

Assessing spatio-temporal rates, patterns and determinants of biological invasions in forest ecosystems. The case of *Acacia* species in NW Spain



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ABSTRACT

Invasive species currently pose a major environmental challenge. Understanding their development and the factors associated with their expansion is the first step towards developing effective control measures. This work proposes the use of detailed spatio-temporal information from forest monitoring systems to assess the demographic rates, spatio-temporal patterns and spread determinants of invasive plants in forest ecosystems. For this purpose, we selected two of the most widespread non-native plants in Europe: *Acacia dealbata* and *Acacia melanoxylon*. Focusing on the forested area of northwest Spain and based on the comparison of two cycles of the Spanish National Forest Inventory, this study analyzes the dynamics of *Acacia* species between 1998 and 2008 in regards to changes in their spatial distribution, dominance, abundance, diametrical (dbh) structure and regeneration. In addition, the forested area was classified into forest types to identify the forests which are more susceptible to invasion. Finally, through general linear models, this study analyzes the relative importance of abiotic and biotic factors determining the spread of *Acacia* species over the studied period. The results confirm a rapid expansion in the presence of *Acacia* species in the forests of NW Spain, with annual spread rates around 0.1%. These two species are increasing their dominance across most forest types in the study area, where they are becoming the dominant species in the regeneration of some of them. Environmental factors and connectivity between *Acacia* populations are identified as the main factors associated with their spread into new areas. Additionally, the combination of disturbances and biotic factors associated with stand structure (total basal area, richness and tree cover) appear to determine the vulnerability or resistance of some forest to their spread. The early stage of invasion detected highlights the potential of *Acacia* species to continue spreading. This aspect, in conjunction with the high degree of disturbances (mainly fires) in this region, could be critical in determining the configuration of future forest landscapes in NW Spain. This study demonstrates the value of considering broad-scale periodic forest surveys to monitor biological invasions in forests ecosystems. The spatially-explicit data obtained from these surveys can contribute not only to furthering our knowledge with regard to invasion biology but also to developing more efficient conservation and management strategies.

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1. Introduction

Invasive alien species pose one of the most important direct threats to the structure and function of ecosystem diversity. The spread of invasive alien species is therefore among the most urgent nature conservation issues to be faced at global scale (UNEP, 2010), the identification of alien spread pathways to prevent their

introduction and establishment being one of the main targets of the EU 2020 Strategic Plan for Biodiversity (EC, 2011).

The considerable research into invasion ecology in recent decades has centered around three main questions: invasiveness (Rejmánek and Richardson, 1996), invasibility (Chytrý et al., 2008) and impacts (Hejda et al., 2009). As a result, our theoretical and practical knowledge of plant invasions has improved substantially, although the capability to address further challenges in this line of research may be hindered by the lack of availability, detail and heterogeneity of information concerning invaders (Pyšek et al., 2002). One of these new challenges is to provide new insights into invasion dynamics (Richardson et al., 2010).

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Although access to detailed lists and maps of non-native species has improved at global level in recent times (Foxcroft et al., 2010), there is a lack of broad scale periodic surveys providing the possibility to identify detailed demographic rates, spatio-temporal patterns and determinants of invasive plant spread.

Statistically-designed inventories such as National Forest Inventories (NFI) based on periodic re-measurements of permanent sample units constitute a valuable tool for monitoring forest dynamics (Lund, 1998). Consequently, the inclusion of non-native species data in these surveys, based on biodiversity monitoring programs, (Corona et al., 2011) provides a valuable opportunity not only to examine the broad-scale evolution of plant invasions in forest ecosystems but also to test ecological hypotheses in invasion biology.

For this study we selected two different *Acacia* species in an attempt to determine general patterns in forest dynamics and invasion ecology over the last decade in the northwest of Spain, one of the most affected regions of the country (Romero Buján, 2007). *Acacia* species are among the most widespread invasive plants in Europe, and two of the most aggressive are *Acacia dealbata* Link and *Acacia melanoxylon* R. Br. in W.T. Aiton. Today, they are widely naturalized and have become an environmental problem in Southwestern Europe (Carballeira and Reigosa, 1999; Hussain et al., 2011) where they pose a threat to native species and have been declared “invaders” (Sanz-Elorza et al., 2004). The invasive success of *Acacia* is mainly attributed to its rapid growth rate, prolific production of seeds with high longevity, germination stimulated by fire, allelopathic effects and the absence of natural enemies (Marchante et al., 2003). In the Iberian Peninsula, these two species have not yet reached their potential distribution range (Gassó et al., 2012), although it is likely that they will be able to reach this potential range in the near future. Identifying the determinants of invasion in the early stages is crucial to the development of realistic predictive models of invasion risk (Kolar and Lodge, 2001) and to mitigate the potential ecological impact.

This study constitutes a first attempt at using national forests monitoring data to study the evolution of biological invasions. Based on the analysis of the sequential broad-scale databases from two cycles of the Spanish NFI, the primary aim of this study is to examine the spatio-temporal changes in the distribution, abundance and dominance of *A. melanoxylon* and *A. dealbata* in the forests of NW Spain over the period 1998–2008. The second objective is to identify the types of forest which are most vulnerable to invasion and the level of invasion reached. Finally, an attempt is made to disentangle the relative importance of the biotic and abiotic factors underlying the spread of these two species in different forest types. For this purpose we test two hypotheses: the first is that *Acacia* species have expanded and increased their dominance in the forests of NW Spain between 1998 and 2008. The second is that the expansion rates and dominance of these species differ from one forest type to another.

2. Material and methods

2.1. Study area

This study is based on NFI information for the provinces which comprise the region of Galicia in the northwest of the Iberian Peninsula (Fig. 1). Due to a combination of bioclimatic and human factors, the percentage of non-native flora in this area of NW Spain (14%) (Romero Buján, 2007) is higher than for the Iberian Peninsula as a whole (12%) (Sanz-Elorza et al., 2004). This region presents a climatic gradient from the coast towards inland areas, but there is a dominant humid Atlantic climate with mild temperatures (mean annual temperature of 13 °C) and abundant

precipitation (mean annual rainfall of 1400 mm). Soils are acidic and the area exhibits a complex topography, with altitudes ranging from sea level up to 2124 m. Today, almost 50% of the forests in NW Spain comprise plantations of non-site-native species such as *Pinus pinaster* Ait., *Eucalyptus* spp., *Pinus sylvestris* L. and *Pinus radiata* D. Don (Table S2 in Supplementary material). The native forest types present in the area are floodplain/riparian forests, scattered coastline forests of *P. pinaster*, atlantic mixed broad-leaved forest where *Quercus robur* L. is abundant and oak forests of *Quercus pyrenaica* Willd. in the transition zone between the Atlantic and Mediterranean biogeoregions (Fig. 1C).

Acacia species are Australian N₂-fixing trees that were introduced into Europe as an ornamental species in the 19th century (Sheppard et al., 2006). In Spain, they are mainly distributed in the most NW territories where *A. melanoxylon* occurs close to the coastline in temperate locations while *A. dealbata*, with a broader ecological valence, can be found in more continental areas (Fig. 1B, Table S2 in Supplementary material).

2.2. Data used

The study is based on spatially detailed information from two consecutive cycles of the Spanish NFI performed in NW Spain in 1998 (NFI3) and in 2008 (NFI4), a time interval of 10 years (13,159 plots). In these Spanish NFI cycles, permanent plots were established systematically in the forested area at the intersections of a 1 km × 1 km grid. Field plots consist of four concentric circular areas with radii of 5, 10, 15 and 25 m.

Depending on the dbh (diameter at breast height) of the tree species, different dendrometric characteristics are measured within each plot and for each radius such as dbh or height of trees with dbh ≥ 7.5 cm and height ≥ 1.30 m. Furthermore, other forest attributes and conditions are measured (tree and shrub species composition, density, covers, recruitment, saplings (trees with 2.5 cm ≤ dbh < 7.5 cm), silvicultural treatments (clear-cutting, groundwork and crown treatments), etc.).

A total of 20 predictors were considered as independent variables to analyze the relative importance of abiotic and biotic factors determining the spread of *Acacia* species over the period considered (Table S1 in Supplementary material). Some of these variables were also used to characterize the climatic and physical ranges of the two *Acacia* species and the different forest types, as well as their disturbance level (Fig. S1 in Supplementary material). As regards the abiotic factors; topographical variables (altitude, aspect, exposure and closest distance to sea) were taken from the digital elevation model of Spain with a spatial resolution of 25 m (U.T.M, ED 50). Climatic variables were extracted from Gonzalo (2010). The impact of human disturbances on the spread of *Acacias* over the time frame considered were discerned using variables such as silviculture treatments obtained from NFI plot databases, the forest-urban and forest-crop interface calculated from land use maps (Heymann et al., 1994; EEA, 2012) and the fire incidence from MODIS burned area products (Boschetti et al., 2009). As for biotic factors, we considered several attributes of forest structure derived from NFI datasets such as species richness, tree cover and basal area at plot level. Furthermore, to analyze the importance of propagule pressure or distance from invasion loci, we consider the connectivity between plots containing *Acacia* species (Fig. S1 in Supplementary material).

2.3. Data analysis

Spanish NFI records of the presence of *A. melanoxylon* and *A. dealbata* (Fig. 1B), along with other cartographical sources such as botanical Atlases (Sanz-Elorza et al., 2004; Anthos, 2012), provided valuable information for mapping the current spatial

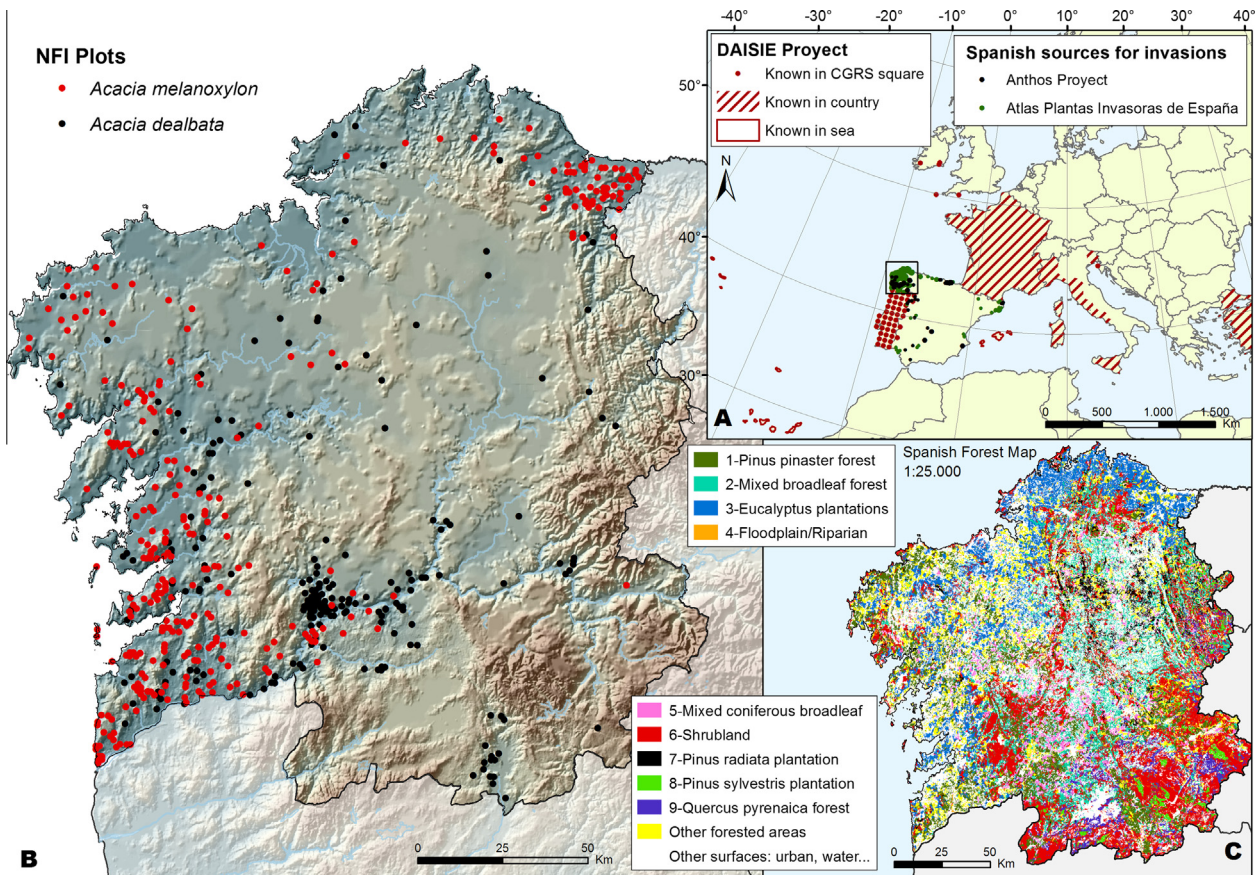


Fig. 1. (A) Known distribution area of *Acacia melanoxyylon* and *Acacia dealbata* in Europe. (B) Known distribution area of *Acacia* species in NW Spain. (C) Distribution of the different forest types in NW Spain.

distribution of the two *Acacia* species in the study area (Fig. 1A). Based on NFI plot information such as species dominance and forest management, the forested area of NW Spain was then classified into nine forest types (see Fig. 1C and Table S2 in Supplementary material for main characteristics and abbreviations) according to the definitions proposed for Europe (Barbati et al., 2007).

The comparison of the information derived from the plots in which *Acacia* species were present in the two sequential NFI allowed the total spatial expansion, density and growing stock rates of *Acacia* species to be assessed (114 plots). To analyze the stage of invasion in the plots during the time frame considered, changes in *Acacia* species abundance by dbh class were also calculated. It must be considered that due to the dynamic nature of this species and the frequency of disturbances in the forests where these two species are found, the number of remeasured plots used in these analyzes was limited and was lower than the proportion used when studying the distribution or spread derived from the presence/absence indicator.

The vulnerability to the invasion in the different forest types was analyzed through the particularized Important Value Index (IVI) from Curtis (1959) as the sum of the relative density and dominance of *Acacia* species in the plots by forest types (114 plots). Relative density was defined as the numerical strength of a species in relation to the total number of individuals of all the species. It was calculated as: [(Number of individual of the species/Number of individual of all the species) × 100]. Relative dominance was determined by the value of the total basal area of a species with respect to the sum of basal area of the rest of the species in the plot and it was calculated as: [(Total basal area of the species/Total basal area of all the species) × 100]. The IVI was used to determine the overall importance of *Acacia* species in the plots, providing a

good indicator of invasive species dominance. In these approaches, only the forest types in which there was a significant number of plots with presence of the two *Acacia* species were considered ($n \geq 5$). Since there were different sample sizes and non-homogeneity of the variance, the mean differences in *Acacia* IVI by forest type were assessed through the Welch Test. Tamhane's T2 test was then used for post hoc multiple comparisons of mean values between forest types (Hollander and Wolfe, 1999).

Two dichotomous dependent variables (*Col*, colonization, and *Dis*, disappearance) (757 plots) were then created to analyze changes in spatial distribution and the level of invasion of the two *Acacia* species in the different forest types in NW Spain during the period (1998–2008).

The current invasibility of the different forest types was partly analyzed through the total number and proportion of saplings of the two *Acacia* species in the regeneration of each forest type according to the last NFI (2008) (92 plots). The proportion of the species in the regeneration defines the numerical strength of that species in relation to the total number of individuals of all the species, indicating conspecific abundance or dominance. The results were then analyzed to show the overall patterns and range of the current regeneration of the two *Acacia* species in the different forest types they have invaded.

Finally, a dichotomous dependent variable *Spr* was created to assess the effect of different biotic and abiotic factors on the spread of the *Acacia* species in the forests of NW Spain over the period 1998–2008 through general linear model (GLM) analysis with binomial error and logit link. This was analyzed in the plots in which *Acacia* species were not present in 1998 but were present in 2008 (251 plots). The logistic regression models provide information on the relationships and strengths among dependent and

independent variables. Furthermore, logistic regression accepts a combination of continuous and categorical variables as well as not normally distributed ones (Hosmer and Lemeshow, 2000). Multicollinearity was verified using Pearson correlation coefficients. Some of the explanatory variables that were highly correlated ($|r| > 0.8$) were excluded prior to building the model. We followed a step-by-step model-building procedure and the fit of the model was tested after the elimination of each variable. Deviance reduction, estimated as: $D^2 = (\text{null deviance} - \text{residual deviance})/\text{null}$, was used as the measure of discrepancy to assess the goodness-of-fit of the model (Crawley, 1993).

ArcGis 10 (ESRI Inc., Redlands, CA, USA) was used as an image analysis tool as well as to extract topographical, climatic, land use and fire variables to the $1 \text{ km} \times 1 \text{ km}$ grid. R software was used to fit the GLM model and SPSS17.0 (SPSS Statistics, 2009) for all the other statistical analysis.

3. Results

3.1. Changes in the distribution of Acacia species

In 1998, *A. melanoxylo*n and *A. dealbata* were present in 2.2% and 1.5% respectively of the total forested area of the study region. By 2008 they had expanded by 1% and 0.83% respectively (Table 1), with an expansion rate (proportion of total hectares invaded per year) of approximately 3100 ha yr^{-1} and 2500 ha yr^{-1} . The intensity of the changes in the spatial distribution of *Acacia* species differs according to forest type. There has been a notable increase in the presence of *A. melanoxylo*n in riparian forests and *Eucalyptus* spp. plantations, reaching 7% and 3.5% of the total forest area of these two forest types respectively (Fig. 2). In these two forest types, the increase was almost four times greater than for other forest types. Conversely, there has been a notable decrease in the presence of this species in mixed broadleaf forests and shrublands, although in 2008, it was present in 1% and 3% of these two forest types respectively. The presence of *A. dealbata* has increased significantly in the majority of forest types in the study region, even occurring in *Q. pyrenaica* oak forest in 2008, where it was absent in 1998. This increase is particularly notable in mixed conifer-broadleaf forests, the most abundant forest type in the study area, where it is present in almost 3.5%. A small decrease in the presence of this species was detected in riparian forest and shrubland, occurring in 3% and 0.4% of each type respectively (Fig. 2).

3.2. Acacia species dynamics and dbh structure

Analysis of the dynamics of NFI plots in which *Acacia* species were present in 1998 and 2008 show that the number of trees per hectare, basal area and growing stock of these two invasive species almost doubled in all cases during this period (Table 1). However, while in the case of *A. melanoxylo*n the increase has been

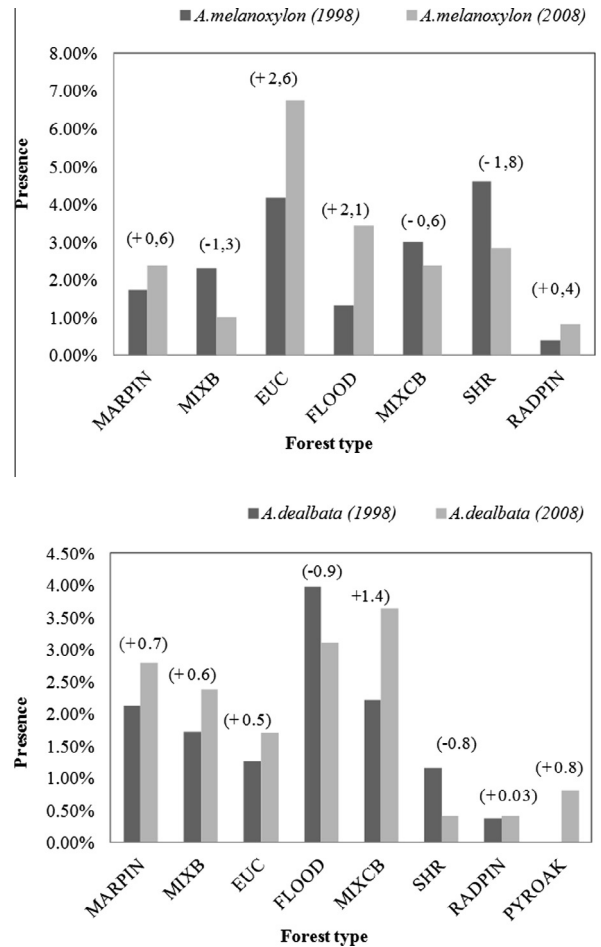


Fig. 2. Changes in the proportion of the *Acacia* species in the different forest types of NW Spain, 1998–2008. See Table S2 in Supplementary material for forest types abbreviations.

greater in terms of basal area and proportion of growing stock in the stands where it occurs, *A. dealbata* has undergone a greater increase in the number of trees per hectare (Table 1).

The pattern of variation in the proportion of trees of different dbh classes over the studied period differs between the two species. In the case of *A. melanoxylo*n, the proportion of trees with the smallest diameters has suffered a slight drop over the period, while the proportion of trees with medium-large diameter has increased (Fig. S2 in Supplementary material). However, in the case of *A. dealbata* the proportion of small diameter trees has risen, whereas the proportion of medium diameter trees has decreased slightly (Fig. S2).

Table 1

Changes in distribution (ΔS) and stock ($\Delta N, \Delta BA, \Delta G$) of *A. dealbata* and *A. melanoxylo*n, 1998–2008. In bold the decennial increments are highlighted.

	<i>A. melanoxylo</i> n			<i>A. dealbata</i>		
	1998	2008	Increment	1998	2008	Increment
Number of plots with presence	167	262	95	129	199	70
Percentage of total forest area (%)	2.2	3.2	1.00	1.5	2.4	0.8
Area (ha)	57,300	88,250	31,000	40,900	66,300	25,400
Mean number of trees per ha	2.6	3.1	0.5	2.4	3.8	1.4
Relative density: % of <i>Acacia</i> sp. in total tree per ha	0.4	0.4	0.02	0.4	0.5	0.1
Mean basal area (m^2/ha)	0.03	0.06	0.03	0.02	0.04	0.02
Relative dominance: % of <i>Acacia</i> sp. in total basal area (%)	0.2	0.2	0.1	0.1	0.2	0.1
Mean growing stock (m^3/ha)	0.2	0.4	0.2	0.1	0.2	0.1
Proportion of <i>Acacia</i> sp. in total growing stock (%)	0.2	0.3	0.1	0.1	0.1	0.03

The analysis of *Acacia* species saplings did not identify significant differences between forest types due to the high level of stochasticity in the associated variables. However, as can be seen from Table 2, the relative and absolute density of the regeneration varied from one forest type to another. *A. melanoxylon* regenerates more abundantly in mixed conifer-broadleaf forests than in *Eucalyptus* spp. plantations, the only two forest types in which saplings of this species were found. In addition, as revealed by the relative results, this species tends to dominate in the regeneration of mixed conifer-broadleaf forests. In the case of *A. dealbata*, despite the high dispersion of the saplings associated variables, the results show a clear tendency to dominate in the regeneration of all the forest types in which this species was found: mixed broadleaf forests, *Eucalyptus* spp. plantations and mixed conifer-broadleaf forest, regenerating in similar abundance.

As indicated by the Welch and Post hoc tests through mean differences in the IVI over the period 1998–2008, the dominance of the two invasive species increased in all the forests types in which they were present (Table 3). However, these changes differed significantly depending on the forest type. The increase in overall importance of *A. melanoxylon* and *A. dealbata* was significantly greater in mixed conifer-broadleaf forests than in other forest types. Additionally, in the case of *A. melanoxylon*, this increase in dominance was also more significant in *Eucalyptus* spp. plantations than in other forest types.

3.3. Factors involved in the spread of *Acacia* species

Among the 20 biotic and abiotic predictors previously considered to explain the spread of the *Acacia* species from 1998 to 2008 (Table S1 in Supplementary material), the best GLM fits were obtained for 11 different predictors in the case of *A. melanoxylon* and 10 for *A. dealbata* with which the spread of the two species over the period displayed significant relationships. The final models accounted for 52% and 48% of the observed variability in the spread of *A. melanoxylon* and *A. dealbata* respectively over the period (Table 4). As regards the climatic abiotic factors, mean annual temperature has significant and positive effects on both species spread over the studied period, while to a lesser extent, annual rainfall and the mean temperature oscillation has a negative one. The factor ‘closest distance to the sea’ also has a

Table 4

Binomial GLM results for the spread of *A. melanoxylon* and *A. dealbata* during the period 1998–2008. See Table S1 of Supplementary material for abbreviations.

Predictors	<i>A. melanoxylon</i>		<i>A. dealbata</i>	
	Effect	D ²	Effect	D ²
Intercept	−0.35	–	5.59	–
Ptot	−0.0125	1.99*	−0.0037	8.22**
Tm	0.31	44.73**	0.22	68.43**
Dsea	4.08E−05	62.89**	–	–
Osc	−0.28	9.7**	−0.42	11.52**
Clearcut	0.96	2.09**	–	–
Connect	−3.18E−04	85.33**	−1.80E−04	66.15**
Treecover	−0.01	12.13**	−0.04	10.48**
Fire	0.93	2.06*	0.68	2.87*
BA	−0.04	4.47**	−0.0407	3.85**
TRichness	0.13	4.35**	0.22	12.31**
FUInt	–	–	0.08	7.23**
Deviance (D²)		51.623%		48.026%

* Significance codes: $p > 0.05$

** Significance codes: $p > 0.01$.

positive relationship with the spread of *A. melanoxylon* in the study zone. Regarding human-mediated and other disturbances, clear-cutting, urban-forest interfaces and fire incidence had a positive and significant effect on both species. Among the biotic factors connectivity between stands shows a strong association with the spread. As for other biotic interactions, stand structure characteristics such as tree cover and total basal area exhibited a negative relationship while total richness has a positive association with their spread.

4. Discussion

The results confirm the prior hypothesis of expansion and upward dominance of *Acacia* species in the forested area of NW Spain over the last decade, revealing different invasion patterns from one forest type to another.

4.1. Spatio-temporal dynamics

The quantification of the area occupied by invasive plants in a given zone, the identification of the stage of invasion, their spread

Table 2

Mean and standard deviation (Stand-Dev) of the absolute (Nsap) and relative (Nsaprel (%)) number of *A. melanoxylon* and *A. dealbata* saplings in the regeneration per hectare. See Table S2 of Supplementary material for forest types abbreviations.

Forest type	<i>A. melanoxylon</i>		<i>A. dealbata</i>	
	Mean Nsap (Stand. Dev.)	Mean Nsaprel (Stand. Dev.)	Mean Nsap (Stand. Dev.)	Mean Nsaprel (Stand. Dev.)
EUC	875.4 (756.7)	0.5 (0.4)	2772.8 (1930.5)	0.7 (0.4)
MIXCB	2018.9 (1036.4)	0.8 (0.3)	2113.6 (1916.2)	0.9 (0.1)
MIXB	–	–	3028.5 (2921.2)	0.9 (0.2)

Table 3

Mean differences in IVI (Importance Value Index) of (1) *A. melanoxylon* and (2) *A. dealbata*, between the invaded forest types of NW Spain. See Table S2 of Supplementary material for forest type abbreviations.

(1) Mean IVI (Stand. Dev.)	Forest type	MARPIN (n = 10)	MIXB (n = 7)	EUC (n = 19)	MIXCB (n = 32)
0.14 (0.08)	MARPIN		−0.227	−0.64*	−0.86*
0.36 (0.23)	MIXB			−0.420	−0.64
0.79 (0.61)	EUC				−0.22
1.00 (0.89)	MIXCB				
(2) Mean IVI (Stand. Dev.)	Forest type		MIXB (n = 7)	EUC (n = 9)	MIXCB (n = 30)
0.62 (0.57)	MIXB			−0.25	−0.66*
0.87 (0.69)	EUC				−0.41
1.28 (0.69)	MIXCB				

* Significant difference at level $p = 0.05$.

rates and the potential to invade new areas are of critical importance in determining the ability of organisms to shift their ranges and to detect their invasive success and persistence (Higgins and Richardson, 1996; Higgins et al., 2001). The percentage of forested area in NW Spain occupied by the two *Acacia* species reached 3.2% and 2.4% in 2008, exhibiting annual rates of invasion (proportion of total area invaded per year) of 0.1% and 0.08% for *A. melanoxylon* and *A. dealbata* respectively. To date, most of the empirical data on invasion rates worldwide are based on estimations from past aerial photographs (Lonsdale, 1993; Higgins et al., 2001) for broad scale studies or, to a lesser extent, from estimates based on field work for local scale studies (Wangen and Webster, 2006). However, to our knowledge this is the first time that these rates have been studied extensively on a detailed spatial grid on such a large scale. Bearing in mind the limitations involved in comparing the spread rates associated with the differing sized areas and populations monitored of previous studies, it would appear that the *Acacia* species in NW Spain exhibit mid-high invasion rates, since similar or lower estimates have been reported for other invasive tree/shrub species; 0.08% for *P. radiata* (Richardson and Brown, 1986), 0.03% for *Acacia cyclops* or 0.06% for *P. pinaster* (Higgins et al., 2001), all in South Africa. The rates of areal spread of the two *Acacia* species ($31 \text{ km}^2 \text{ yr}^{-1}$ and $25 \text{ km}^2 \text{ yr}^{-1}$) are close to the average for other tree/shrub life forms worldwide, which present a mean spread rate of around $27 \text{ km}^2 \text{ yr}^{-1}$, ranging from $0.02 \text{ km}^2 \text{ yr}^{-1}$ to $179 \text{ km}^2 \text{ yr}^{-1}$ (from a review carried out by Pyšek and Hulme, 2005).

The aforementioned spatio-temporal spread was concomitant with a substantial increase in growing stock and dominance over the period 1998–2008, doubling in all the cases the preceding values but displaying different traits. Whereas *A. melanoxylon* seems to be increasing its dominance in forests where it was present through increments in growing stock and basal area, *A. dealbata* displays a greater increase in density and regeneration. Although this rise in dominance is general for all forest types analyzed, a significant increase is observed in disturbed forest types (according to our characterization) such as *Eucalyptus* spp. plantations and mixed conifer-broadleaf forests, but also in habitats which in principle are less altered by human activity such as native mixed-broadleaf forests. This pattern is also observed in the relative proportion of trees in the regeneration where *Acacia* species tend to dominate and to homogenize this important forest stratum supporting previous results at local scale in the region (Hussain et al., 2011; González-Muñoz et al., 2012; Lorenzo et al., 2012). The concurrence of our findings with those of the aforementioned studies may have important implications for the future composition and functional diversity of forests in which *Acacia* species are becoming naturalized and spreading and where a decrease in structural and compositional complexity is expected.

The dbh distribution structure of *Acacia* species over the studied period suggest an early stage of invasion in the forests of NW Spain being saplings the dominant class. This finding is in accordance with the general increase of *Acacia* species occurrence observed in the majority of forest types of NW Spain in the last inventory. Bearing in mind the capacity of *Acacia* species to flower throughout the year and their strong resprouting ability (Lorenzo et al., 2010), these results highlight the potential of *Acacia* species to continue spreading in the near future, confirming previous predictions suggesting that these species have not yet reached their potential area of distribution within the Iberian Peninsula (Gassó et al., 2012).

4.2. Factors associated with *Acacia* species spread and invasibility

The results of the GLMs point to connectivity and environment as the key factors associated with the expansion of the two invasive species.

It is not surprising that connectivity between *Acacia* populations has a strong association with the spread since increased availability of propagules between proximate populations raises the chances of establishment, persistence, naturalization and invasion (Alston and Richardson, 2006). Furthermore, this result is in accordance with the non-long distance dispersal adaptation more common in *Acacia* species which are usually dispersed by animals such as birds and ants (Davidson and Morton, 1984; Lorenzo et al., 2010).

With regard to environmental factors, temperature and distance to the sea are revealed as the most important filters constraining the colonization of new areas. This finding agrees with the habitat compatibility hypothesis (Rejmánek et al., 2005) which states that habitats globally tend to be invaded by species from similar environments at source. The natural distribution range of *A. melanoxylon* and *A. dealbata*, mainly in south-eastern Australia, illustrates their preference for oceanic climate locations (Costermans, 1985). This partly explains the absence of both *Acacia* species in certain forest types characterized by higher temperature oscillations, such as *P. sylvestris* plantations located at higher altitudes. Similarly *A. melanoxylon* is completely absent in oak forests of *Q. pyrenaica* in submediterranean climatic transition zones although the most recent inventory indicated a small presence of *A. dealbata* in these forests. The broader ecological valence of the latter allows this species to invade more continental locations, away from the influence of the coast. However, this significant relationship with certain environmental factors does not necessarily explain the degree of invasion in the different forest types. Moreover, forest types with similar environmental conditions exhibit dissimilar levels of invasion, suggesting that other mechanisms render them more or less susceptible to invasion.

Disturbances are considered one of the most important factors behind the invasive spread of *Acacia* species (Brooks et al., 2004; Lorenzo et al., 2010; Le Maitre et al., 2011). The significant positive association found between the spread of *A. melanoxylon* and *A. dealbata* and disturbance events such as fires, clear-cutting and urban-forest interfaces would appear to support this idea. Davis et al. (2000) suggest that habitats might be more susceptible to invasion when there is an increase in the amount of unused resources resulting from disturbance events. Accordingly, some of the habitats with higher levels of disturbance correspond to forest types with a higher degree of invasibility. *Eucalyptus* spp. plantations are located close to the coast where population is concentrated and where intuitively there would be a high propagule pressure (Di Castri, 1989) due to their proximity to urban-forest interfaces and communication networks. Furthermore, *Eucalyptus* spp. plantations and mixed conifer-broadleaf forests, two of the most invaded forest types, had the highest fire incidence over the period (affecting almost 10% and 8% respectively of their extent). Forest fires are one of the main disturbance factors in forest ecosystems across large areas of Spain, including NW Spain (Moreno et al., 1998; de la Cueva et al., 2006). *Acacia* species are highly resilient to fires and are capable of regenerating both through germination and sprouting from roots and stems after fires (Ough, 2001). Some authors (e.g. Lorenzo et al., 2010) have already suggested that the spread of *A. dealbata* in NW Spain may be assisted by human disturbances such as fires, although this hypothesis has not yet been tested at larger scales (see however de la Cueva (2014) for a local scale study). Hence, one of the key findings of the present study is the positive relationship found between the spread of both *Acacia* species and fire incidence, which confirms that areas currently occupied by *Acacia* are often areas which have been affected by fire.

Disturbances seem to be an important factor associated with the spread of invasive species, however not always the more anthropogenic disturb forests are the ecosystems with a higher degree of invasion. In such cases, as suggested by Alpert et al.

(2000) or *Blossey and Nötzold (1995)*, community structure traits might be influencing the invasibility of some ecosystems. This is the case of *P. radiata* and *P. pinaster* plantations, which present lower levels of invasion than other forests even though they are intensively managed and occupy large areas with as suitable environmental conditions as other more invaded forests. Pine plantations form monospecific forests with higher stand basal area and an evergreen canopy which is more closed than that of *Eucalyptus* spp. plantations, resulting in a general absence of understorey. In these forests, *Acacia* species would face strong competition for resources, which may be associated with negative relationships found between the spread of these species and both total stand basal area and tree cover. This pattern is also corroborated by the significantly lower increase in dominance found in *P. pinaster* plantations compared with other forest types. Furthermore, these results support the findings of previous studies that identified important relationships between invasion by alien species and percentage of overstorey cover (*Alston and Richardson, 2006*) and canopy closure (*Fuentes-Ramírez et al., 2011*).

As regards other community structure traits which influence the spread of *Acacia* species; total richness per plot shows a significant positive relationship supporting previous studies at similar scales (*Alpert et al., 2000; Stohlgren et al., 2003; Souza et al., 2011*). In accordance with this finding, forest types with higher values of richness such as mixed conifer-broadleaf forests, mixed-broadleaf forests and riparian forests, show some of the highest levels of invasion. *Levine and D'Antonio (1999)* suggested that species richness may be positively correlated with invasion, because both are promoted by the same factors. Like floodplain forests, the conifer-broadleaf and mixed-broadleaf forests of NW Spain form transitional, dynamic ecosystems that act as corridors for species between adjacent habitats (*Richardson et al., 2007*) and therefore, support high levels of diversity. The current mixed conifer-broadleaf forests of NW Spain are the result of natural colonization by native species of abandoned monospecific plantations (*Saura and Carballal, 2004*) and the mixed-broadleaf forests are usually found in valleys near populations, with a rich mosaic of land uses and where there would be a strong propagule pressure and more opportunities for *Acacia* species to be established. In mixed forests, our results also show an alarming tendency for *Acacia* species to dominate in the regeneration which lead us to suggest that in these cases, once established in the understorey, other processes such as competitive ability (*Blossey and Nötzold, 1995*) and allelopathy (*Callaway and Aschehoug, 2000*) may facilitate their persistence and dominance.

5. Conclusions

Acacia species are spreading rapidly and are becoming the dominant tree species across large areas of forest in NW Spain. As this study suggests, the success of *Acacia* species in spreading to and invading new areas is not due to a single mechanism but rather to a group of interrelated processes. The distribution ranges of the species in the forests of NW Spain are mainly constrained by environmental filters and the connectivity or propagule pressure between proximate populations. Additionally, the combination of disturbance events and stand structure traits seem to play an important role in determining the level of invasion of the different forests. Our results point to an early stage of invasion, highlighting the potential of *Acacia* species to continue spreading. This fact, together with the high frequency of disturbances such as fire, may be critical in determining the configuration of future forest landscapes in the region (e.g. *de la Cueva et al., 2012*).

The empirical results from this research will contribute to the growing reference database on plant invasion rates and may

provide practical help in the assessment of level and severity of biological invasions worldwide. Furthermore, the detailed data obtained from this type of study, such as spread rates, spread determinants and forests invisibility is crucial to improving spatially-explicit information on the risk of invasions as well as facilitating the development of efficient policies and management measures for forest conservation. Although limited to forest ecosystems, this work highlights the suitability of using broad-scale periodic forest surveys to monitor invasive plants, as well as their potential to contribute in the future to the necessary practical and theoretical understanding of biological invasions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.05.058>.

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