Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities

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**Abstract.** *Acacia dealbata* Link (Mimosaceae) is a woody leguminous tree introduced to Europe from Australia that has become a serious environmental problem in north-western Spain, where it forms dense monospecific patches threatening native-plant biodiversity. We describe the effects of invasion by *A. dealbata* on understorey plant composition in shrubland, oak- and pine-forest communities in north-western Spain. Plant species richness and composition, plant density and total plant cover were measured and compared among patches with different invasion status (invaded, transition and non-invaded patches) in each studied community. A clear effect of the community type and invasion on the understorey vegetation was observed. In general, composition of shrubland was different from that of oak and pine forests. We found significant effects of invasion status on species richness, plant density and total plant cover; values were significantly lower in invaded than non-invaded patches. Invasion by *A. dealbata* also was associated with changes in species composition. In total, eight native species, including the endemic *Daboecia cantabrica* (thuds) K. Koch, were confined to non-invaded patches and were replaced by other natives in invaded and transition patches. Our results suggest that although *A. dealbata* represented a serious threat to all of the study communities, the severity of the impact depended on the community type.

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**Introduction**

In many parts of the world, invasions by exotic species have been recognised as a major threat to natural ecosystems and a major cause of biodiversity loss (Keane and Crawley 2002; Callaway et al. 2005; Hierro et al. 2005; Lorenzo et al. 2008). Plant invaders of natural ecosystems displace native species, leading to extensive changes in ecosystem processes and community structure (Yelenik et al. 2004; Callaway et al. 2005; Hierro et al. 2005; Gooden et al. 2009a). Although the number of studies assessing the effects of invasive species at community level throughout the world is increasing (e.g. Gooden et al. 2009a, 2009b; Hejda et al. 2009; Jäger et al. 2007, 2009), studies on the impact of invaders in multiple sites are quite scarce (Vilà et al. 2006). The amount of time that has passed since the invasion determines the magnitude of invasion impacts (Strayer et al. 2006). However, the quality and magnitude of these impacts on resident communities differs among invasions. For example, sometimes plant invasions have an impact on soil chemical properties that are increased over time (Marchante et al. 2008a, 2008b). Other times, impacts are at soil microorganism level (Rodríguez-Echeverría et al. 2007, 2009) or in the accumulation of exotic litter and interactions with abiotic variables (Strayer et al. 2006). Studying the impacts at community level in the field, by comparing invaded and non-invaded areas, may help us identify the potential effects of an invasive species and provide useful information for nature conservation (Hejda et al. 2009). This may help us understand the invasive ability of an exotic species; invaders with a high impact should be targeted for earlier eradication than invaders with weak effects (Strayer et al. 2006). However, both strong and weak impacts by exotics are equally important to take into account when the invaded ecosystems are located in protected areas. Accordingly, the control of an exotic species should begin in these areas, because, as defined by the International Union for Conservation of Nature (IUCN), a protected area is an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, managed through legal or other effective means (FAO 2000).

Galicia is a Spanish region with a large number of protected areas because of their high ecological and cultural value. These areas include Biosphere Reserves, National Parks, the ‘Nature 2000 Network’, Natural Parks and Protected Landscapes, representing almost one-quarter of its total territory (Regional Government, http://www.xunta.es, verified 12 May 2012). Some of these areas are currently threatened by the invasive expansion...
of *Acacia dealbata* Link (hereafter, *Acacia*). *Acacia* is an Australian N₂-fixing tree that grows up to 15 m tall in the studied invaded areas. This woody legume was introduced into Europe as an ornamental species in the 19th century (Reigosa 1987) and, today, has become a serious environmental problem in north-western Spain, where it has invaded protected areas of native forests, abandoned arable land and watercourses, to the detriment of native understory species (Carballeira and Reigosa 1999; Lorenzo et al. 2008; González-Muñoz et al. 2012) – a phenomenon which is at least partially related to the release of allelopathic compounds by *A. dealbata* (Carballeira and Reigosa 1999; Lorenzo et al. 2008, 2010b, 2010c). Moreover, *A. dealbata* has been shown to alter nutrient pools, soil-microbe structure and the diversity and richness of soil microorganisms (Souto 1997; Lorenzo et al. 2010d; González-Muñoz et al. 2012). Quantitative studies are necessary to determine whether this invasive species displaces native species and reduces local biodiversity, because the impact of *Acacia* invasion on understory plant composition in invaded patches at field level is poorly understood.

The present study was carried out with the aim of testing the hypothesis that invasion by *Acacia* leads to changes in the composition of aboveground plant communities and decreases the plant species diversity of the invaded patches in comparison to pre-existing vegetation. To test this hypothesis, we sampled patches dominated by native species, patches dominated by the invasive *Acacia*, and mixed patches in different plant communities.

**Materials and methods**

**Study plots and invasion status**

We carried out our study in Galicia, north-western Spain, in areas of ecological interest and threatened by *Acacia* invasion (Biosphere Reserves, Natural Parks, autochthonous forests). We surveyed 11 plots threatened by *Acacia* covering shrubland, oak-forest and pine-forest vegetation communities. The main biological and climatic characteristics and location of the studied plots are shown in Table 1. Photosynthetically active radiation (PAR) was determined at nine points (15 m apart) in each studied plot with a Hansatech light meter (QRT1, Hansatech Instruments, Norfolk, UK) (Table 2).

We differentiated the following three types of invasion status in each plot: (1) ‘invaded patches’, which were stands invaded by *Acacia*, with the invader as the dominant species, consisting of adult trees with similar trunk density, (2) ‘non-invaded patches’, consisting of contiguous mature community (shrubland, oak forest and pine forest) with a predominantly native understory without *Acacia*, and (3) ‘transition patches’ found between the invaded and non-invaded patches (2 m wide), consisting of both small *Acacia* trees and native plants.

<table>
<thead>
<tr>
<th>Plot geographic coordinates</th>
<th>Type of threatened plant community</th>
<th>Main species</th>
<th>Origin</th>
<th>Soil classification</th>
<th>Climate</th>
<th>Altitude range (m)</th>
<th>Accumulated annual rainfall (mm)</th>
<th>Mean annual temperature range (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>29T5594678 Oak forest</td>
<td>Quercus robur L.</td>
<td>Native</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with a central European trend</td>
<td>590–610</td>
<td>814</td>
<td>8.1–19.1</td>
<td></td>
</tr>
<tr>
<td>29T5994670 Shrubland</td>
<td>Cytisus psilosepalus Sweet, Cytisus striatus (Hill) Rothm</td>
<td>Native</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with a central European trend</td>
<td>540–600</td>
<td>814</td>
<td>8.1–19.1</td>
<td></td>
</tr>
<tr>
<td>29T5684684 Shrubland</td>
<td>Erica cinerea L., Ulex gallii subsp. breoganii (Castrov. et Valdés Berm.) Rivas Mart. et al.</td>
<td>Native</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>85–300</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5684683 Oak forest</td>
<td>Quercus robur</td>
<td>Native</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>125–300</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5684683 Pine forest</td>
<td>Pinus pinaster Aiton</td>
<td>Naturalised</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>85–275</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5714687 Pine forest</td>
<td>Pinus pinaster</td>
<td>Naturalised</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>100–150</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5714687 Oak forest</td>
<td>Quercus robur</td>
<td>Native</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>100–300</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5714687 Pine forest</td>
<td>Pinus pinaster</td>
<td>Naturalised</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>90–250</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5684684 Shrubland</td>
<td>Halimum lasianthum (Lam.) Spach Ulex gallii subsp. breoganii</td>
<td>Native</td>
<td>Umbrisoils</td>
<td>Subhumid Mediterranean, with an Atlantic trend</td>
<td>125–300</td>
<td>1135</td>
<td>6.7–18.0</td>
<td></td>
</tr>
<tr>
<td>29T5284661 Pine forest</td>
<td>Pinus pinaster</td>
<td>Naturalised</td>
<td>Umbrisoils</td>
<td>European Atlantic</td>
<td>80–629</td>
<td>1424</td>
<td>9.4–19.6</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Photosynthetically active radiation (PAR) measured in invaded, transition and non-invaded patches

<table>
<thead>
<tr>
<th>Community type</th>
<th>PAR (µmol m⁻² s⁻¹)</th>
<th>Radiation reduction (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Invaded patch</td>
<td>Transition patch</td>
</tr>
<tr>
<td>Shrubland</td>
<td>63.6 ± 8.3</td>
<td>361.5 ± 72.5</td>
</tr>
<tr>
<td>Oak forest</td>
<td>9.5 ± 1.7</td>
<td>25.2 ± 4.6</td>
</tr>
<tr>
<td>Pine forest</td>
<td>41.6 ±9.8</td>
<td>92.5 ±20.7</td>
</tr>
</tbody>
</table>

Sampling of plant communities

To determine the effect of *Acacia* invasion on plant communities in each patch, the understorey vegetation, herbs, shrubs and immature and small tress, including vascular and non-vascular plant species, were sampled during late spring of 2007, because spring is the season with the highest number of plant species, including annuals. In each plot, we randomly established two transects (at least 20 m apart) from the invaded patch (2 m long) through the transition zone (2 m long) to the non-invaded patch (2 m long). In each transect, we sampled four quadrats (0.5 x 0.5 m) per patch-invasion status (invaded, transition and non-invaded) and per plant community (three plots from shrubland, three plots from oak forest and four plots from pine forest). The vegetation attributes recorded in each quadrat were (1) species richness, which was calculated as the number of all plant species, (2) plant density, obtained by adding the number of individual plants of each plant species per quadrat, (3) total plant cover (%), estimated as the area covered by all vascular and non-vascular plant species, and (4) species diversity calculated using Shannon's index (Shannon and Weaver 1949), computed as \( H' = -\sum (p_i \times \ln(p_i)) \), where \( p_i \) corresponds to the relative abundance of each species in the quadrat.

Statistical analyses

To test whether plant communities (shrubland, oak and pine forests) were similarly affected by *Acacia* invasion, we carried out generalised linear mixed models (GLMMs) via restricted maximum likelihood (REML). We analysed the data, considering quadrats nested within plots as variance components (random factors) and community type and patch-invasion status as explanatory variables (fixed factors). We considered the following response variables: species richness, plant density and total plant cover (assuming a Poisson error distribution with a log-link function) and species diversity (assuming binomial error distribution with a logit-link function). Differences between least-squares means were tested pairwise for each community, patch-invasion status or their interaction by using the DIFF option in the LSMEANS statement of the GLIMMIX procedure. The GLMMs were performed with the GLIMMIX procedure of SAS (SAS Statistical package 9.2, SAS Institute, Cary, USA).

To determine whether species composition varies according to the patch-invasion status, we performed a series of correspondence analyses (CAs) for the studied plant communities on the basis of the species abundance data. All of the plant species found were used to perform a global CA, because of the fact that the three plant communities shared several plant species. Individual CAs were then performed for each community type. The purpose was to provide a simple graphical interpretation of the species and invasion status in a two-dimensional space. Because this type of statistical analysis is sensitive to rare species that have a disproportionate effect on the ordination, we restricted our analysis to the 52 species that had at least four individuals. CAs were carried out using IBM-SPSS statistics 19, IBM Corporation, Armonk, USA). The level of significance was set at \( P = 0.05 \) for all analyses.

Results

Fifty-two plant species (including three unidentified species) were found in the different communities, of which 49 were vascular species and three were non-vascular species (Table S1, available as Supplementary Material). In all, 8 of 52 species (15%) appeared exclusively in the non-invaded patch, four (8%) were only in the invaded patch and five (10%) were restricted to the transition patch. The remaining 35 (67%) species were found in the three invasion statuses.

The GLMM found a significant effect of community type and patch-invasion status on species richness, but there was no interaction between these factors (Table 3, Fig. 1). The number of plant species per square metre was significantly higher in the shrubland than that in the oak and pine forests. The non-invaded patch had significantly higher richness species than did both the invaded and transition patches (Fig. 1).

Plant density was significantly affected by community type, patch-invasion status and the interaction between these two
Plant density was generally higher in the shrubland than in the other two forests. Within each community, plant density in the non-invaded patch was significantly higher than that in both transitional and invaded patches, whereas transition patches had higher density than did invaded patches (Fig. 2). The mean plant density value of the non-invaded patch was 3.1 and 4-fold higher than in the transitional and invaded patches, respectively. The same pattern, with a higher plant density in the non-invaded patches, was observed in the other two plant communities. The increase was 2.8 and 4.5 times for the oak forest, whereas it was 1.1 and 1.7 times for the pine forest.

Community type and patch invasion status had significant effects on total plant cover. There was also a significant interaction between these two factors (Table 3). Shrubland showed the highest values of total plant cover. In shrubland and oak forest, plant cover was higher in non-invaded than both transitional and invaded patches, whereas transition patches had higher plant cover than did invaded patches (Fig. 3). In the pine forest, total plant cover in the non-invaded and transitional patches was the same and significantly higher than that in the invaded patch (Fig. 3).

Species diversity was significantly affected by community type and only marginally affected by invasion status, although there was no interaction between these factors (Table 3). Species diversity was significantly higher in shrubland than in pine forest. There were no differences in species diversity between oak forest and the other two plant communities (Fig. 4). Species diversity was lower in invaded than in non-invaded patches.

The global CA performed to evaluate the relationship between species composition and patch-invasion status accounted for 26% of the total variance on Axis I, whereas 9% of the variation was explained by the second ordination axis (Fig. 5). The Chi-square value ($P \leq 0.001$) indicated that the patch invasion status exerted a strong influence on species composition. The CA diagram showed that the patches with different invasion status were clearly separated along the first dimension axis (Fig. 5). However, the majority of species did not seem to follow a clear trend in distribution related to invasion status, with few species associated with each patch-invasion status (Fig. 5). Analysing each community type individually, the patterns of plant species distribution were similar to that found in the global CA, with a high number of species shared by the three
Discussion

The presence of *Acacia* seems to affect the understorey vegetation of the communities we studied. *Acacia* apparently reduced the species richness, plant density and total plant cover in all of the communities and also tended to reduce the species diversity. Our results were similar to those from previous studies comparing vegetation in native patches of forests and closed patches invaded by *Acacia* (Fuentes-Ramírez et al. 2010; González-Muñoz et al. 2012), which showed negative effects of *Acacia* presence on native plant communities. In addition, *Acacia* can invade a wide range of plant communities (Lorenzo 2010). Although it is assumed that the invasion process of *Acacia* is facilitated by environmental disturbances (Lorenzo et al. 2010a), recent studies have shown that *Acacia* is able to invade communities, where no obvious alterations were observed (Lorenzo 2010; Fuentes-Ramírez et al. 2011; González-Muñoz et al. 2012). In the present study, plant communities did not seem recently disturbed (P. Lorenzo, pers. obs.). However, our results showed that the impact of *Acacia* invasion varied, depending on the variable and plant community that were analysed. These differences seem to be related to the initial properties of plant communities. In fact, we found differences for understorey vegetation features between the shrubland and woodland plant communities. Historical disturbances of plant communities, such as how long the invasion process lasts, may also be influencing the differences found between the community types (Marchante et al. 2008b).

Competitive interaction for space, light and nutrients between the invaders and native plants may be responsible for the negative effects of invasion (Jäger et al. 2009). Invasive plants often change light availability in a given community (Jäger et al. 2009), which affects community composition in the natural forest (Reinhart and Callaway 2006). In the current study, *Acacia* apparently resulted in a PAR reduction of at least 69.6% on the understorey across the communities studied. This reduced PAR in invaded patches was associated with lower species richness, plant density and total plant cover, suggesting that these changes in understorey communities were at least partially accounted for by a reduction in light availability brought about by *Acacia* invasion.

Another potential explanation for a reduction in the understorey species abundance is the presence of allelopathic compounds released by *Acacia* (Lorenzo 2010; Lorenzo et al. 2010b, 2010c). These allelochemicals have been shown to interfere with the germination, seedling growth and photosynthesis and respiration rates of model bioassay species, and agricultural and native understorey species (Carballeira and Reigosa 1999; Lorenzo et al. 2008; Lorenzo 2010). The allelopathic effects on understorey species were found throughout the year (Lorenzo et al. 2010b, 2010c), although the strongest effects occur when *Acacia* blooms, a period that coincides with the germination of the majority of the autochthonous understorey species (Carballeira and Reigosa 1999).

Changes in the native plant–soil mutualistic interactions could be a further source of species displacement. It has been previously

![Fig. 4.](image1)

Effects of (a) community type and (b) invasion status on the species diversity in studied communities threatened by the invasion of *Acacia dealbata*. Bars are means ± s.e. Different letters indicate statistical significance at *P* = 0.05 level. Letters in parentheses indicate marginal statistical differences (*P* = 0.07).

![Fig. 5.](image2)

Species distribution obtained with the global correspondence analysis (*χ*², *P* = 0.000) carried out with plant species found in all studied plant communities. Species within the circles indicate a strong relationship between these species and each sampling patch, whereas the species outside are weakly related with all studied patches.
reported that the invasion by *Acacia* can alter the soil-microbe communities of shrublands and grasslands (Lorenzo et al. 2010). It is well documented that invasive species modify the soil microbiota (e.g. Reinhart and Callaway 2006; Jordan et al. 2008; Rodríguez-Echeverría et al. 2009; Sanon et al. 2009), especially by establishing positive feedbacks that disrupt mutualistic associations between native symbionts and seedlings of native plants (Inderjit and van der Putten 2010).

We found altered species distribution among different patch-invasion statuses. Whereas shrubs and herbs were predominant in the non-invaded patches, seedlings of *Acacia* and native woody species were found in invaded patches, albeit with a relatively small shrub typology. The lower number of herb species in invaded patches could indicate that herbaceous species are more sensitive to tree invasion than are other plant types, as found by Jäger et al. (2007, 2009). In the CAs, we can see that a few particular species were associated with a particular patch-invasion status. This fact suggests that these species require the specific environmental conditions that occur in each invasion status where they appear, and that some species could be replaced by others as the invasion of *Acacia* progresses.

The alteration of soil-nutrient dynamics as a result of the introduction of exotic species may drive changes in community composition in the invaded range (Ehrenfeld 2003). *Acacia* modifies soil characteristics by increasing soil nutrient content, mainly nitrogen, carbon, organic matter and exchangeable phosphorous (Lorenzo et al. 2010; González-Muñoz et al. 2012). These changes could cause the disappearance of some species adapted to pre-invasion conditions, as some species are more easily excluded from invaded communities than are others (Standish et al. 2001; Stinson et al. 2007). In the current study, the endemic-native *Daboecia cantabrica* (Ericaceae) was found only in the non-invaded patches. This may be indicating that this species is sensitive to the conditions caused by the invasion, and is displaced from invaded patches and confined to patches without *Acacia*. These results agree with those of González-Muñoz et al. (2012), because that study explored the replacement of native plants by exotic species under *Acacia* canopies. Therefore, as resident species disappeared under the *Acacia* canopy, it seems quite likely that local extinctions could occur in the future as the invasion progresses, as suggested by Jäger et al. (2009).

Conclusions

The present study has provided evidence for the adverse effects of a woody plant invader, *Acacia dealbata*, on understorey plants of different community types. *Acacia* seemed to displace native species, including the endemic *Daboecia cantabrica*, and reduce the presence of understorey native species in invaded patches in all of the communities we studied. The results obtained in the transition patch showed that these changes are gradual and depend on the type of community. The results of the present study suggested that natural communities are sensitive to invasion by *Acacia* and that immediate action is needed to protect and maintain the diversity of plant communities, especially in native communities.

Supplementary material

Supplementary material showing the characteristics of species found in the understoreys of plant communities threatened by *Acacia dealbata* invasion is available at the Journal’s website.

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References


