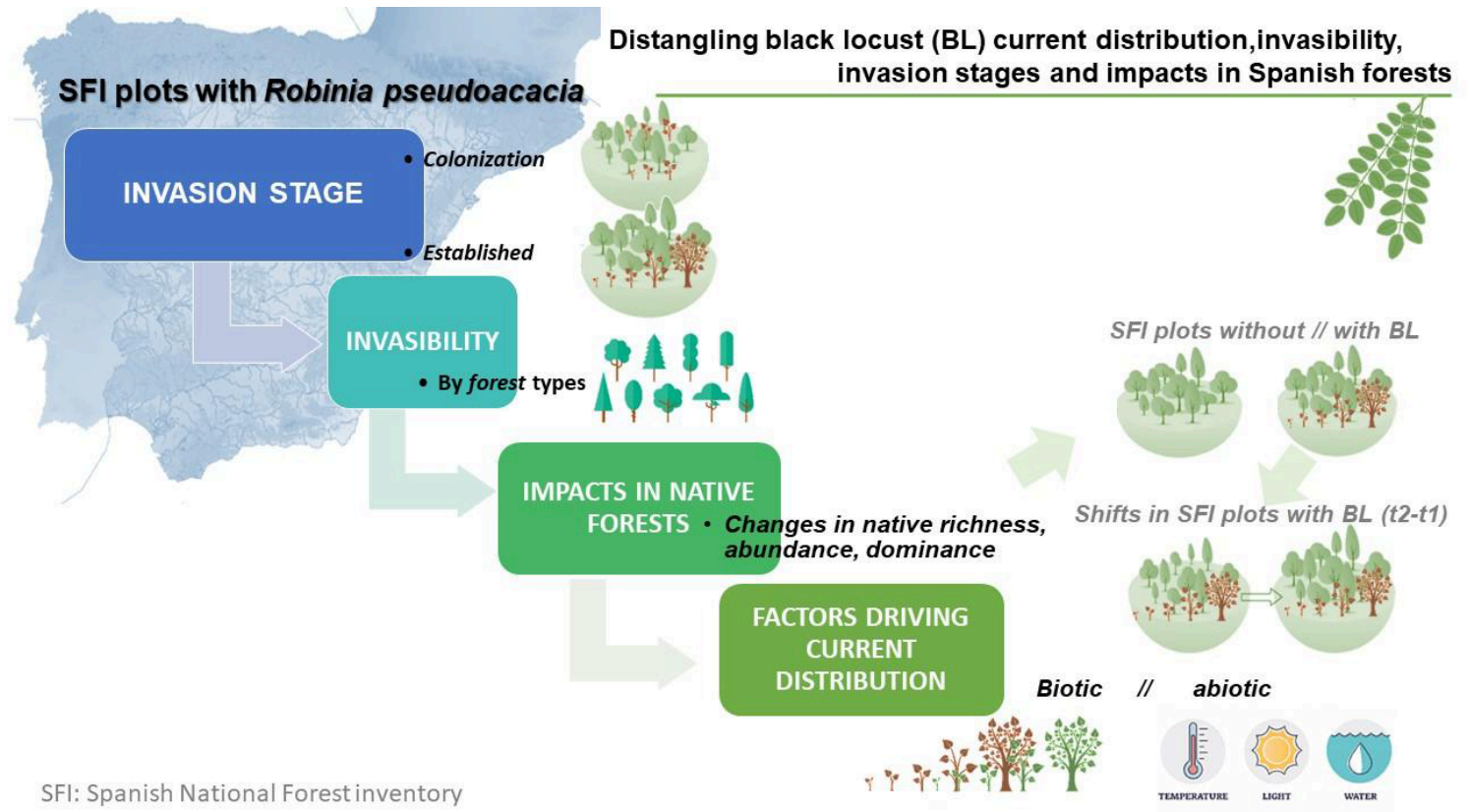


Figure 1

Schematic diagram of the analysis performed based on Spanish National Forest Inventory (SFI) cycles data to disentangle the current distribution, invasibility degree, invasion stages and impacts of black locust (*Robinia pseudoacacia* L.) in southern European forests.

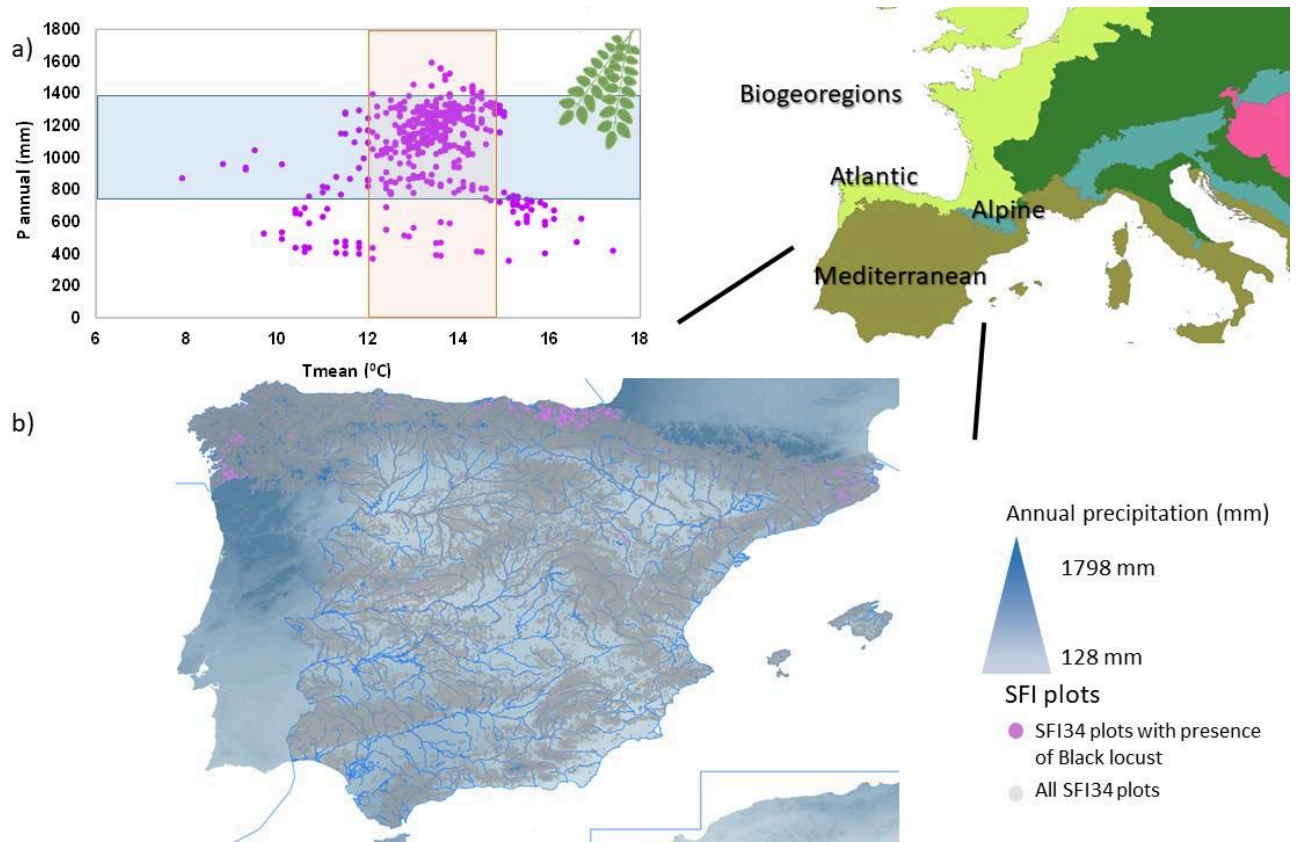


Figure 2

a) Annual precipitation and mean temperature of black locust distribution in Spain based on BL occurrence in SFI plots; b) Location of Spanish Iberian Peninsula in SW Europe within the three biogeographical regions. SFI plots in purple show the distribution of black locust in Spain. The gradient of total annual precipitation along the Iberian Peninsula is also shown.

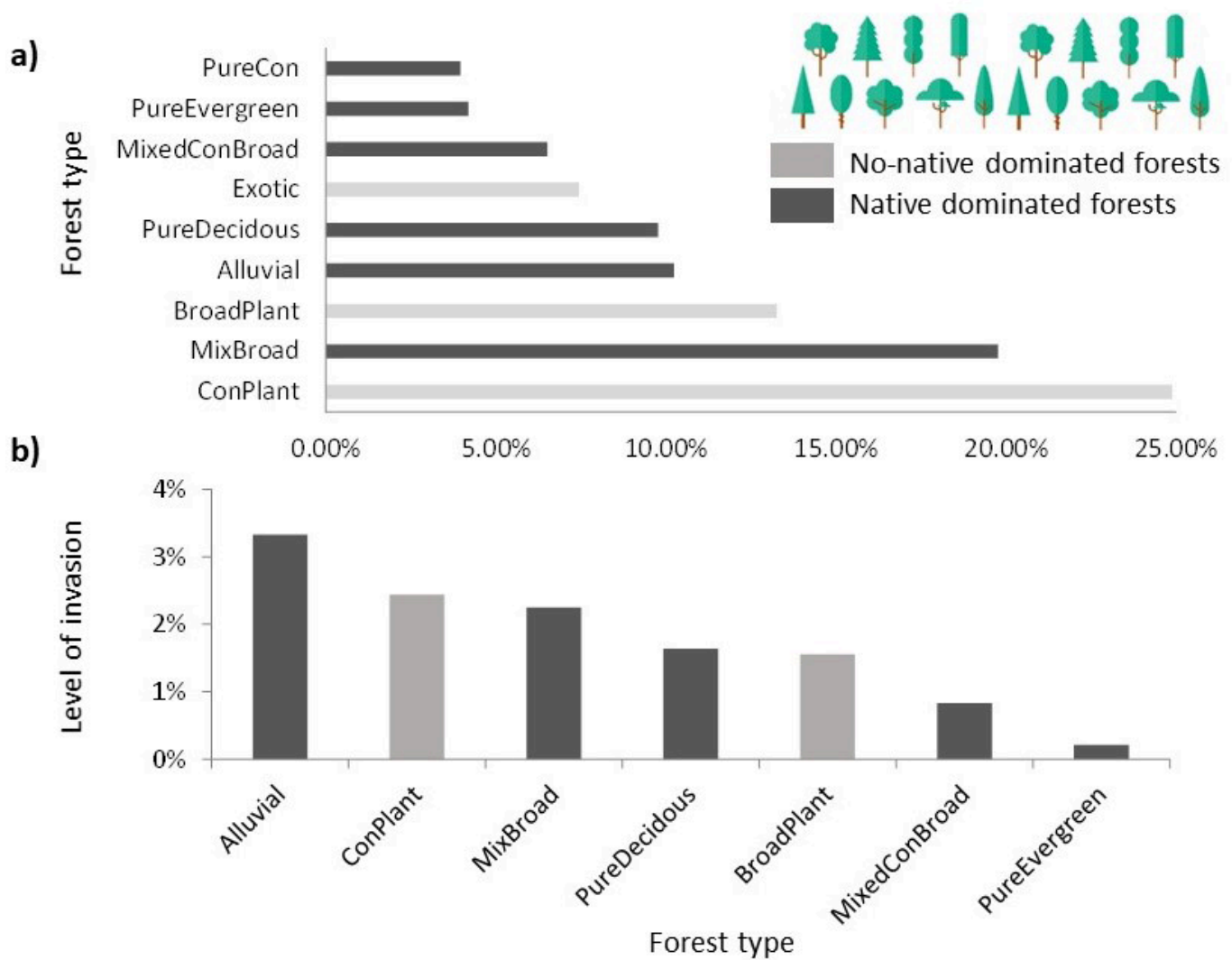


Figure 3

a) Invasibility of forest types: total distribution of BL in SFI plots classified by forest types (N: 430); and;
 b) Level of invasion at national scale: percentage of SFI plots by forest type with black locust presence (N: = 24,043).

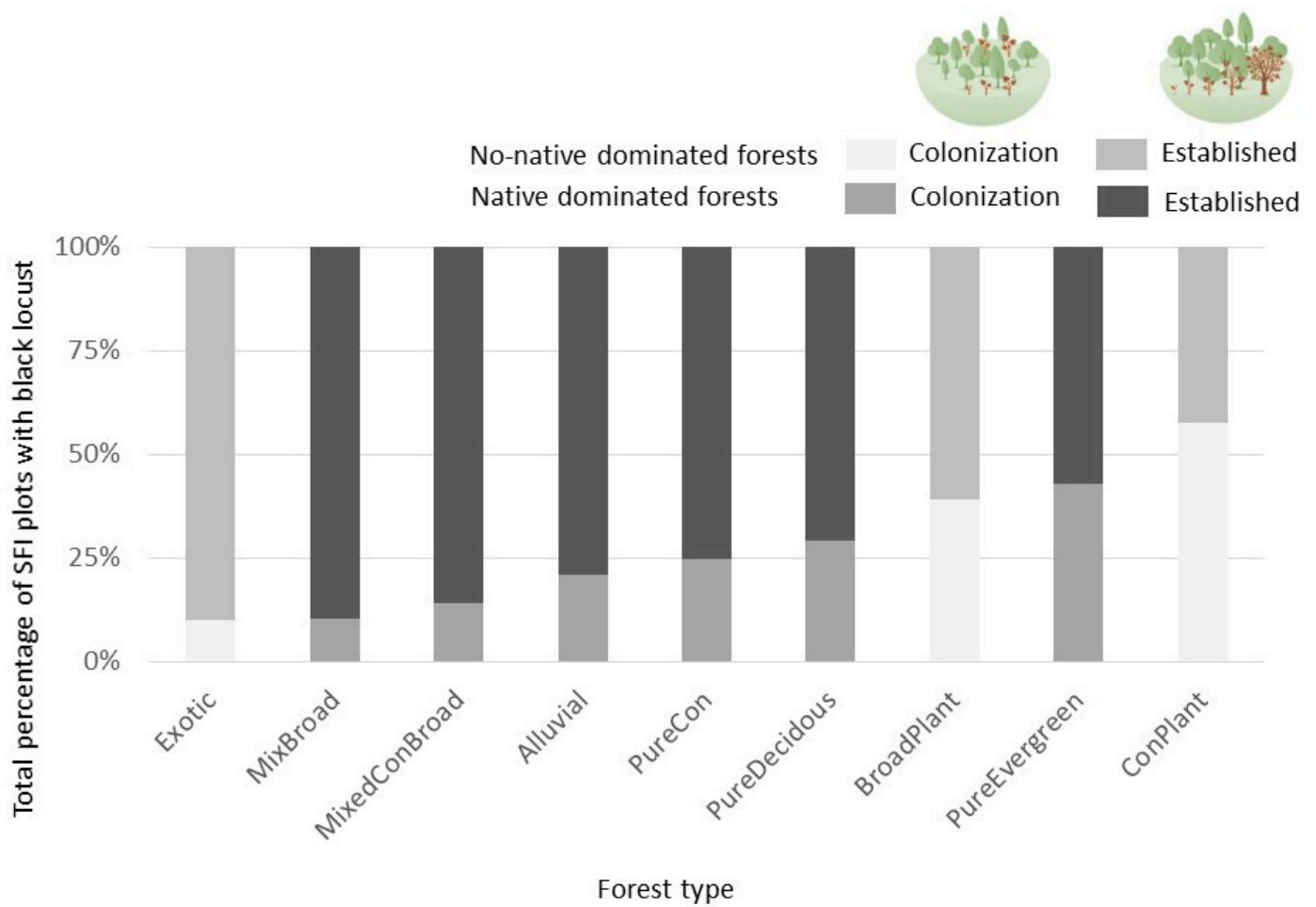


Figure 4

Invasion stages (established and colonization) of the total distribution of black locust in Spain by forest types (N=225).

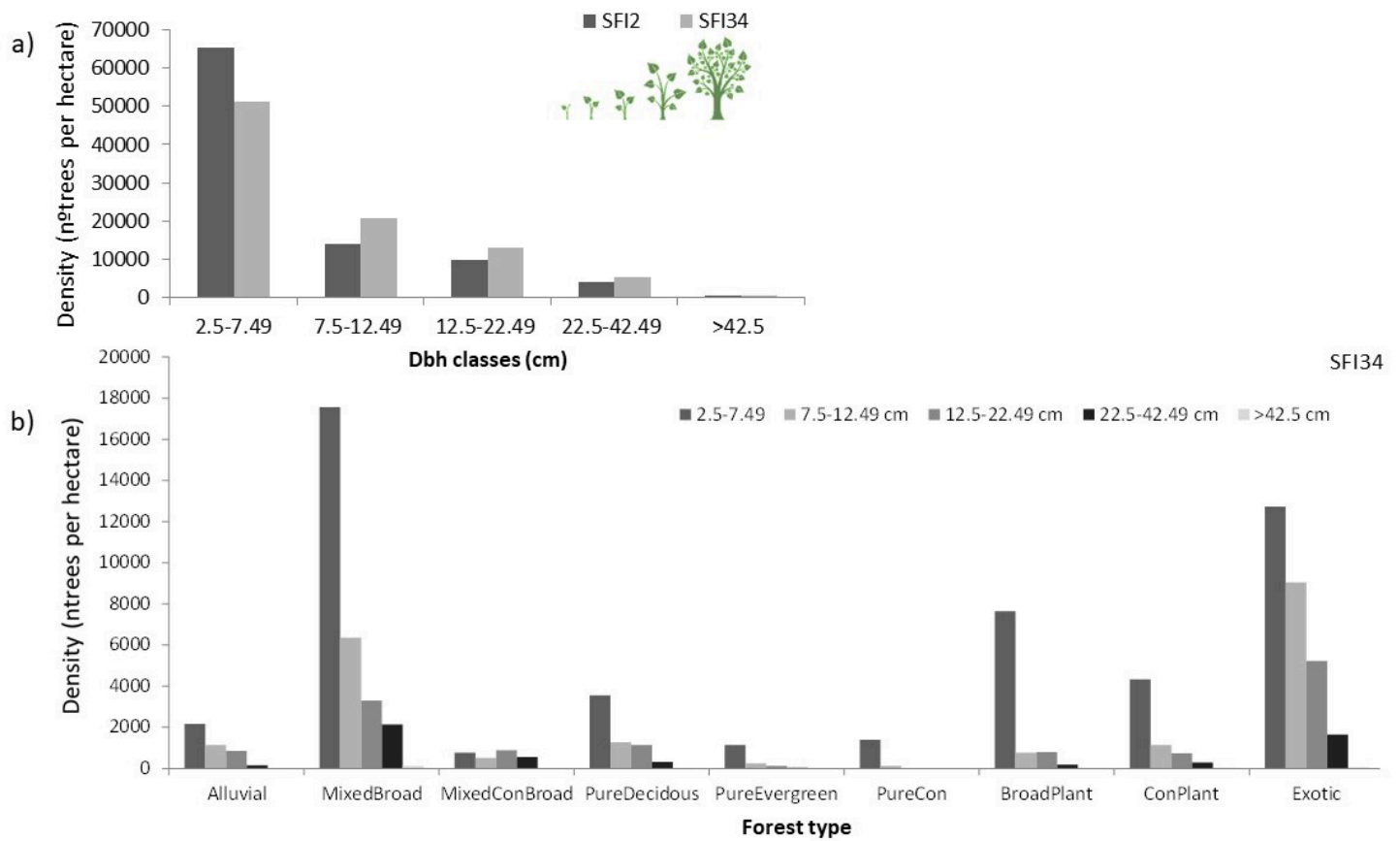


Figure 5

Diametrical (dbh) distribution of black locust in a) Spain in the two consecutive SFI cycles considered, and b) in the different forest types where it is presented in the most up to date SFI database.

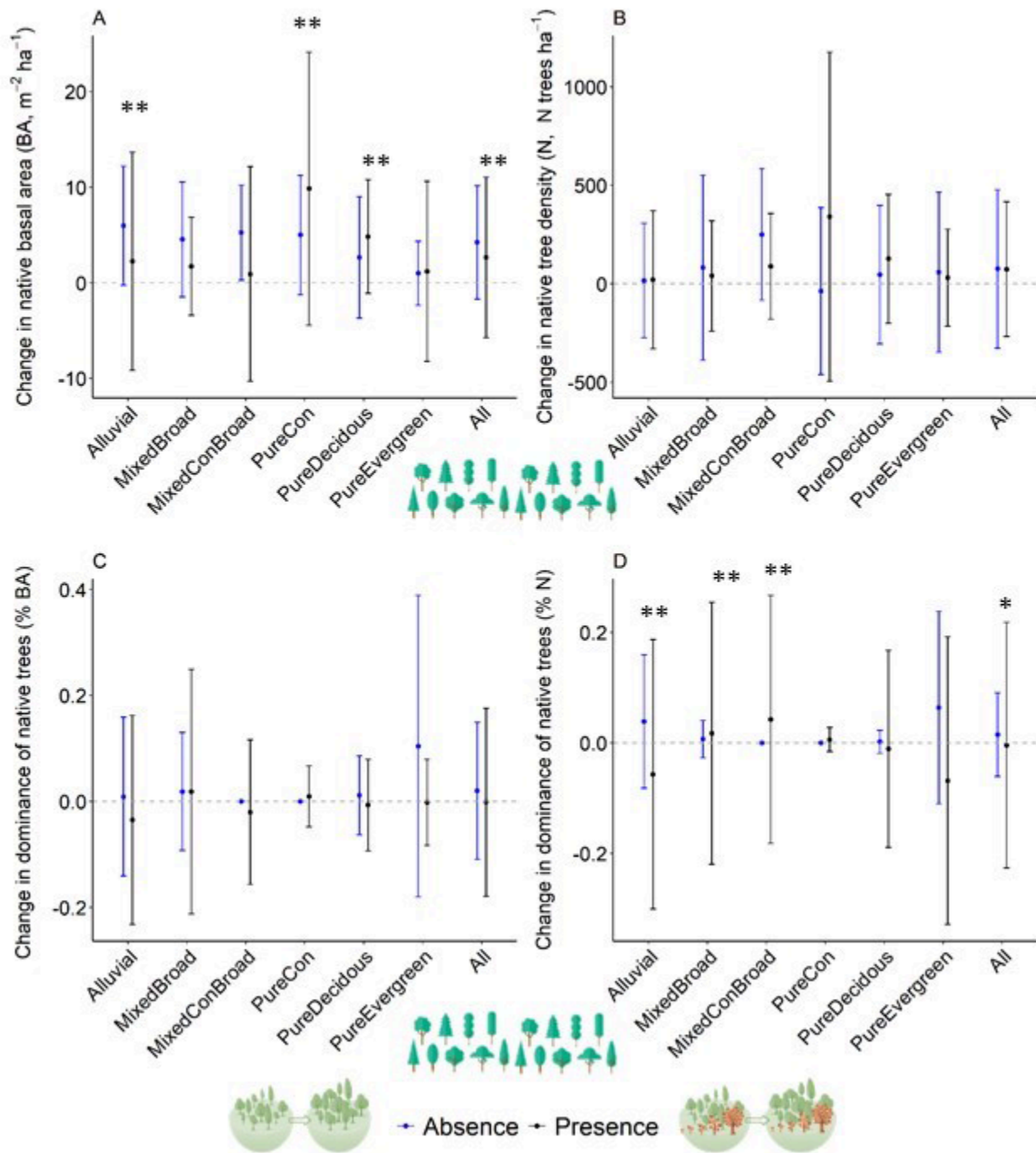


Figure 6

Mean differences and standard deviation in tree native attributes shifts by forest type between re-measured SFI plots with /without black locust presence. Change in tree stratum abundance a) basal area, b) density; and; dominance as proportion of native c) basal area, and d) density. (Signif. codes: **0.01; *0.05.)

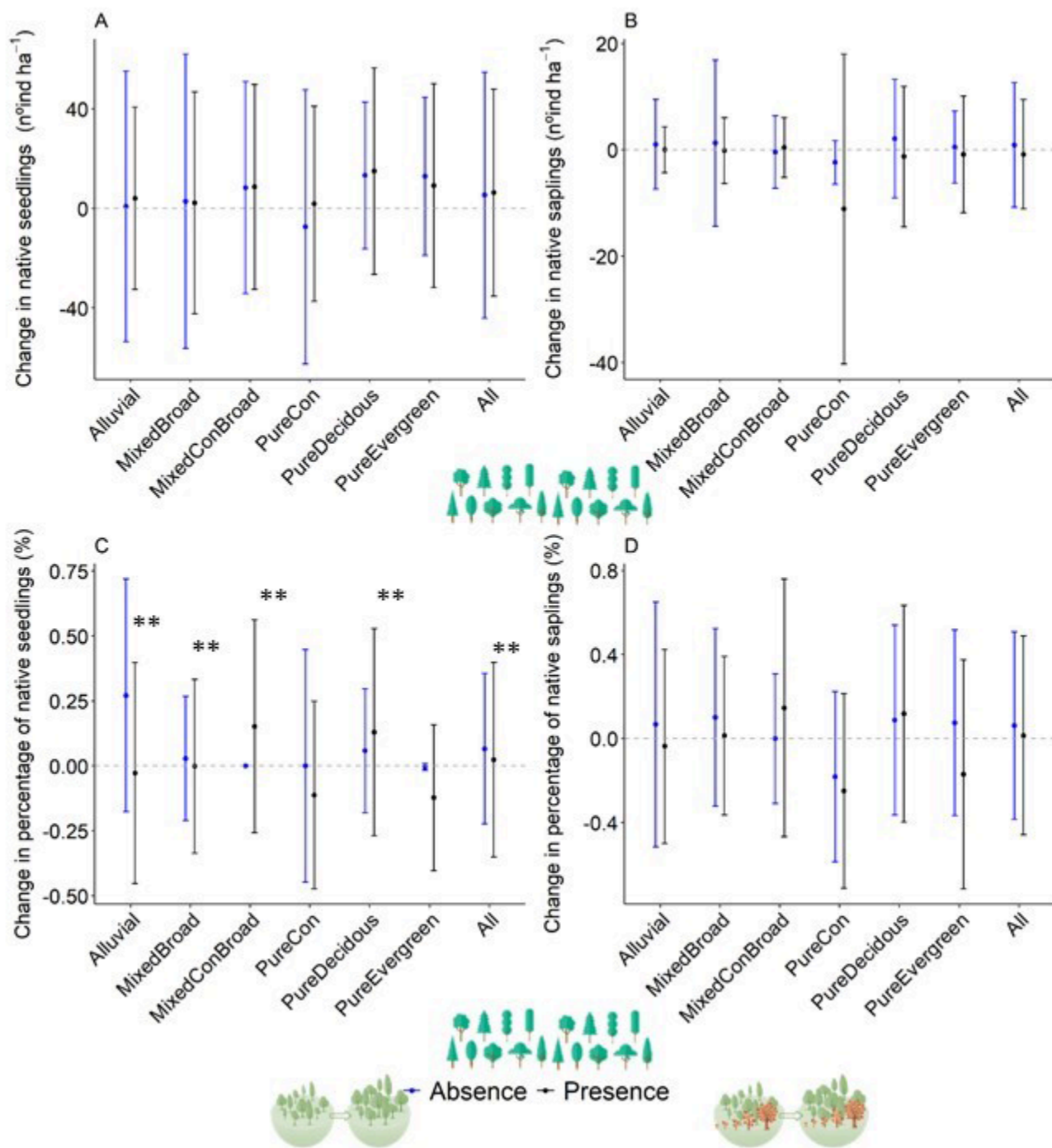


Figure 7

Mean differences and standard deviation in tree native attributes shifts by forest type between re-measured SFI plots with /without black locust presence. Change in regeneration stratum abundance as number of individuals per hectare: a) seedlings, b) saplings; and; in dominance as proportion of native number of individuals c) seedlings; and; d) saplings. (Signif. codes: **0.01; *0.05.)

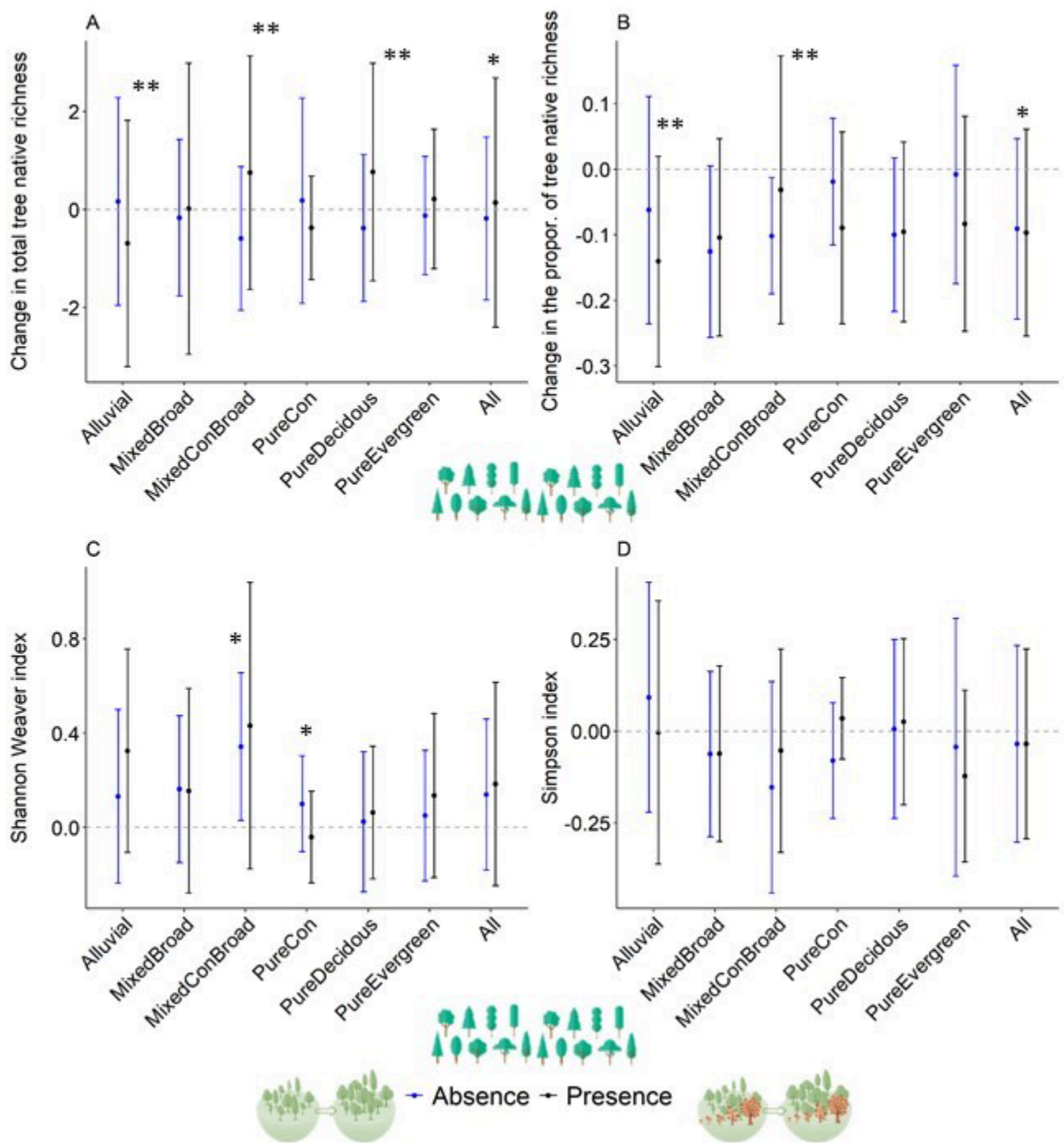


Figure 8

Mean differences and standard deviation in tree native attributes shifts by forest type between re-measured SFI plots with /without black locust presence. Change in a) total tree native richness and b) proportion at plot level; c) Shannon- Weaver index; and d) Simpson index. (Signif. codes: **0.01; *0.05.)

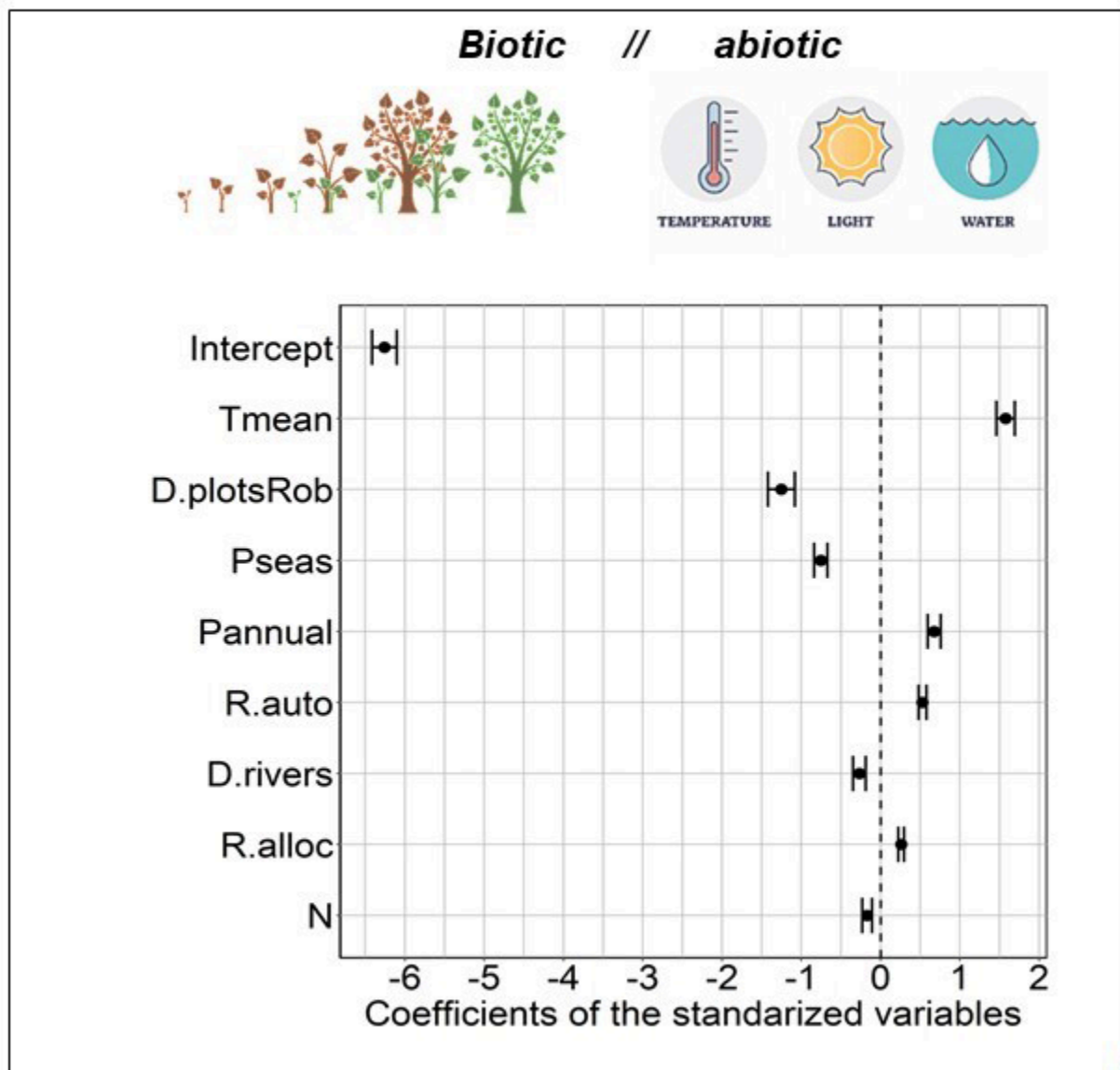


Figure 9

Coefficients and standard errors of the standardized variables selected by the backward variables selection process. Variables are ordered according to their standardized coefficient in absolute terms. **Tmean** = mean annual temperature; **D.plotsRob** = distance to black locust plots; **Pannual** = cumulative annual precipitation; **Pseas** = precipitation seasonality; **R. nat** = richness of native tree species, **R. no-nat** = richness of no-native tree species; **D.rivers** = distance to the rivers; **N** = plot tree density.