



Invasiveness, ecological impacts and control of acacias in southwestern Europe – a review

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Abstract. The most prolific acacias in southern Europe (*Acacia dealbata*, *A. melanoxylon* and *A. longifolia*) are rapidly spreading in its westernmost area: Portugal and NW Spain, where congeners with invasion potential are already established. We performed a bibliographic search of acacia invasions in southern Europe and used spatial data on acacia distribution and abiotic parameters in Iberia to check the influence of abiotic factors on acacia invasion. According to our results, in Iberia *A. dealbata* and *A. melanoxylon* seem limited by high soil pH ($\text{pH}_{\text{CaCl}_2} > 5.5$), frequent frosts (> 21 to 40 d yr^{-1}) and low annual precipitation (< 500 to 1000 mm); data were inconclusive for *A. longifolia*, while *A. saligna* prefers neutral soils in the driest and warmest areas. The percentage of area occupied by *A. dealbata* and *A. melanoxylon* increases significantly with the percentage of burnt surface. In the literature, acacias' invasiveness is usually attributed to their high resprouting and seeding capacity and to native exclusion through their allelopathic potential; symbiotic promiscuity with rhizobia; high environmental plasticity; and adaptation to burnt, cleared and resource-poor land. However, it is unknown how acacias became so invasive in western Iberia, where native Fabaceae shrubs with similar ecological traits (and invaders outside their natural range) are abundant. Invasive acacias can modify fire and water regimes, above-ground biodiversity, and topsoil characteristics (microbial communities, pH, organic matter and macronutrients levels); nevertheless, sound comparisons with mature stands of Iberian legumes for these and other soil properties (N fluxes, micronutrients) are lacking. As several acacias outcompete Iberian Fabaceae shrubs partly thanks to enemy release, the introduction of biocontrol agents (as for *A. longifolia* in Portugal) can be useful for invasion control.

1 Introduction

Acacia species belong to the subfamily Mimosoideae and family Fabaceae and include roughly 1300 species (Maslin, 2001). Around 1012 of these species are native to Australia and belong to the subgenus *Phyllodineae* (Richardson and Rejmánek, 2011), presenting traits that make them more invasive than their African relatives (Low, 2012). A third of the Australian acacias are exotic (i.e. present outside their native distribution; Richardson et al., 2011), and 24 of these species are invasive (Richardson et al., 2015). *Acacia* species outside their natural range whose introduction and posterior spread implies an environmental impact can be considered invasive (European Parliament and Council, 2014). Casual and naturalized *Acacia* species (i.e. able to establish new self-

perpetuating populations; Richardson et al., 2000) are phylogenetically distant (Yessoufou et al., 2016), and the invasive species form small clusters in the phylogeny (Miller et al., 2011). The *Acacia* genus is one of the most invasive tree genera (Richardson and Rejmánek, 2011), particularly in disturbed environments (Fuentes-Ramírez et al., 2011; Morris et al., 2011; Hernández et al., 2014) and Mediterranean climates (Carvalho et al., 2010; Morris et al., 2011; Lazzaro et al., 2014), which are usually linked to a scarcity of water and nutrients (Morris et al., 2011).

Acacia species have industrial (tannin and pulp production), agroforestry and ornamental uses (Griffin et al., 2011). They were introduced for economic purposes or for rehabilitation of degraded land, but subsequent invasion has resulted in significant economic and environmental impacts (as cal-

culated in De Wit et al., 2001) that outweigh the economic benefits (Low, 2012; Duponnois et al., 2013; Richardson et al., 2015). However, their use is expected to increase, which could entail a further expansion in their distribution (Griffin et al., 2011). This highlights the importance of carrying out a risk assessment before introducing new species (Low, 2012; Richardson et al., 2015).

In Europe, *Acacia* species tend to colonize sensitive habitats such as dunes, riverbanks and natural reserves (Lorenzo et al., 2010a). Moreover, invasion of protected areas by *Acacia* spp. is predicted to increase according to some species distribution models, facilitated by a higher connectivity of protected areas (Vicente et al., 2013). In southern European countries, up to 14 *Acacia* species, 8 of them with invasive potential, have been introduced (Lorenzo et al., 2010a). The most prolific at present are *A. dealbata* Link, *A. melanoxylon* R. Br. and *A. longifolia* (Andrews) Willd (Lorenzo et al., 2010a), although other congeners are potential invaders (Table 1).

With 13 introduced species (Table 1), half of which are potential invaders and 4 of which are already invading wide zones including most of the natural and national parks (Tables 2 and 3), western Iberia (Portugal, NW Spain) is by far the European region most widely invaded by *Acacia* species although the mechanisms underlying the invasion process are not fully understood (e.g. how they are able to outcompete Iberian Fabaceae shrubs). Therefore, the purpose of this article is to review the available information on *Acacia* species invasions which can help (a) to explain why these exotic plants are so successful in western Iberia; (b) to determine the current state of knowledge and to identify knowledge gaps about their effects on the invaded ecosystems; and (c) to discuss the proposed methods for *Acacia* spp. control and subsequent restoration of the invaded areas, in terms of efficiency and limitations.

2 Methods

An exhaustive bibliographic search was carried out with Scopus, Web of Science and Google Scholar to find scientific and technical articles as well as governmental documents on *Acacia* species invasions in southern Europe, with a special focus on western Iberia. For this purpose, the following keywords were combined with Boolean operators (AND, OR) in the searches: *acacia**, *biodiversity*, *climate*, *control*, *Croatia*, *dispersal*, *distribution*, *effect**, *enemy*, *eradication*, *Europe*, **fire**, *France*, *Greece*, *Iberia*, *impact**, *invas**, *Italy*, *Portugal*, *soil**, *Spain* and *water*. These keywords included the most invaded countries in Europe by acacias, as well as abiotic and biotic factors that could potentially affect *acacia* invasiveness or be affected by the invasion and control methods.

To determine the influence of some abiotic factors on *Acacia* spp. invasion, we focused on the Iberian Peninsula, lo-

cated in SW Europe (Fig. 1). It comprises continental Portugal and Spain with an extent of almost 600 000 km² and large high- or medium-elevation areas in the centre and the north (Loidi, 2017). The peninsula includes two macrobioclimates – Mediterranean, in almost 80 % of the area, and Temperate, mostly in the north (Rivas-Martínez et al., 2017). Its flora comprises more than 6000 species, around 20 % of them endemic and 12 % exotic (Aedo et al., 2017).

The distributions of the most widespread species in Spain (UTM 10 km × 10 km grid from Sanz-Elorza et al., 2004) and Portugal (presence of *Acacia* genus in a 10 km × 10 km grid; Fernandes et al., 2013) were compared with the most detailed data available on soil pH (CaCl₂; 5 km resolution; a geostatistical framework based on regression-kriging was used; European Commission, 2010), fire incidence (25 km × 25 km resolution; data from the European Forest Fire Information System; Borrelli et al., 2016), and frost risk and annual precipitation (data collected from 1971 to 2000; AEMET-IMP, 2011). These two maps of *acacia* presence used for the spatial analysis were chosen on the grounds that they were the ones available with the same resolution (10 km × 10 km grid) and covered the entire continental area of Spain and Portugal. However, as the *acacia* map for Portugal did not differentiate between *Acacia* species, and to help interpretations of results, we overlapped the Portugal map with a second *acacia* layer for Portugal (Invasive Plants in Portugal, 2019; Fig. 1) that differentiated the species, although with a lower resolution (province level).

All the aforementioned data were georeferenced and converted to polygons with ArcGIS 9.2. Each colour of the abiotic layers that were georeferenced was attributed to the corresponding value in the original map in the attribute table. These numeric data from abiotic variables were discretized in equal-width intervals. Then, using the “Intersect” function, the overlapping areas (in square kilometres) between each *Acacia* species presence and the different levels of each abiotic factor were calculated. For each *Acacia* species, its presence frequency (percentage of occupied area) for each interval of an abiotic factor was calculated as

$$f = \frac{A_i}{A_{sp}}, \quad (1)$$

where A_i is the area of the intersect and A_{sp} is the total area of the species. The significance of the differences between presence frequencies was tested with the arcsine test of equality of percentages (Sokal and Rohlf, 1979).

Results for the Iberian Peninsula were presented without differentiated *acacia* species (*Acacia* spp.), while results for the different species were based only on the Spanish data (due to the limitations in Portugal *acacia* data specified before).

Table 1. Origin and status of the *Acacia* species registered in Europe in the wild as invasive (I), established or naturalized (E; as in Richardson et al., 2000), non-established (NE), or unknown (U).

Species	Origin	Status	European country (<i>island</i>)
<i>A. baileyana</i> F. Muell.	Australia ¹	E NE	Spain ⁴ , France (<i>Corsica</i>) ⁴ , Portugal (<i>Madeira</i>) ⁴ Portugal ⁴ , France ^{4,5}
<i>A. cultriformis</i> A. Cunn. ex G. Don	Australia ²	NE	Portugal ⁴ , France ⁵
<i>A. cyclops</i> A. Cunn. ex G. Don fil.	Australia ¹	E NE	Portugal ⁴ , Spain ⁴ Portugal (<i>Madeira</i>) ⁴ , France ⁵
<i>A. dealbata</i> Link	Australia ¹	I E NE	Portugal ⁶ , Spain ⁷ , France ⁵ Portugal (<i>Azores, Madeira</i>) ⁴ , Italy (continental, <i>Sardinia</i>) ⁴ Spain (<i>Balearic Islands</i>) ⁴ , France (<i>Corsica</i>) ⁴
<i>A. farnesiana</i> L. Willd.	Neotropical ¹	E NE U	Portugal (<i>Azores, Madeira</i>) ⁴ , France ⁴ , <i>Cyprus</i> ⁴ Spain ⁴ , Italy (<i>Sardinia</i>) ⁴ , Greece ⁴ France (<i>Corsica</i>) ⁴
<i>A. longifolia</i> (Andrews) Willd.	Australia ¹	I E NE U	Portugal ⁶ Portugal (<i>Azores, Madeira</i>) ⁴ , Spain ⁴ , Italy ⁴ Spain (<i>Balearic Islands</i>) ⁴ , France ⁵ , Italy (<i>Sardinia</i>) ⁴ France (<i>Corsica</i>) ⁴
<i>A. mearnsii</i> De Wild.	Australia ¹	I E	Portugal ⁶ , France ⁵ , Italy ⁵ Spain ⁴
<i>A. melanoxylon</i> R. Br.	Australia ¹	I E NE	Portugal ⁶ Portugal (<i>Azores, Madeira</i>) ⁴ , Spain ⁴ , France ^{4,5} , UK ⁴ Italy (<i>Sardinia, Sicily</i>) ⁴
<i>A. pycnantha</i> Benth.	Australia ¹	I E NE U	Portugal ⁶ Spain ⁴ Portugal (<i>Madeira</i>) ⁴ , Italy (continental, <i>Sardinia</i>) ⁴ France ⁴
<i>A. salicina</i> Lindley	Australia ³	NE	France ⁵
<i>A. saligna</i> Labill. H. L. Wendl.	Australia ¹	I E NE U	Portugal ⁶ , France ⁵ Portugal (<i>Azores</i>) ⁴ , Spain (continental, <i>Balearic Islands</i>) ⁴ , Italy (continental, <i>Sardinia, Sicily</i>) ⁴ , Greece ⁴ , <i>Cyprus</i> ⁴ <i>Malta</i> ⁴ France (<i>Corsica</i>) ⁴
<i>A. retinodes</i> Schltld.	Australia ¹	I E NE U	Portugal ⁶ Spain ⁴ , France ^{4,5} , Italy ⁴ , UK ⁵ , <i>Cyprus</i> ⁵ Spain (<i>Balearic Islands</i>) ⁴ , Italy (<i>Sardinia</i>) ⁴ Portugal (<i>Azores</i>) ⁵ , France (<i>Corsica</i>) ⁴
<i>A. verticillata</i> (L'Hér.) Willd.	Australia ¹	E NE	Portugal (continental, <i>Madeira</i>) ⁴ Spain ⁴ , France ⁸

¹ Sheppard et al. (2006). ² ANPSA (2012). ³ MAPAMA (2013). ⁴ DAISIE Project (2016; Delivering Alien Species Inventories for Europe). ⁵ ISSG (2016). ⁶ Ministério do Ambiente (1999). ⁷ MAGRAMA (2013). ⁸ Muséum National d'Histoire Naturelle (2016).

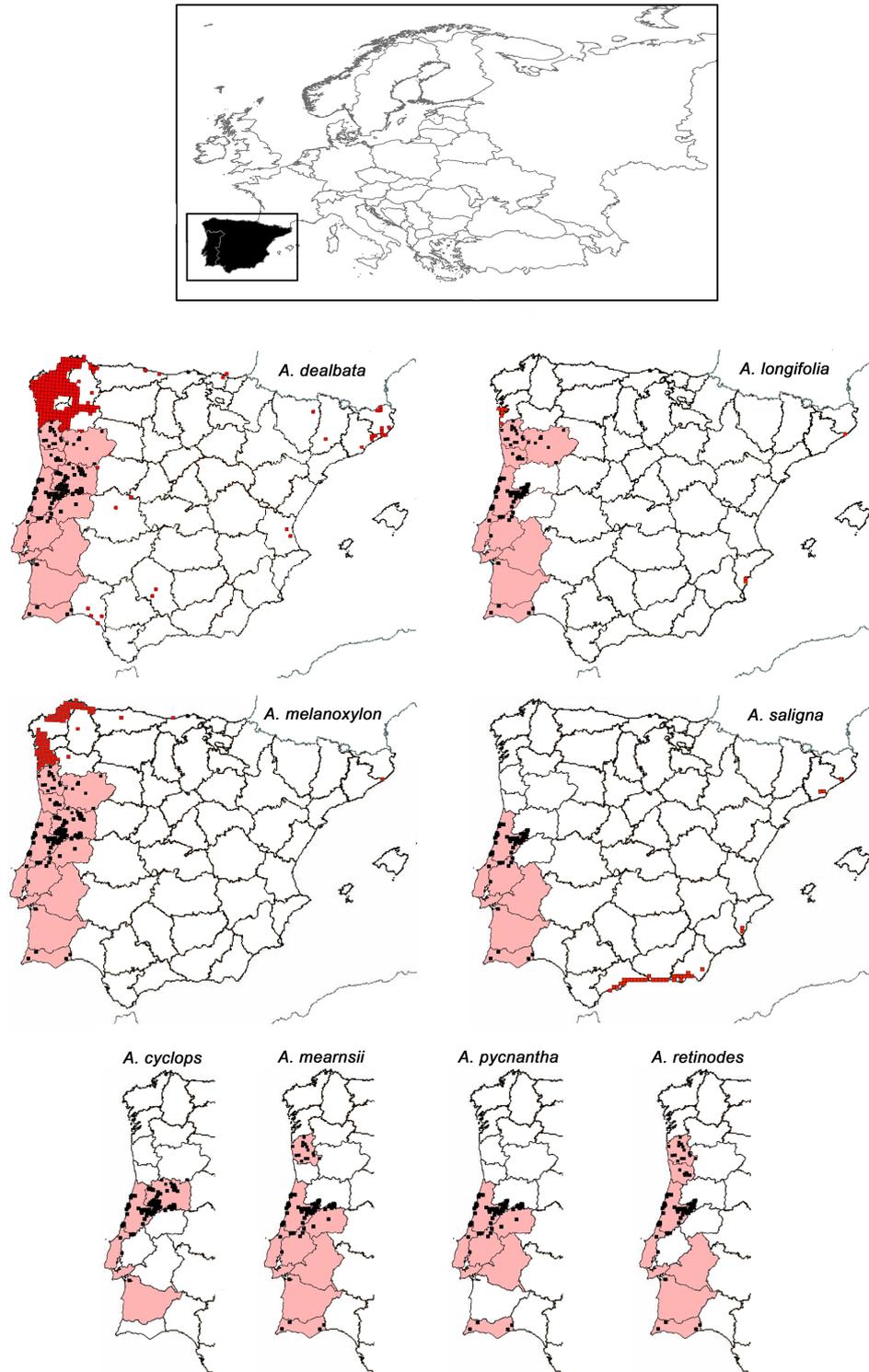


Figure 1. Distribution of invasive Australian *Acacia* species in the Iberian Peninsula. Data of the distribution of each *Acacia* species in Spain ($10\text{ km} \times 10\text{ km}$ UTM red squares) are taken from Sanz-Elorza et al. (2004). For Portugal we did not find published such detailed information at a species level; therefore, for a given species its presence–absence data per province (invaded provinces in pink; adapted from Invasive Plants in Portugal, 2019) are combined with data of *Acacia* genus presence on a more detailed scale ($10\text{ km} \times 10\text{ km}$ black squares; adapted from Fernandes et al., 2013). At the top of the figure is a map of Europe with the Iberian Peninsula (continental Portugal and Spain) highlighted in black.

Table 2. Invasive Australian acacias in western Iberia: date and purpose of the introduction, habitats preferentially invaded, and current situation.

	<i>A. dealbata</i>	<i>A. melanoxylon</i>	<i>A. longifolia</i>	<i>A. saligna</i>
Introduction in Portugal	19th century (second half) ¹	19th century (first half) ⁵	19th century (second half) ⁷	–
Introduction in NW Spain	20th century ²	20th century (first half) ⁶	20th century (second half) ⁶	–
Purpose of introduction	Stabilize railway margins, guides in vineyards ^{2,3}	Ornamental, dune fixation, improve <i>Eucalyptus</i> production ⁶	Ornamental, dune fixation ⁷	Ornamental, control dune erosion ⁹
Preferential habitat of invasion	Forest ecosystems ²	Riparian forests, <i>Eucalyptus</i> plantations ⁴	Dunes, pine plantations ⁸	Coastal warm arid areas ⁹
Current situation	Expansion (2500 ha yr ⁻¹ in NW Spain) ⁴	Expansion (3100 ha yr ⁻¹ in NW Spain) ⁴		

¹ Fernandes (2012). ² Vazquez-de-la-Cueva (2014). ³ Lorenzo et al. (2010a). ⁴ Hernández et al. (2014). ⁵ Heywood and Ball (1968). ⁶ Sanz-Elorza et al. (2004). ⁷ Neto (1993). ⁸ Fernandes et al. (2015). ⁹ Marchante et al. (2014).

Table 3. Protected areas in western Iberia invaded by Australian *Acacia* species. Key: N, naturalized; P, present; I, increasing; CU, control unsuccessfully attempted; NB, nearby populations.

Protected area	<i>A. dealbata</i>	<i>A. melanoxylon</i>	<i>A. longifolia</i>	<i>A. saligna</i>	<i>Acacia</i> sp.
Atlantic Islands of Galicia National Park ^{1–3}	–	P, N	P, N	–	–
Picos de Europa National Park ⁴	–	P, CU	–	–	–
Peneda-Gerês National Park ^{5–8}	P, I, CU	P, I, CU	–	–	–
Baixa Limia – Serra do Xurés Natural Park ^(personal observation)	P, I	P, I	–	–	–
Fragas do Eume Natural Park ^{9–10}	NB	P	–	–	–
Monte Aloia Natural Park ¹¹	P, I	P, I	–	–	–
Alvão Natural Park ¹²	P	–	–	–	–
Montesinho Natural Park ¹³	P	P	–	–	–
Northern Littoral Natural Park ¹⁴	–	–	P	–	–
Southwest Alentejo and Vicentine Coast Natural Park ¹⁴	P	–	–	P	–
Sintra-Cascais Natural Park ¹⁴	–	–	–	–	P

¹ Bañares et al. (2004). ² GEIB (2006). ³ Fernández-Bouzas et al. (2005). ⁴ TRAGSA (2009). ⁵ Fernandes-Fontes and Bento-Gonçalves (2005). ⁶ Viana and Aranha (2008). ⁷ ICNB (2011). ⁸ Fernandes et al. (2013). ⁹ Pulgar-Sañudo et al. (2006). ¹⁰ Xunta de Galicia (2014). ¹¹ Lorenzo-Fernández et al. (2000). ¹² Coelho and Alves (2004). ¹³ Gonçalves-Aguiar (2000). ¹⁴ ICNF (2016).

3 Invasiveness of *Acacia* species in western Iberia

3.1 Abiotic factors influencing establishment–spread success

3.1.1 Results of the spatial analysis

All four abiotic factors considered in the spatial analysis (burnt area, soil pH, frost days per year, precipitation) affected acacia presence in the Iberian Peninsula (Table 4). Our results showed that the percentage of occupied area of *A. dealbata* and *A. melanoxylon*, but not that of *A. saligna* and *A. longifolia*, increases significantly with the percentage of burnt surface in the 25 km × 25 km grids, especially in those over the threshold of 4 % of burnt surface (Table 4, Figs. 1 and 2). Both *A. dealbata* and *A. melanoxylon* are by far more frequent in soils with pH_{CaCl2} < 5.5, while *A. saligna* seems to prefer soils with pH_{CaCl2} = 5.5–7.0, and no conclusive data were obtained for *A. longifolia* (Table 4, Figs. 1 and 2).

The percentage of occupied area of *Acacia* species decreases progressively with the number of frost days per year, but the sensitivity to frost was the lowest in *A. dealbata*, intermediate in *A. melanoxylon* and the highest in *A. saligna*; again, the available data were not conclusive for *A. longifolia* (Table 4). Whereas the highest percentage of occupied area of *A. saligna* was found in the driest areas (precipitation < 500 mm yr⁻¹), *A. dealbata* and *A. melanoxylon* were much more frequent in the rainiest areas (precipitation > 1000 mm yr⁻¹; Table 4, Figs. 1 and 2), although these results must be interpreted with care due to the low resolution of the precipitation layer.

3.1.2 Soil characteristics

In both France and Croatia, acacia spread is limited by high soil pH (Kull et al., 2011; Giovanetti et al., 2014), as we found in our results in the Iberian Peninsula, especially for

Table 4. *Acacia* presence frequency (percentage of occupied area) depending on site characteristics. For each species and site characteristic, different letters show significant differences ($a > b > c$, $p < 0.05$; test for equality of percentages of Sokal and Rohlf, 1979).

	<i>Acacia</i> spp. ¹	<i>A. dealbata</i> ²	<i>A. melanoxylon</i> ²	<i>A. saligna</i> ²	<i>A. longifolia</i> ²
Burnt area³					
< 1.6 %	4.24 ^c	2.87 ^c	1.16 ^b	0.75 ^a	0.00 ^a
1.6 %–4 %	5.07 ^{bc}	3.81 ^{bc}	0.04 ^b	0.45 ^a	0.05 ^a
4 %–12 %	10.15 ^{ab}	10.24 ^{ab}	2.84 ^{ab}	0.65 ^a	1.36 ^a
> 12 %	16.00 ^a	20.20 ^a	11.57 ^a	0.00 ^a	0.00 ^a
pH (CaCl₂)⁴					
< 5.5	12.02 ^a	11.59 ^a	4.72 ^a	0.01 ^b	0.31 ^a
5.5–7.0	1.44 ^b	0.63 ^b	0.01 ^b	1.26 ^a	0.05 ^a
> 7.0	0.91 ^b	0.16 ^b	0.00 ^b	0.76 ^{ab}	0.12 ^a
Frosts⁵					
< 10 d yr ⁻¹	9.72 ^a	7.35 ^a	5.09 ^a	3.02 ^a	0.64 ^a
11–20 d yr ⁻¹	9.17 ^a	6.44 ^a	2.69 ^{ab}	0.64 ^{ab}	0.17 ^a
21–40 d yr ⁻¹	6.23 ^a	4.82 ^a	0.74 ^{bc}	0.08 ^b	0.06 ^a
> 40 d yr ⁻¹	1.62 ^b	1.49 ^b	0.10 ^c	0.08 ^b	0.00 ^a
Precipitation⁵					
< 500 mm yr ⁻¹	1.04 ^c	0.05 ^c	0.00 ^b	0.91 ^a	0.07 ^a
500–1000 mm yr ⁻¹	3.02 ^b	1.27 ^b	0.12 ^b	0.51 ^a	0.01 ^a
> 1000 mm yr ⁻¹	24.87 ^a	20.41 ^a	9.16 ^a	0.00 ^a	0.74 ^a

¹ Data from Portugal (Fernandes et al., 2013) and Spain (Sanz-Elorza et al., 2004; see Fig. 1). ² Data from Spain (Sanz-Elorza et al., 2004; see Fig. 1). ³ Calculated on the basis of data from Borrelli et al. (2016), adapted (see Fig. 2). ⁴ Data from the *Soil pH in Europe* map (European Commission, 2010), adapted (see Fig. 2). ⁵ Data from the Iberian climate atlas, 1971–2000 (AEMET-IMP, 2011), adapted (see Fig. 2).

A. dealbata and *A. melanoxylon*, neither of which are present in soils with neutral pHs. However, care should be taken with our results due to the limited resolution of the available soil pH layer at the continental scale we used.

3.1.3 Climate

As Kull et al. (2011) found for France, in the Iberian Peninsula acacia presence is limited by the number of frost days per year (Table 4, Figs. 1 and 2). Richardson et al. (2011) consider that *Acacia* distribution can potentially expand to other areas that meet the species' climate requirements. Climate change can modify the phenology of invasive species (Morais and Freitas, 2015) and can also increase their invasive potential (Morris et al., 2011). Schortemeyer et al. (2002) found that when Australian acacias are not limited in water and nutrient resources, an increase in CO₂ concentration could enhance the growth of most of the studied species (including *A. dealbata* and *A. melanoxylon*) and increase N₂ fixation (in *A. melanoxylon* among others but not in *A. dealbata*). However, water deficiency due to the variation in climate parameters could favour native species over *Acacia* invasive species, as predicted for *A. dealbata* (González-Muñoz et al., 2014). In NW Iberia, regional cli-

mate change models for the second half of the 21st century predict a temperature increase of 2–3 °C, especially in summer and interior areas, and a decrease in precipitation, especially in spring and summer (Álvarez et al., 2011). Therefore, integrated studies at a regional level on the effects of CO₂ increase, changes in temperature (including frost risk) and water availability are needed to provide reliable projections of the effect of climate change in these invasive species. In such projections, the higher variability in environmental conditions derived from global change must also be taken into account (Parepa et al., 2013).

3.1.4 Disturbances

Acacias present high phenotypic plasticity to environmental factors (Pohlman et al., 2005; Fuentes-Ramírez et al., 2011; Vazquez-de-la-Cueva, 2014), which has been seen to be especially important in other invasive species in coping with disturbances (Daehler, 2003), although it does not always increase competitiveness in limited-resource or high-stress habitats (Davidson et al., 2011). Acacia expansion benefits from disturbances such as vegetation clearance carried out in agricultural areas, at roadsides or in abandoned fields (Sanz-Elorza et al., 2004), as well as in burnt areas, where

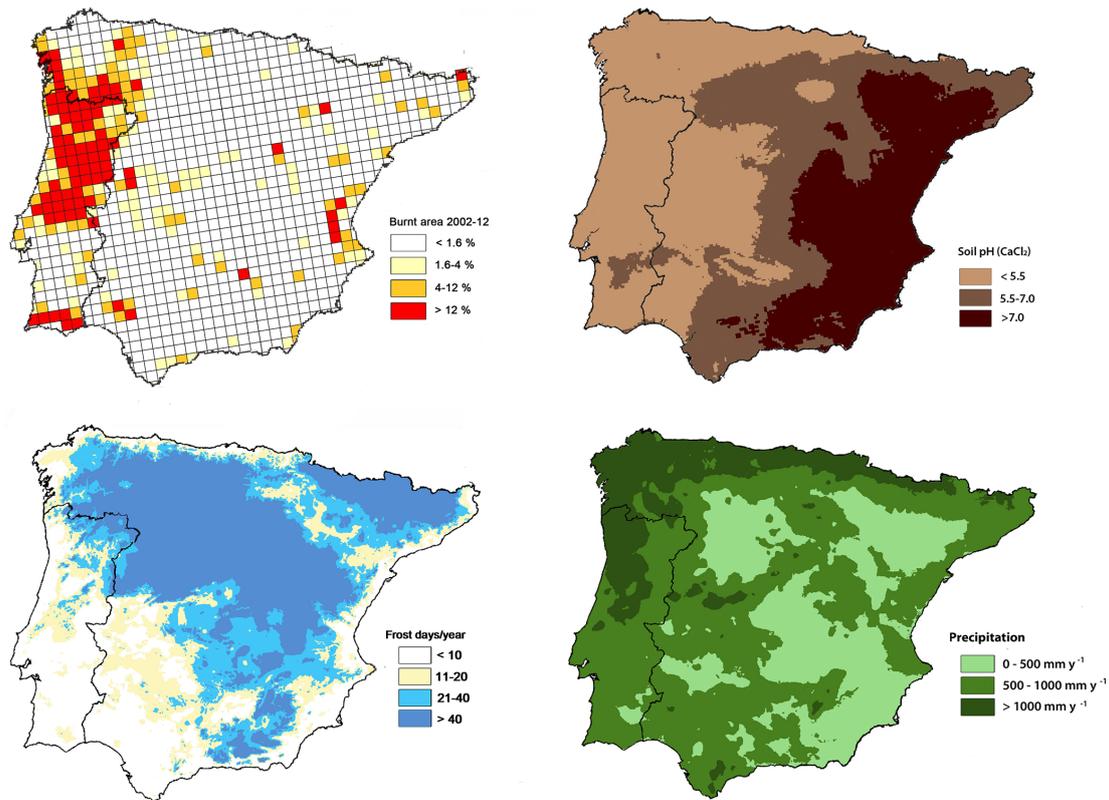


Figure 2. Maps of the Iberian Peninsula for several abiotic characteristics related to *Acacia* spread: burnt area during the period 2002–2012, adapted from Borrelli et al. (2016); soil pH, adapted from European Commission (2010); frost risk and annual precipitation, both adapted from AEMET-IMP (2011).

a transitory increase in nutrient concentration is coupled to a decrease in nutrient demand due to the absence of vegetation (Keeley et al., 2005). Moreover, the clearing of vegetation can facilitate the establishment of the light-demanding *A. dealbata* (Sanz-Elorza et al., 2004). Changes in the interactions between plant and soil microorganisms produced by wildfires can increase competitiveness of invasive species over natives, as seen for *A. longifolia* in a Portuguese dune environment, which could be due to the decrease in soil-specific pathogens (Giovanetti et al., 2014). Wildfires have been related to the expansion of *A. dealbata*, *A. melanoxylon* and *A. longifolia* in southern Europe (Marchante et al., 2003; Lorenzo et al., 2010a; Silva and Marchante, 2012; Hernández et al., 2014; Vazquez-de-la-Cueva, 2014). In western Iberia, where the highest fire incidence in Europe is recorded (Borrelli et al., 2016), *Acacia dealbata* and *A. melanoxylon* were found to be favoured by high fire incidence.

The high invasiveness of *A. dealbata*, *A. melanoxylon* and *A. longifolia* in burnt areas has been related to their ability to exclude natives through (a) a massive bank of pyrophyte seeds that allow them to regenerate by germination after a disturbance (Richardson and Kluge, 2008; Le Maitre et al., 2011; Wilson et al., 2011), (b) vigorous resprouting (Shepherd et al., 2006) and (c) fast growth rates (as seen in *A.*

dealbata, May and Attiwill, 2003). To these advantageous traits, other acacia capacities can be added such as fixing N_2 (Lorenzo et al., 2010a; Morris et al., 2011), with high symbiotic promiscuity (Rodríguez-Echeverría et al., 2003), forming dense monospecific stands (Lorenzo et al., 2010b; Werner et al., 2010), and allelopathic potential (Carballeira and Reigosa, 1999; Lorenzo et al., 2010a, 2011; Hussain et al., 2011; Aguilera et al., 2015). All the aforementioned abilities are also present in several native shrubs (*Ulex*, *Pterospartum* and *Cytisus* genera) that have been largely favoured by fires in NW Iberia for at least 6000 years (Kaal et al., 2011). Therefore, it is an unsolved question how *A. dealbata*, *A. melanoxylon* and *A. longifolia* became so invasive in NW Iberian ecosystems, especially taking into account that some Iberian *Ulex* (Leary et al., 2006; Perry et al., 2014) and *Cytisus* (Parker, 2000) species are considered dangerous invaders in other countries throughout the world, up to the point of displacing some *Acacia* species after disturbances such as fire in Australia (Fogarty and Facelli, 1999).

In burnt South African fynbos and other Mediterranean ecosystems, a decline in native legume abundance has been recorded once the post-fire flush of available phosphorus is exhausted, presumably due to a low uptake capacity of the less accessible phosphorus pools (Power et al., 2010). *Ac-*

According to these authors, despite being also legumes, invasive Australian acacias do not show such a decline after fire, possibly because they have broader root and mycorrhizal systems. Nevertheless, in NW Spain native Fabaceae species such as *U. europaeus* can widely dominate post-fire secondary succession for at least 10 years in some areas (Casal, 1987), pointing again to the intriguing ability of some Australian acacias to invade burnt areas in western Iberia.

Despite multiple *Acacia* adaptations to fire, Vicente et al. (2019) found that climatic factors (for seedlings, saplings and small trees), bedrock and land cover (for medium to large trees) were better predictors of *A. dealbata* invasion in northern Portugal than fire regime.

The high invasiveness of Australian acacias in western Iberia (Portugal and NW Spain; Sanz-Elorza et al., 2004; Fernandes et al., 2013) contrasts with the rest of the Iberian Peninsula and other southern European countries, where they do not present such invasive behaviour or they are more localized (e.g. in acidic soils of Mediterranean France; see Kull et al., 2011). Besides the fact that more species have been introduced there, their invasiveness in western Iberia is partially related to several abiotic factors (Table 4).

3.2 Biotic factors influencing establishment and spread success

3.2.1 Adaptations to low resource availability

Several traits of acacias can help to explain their success as invasive species in western Iberia and elsewhere. In resource-poor environments, Australian acacias show competitive abilities such as an important allocation of resources to roots (Morris et al., 2011); N₂ fixation (Marchante et al., 2003); mycorrhizal associations (Belay et al., 2013); and heteroblasty in some species, such as *A. melanoxylon*, with phyllodes in the adult stage that increase plant tolerance to drought (Brodrigg and Hill, 1993) and nutrient conservation (Morris et al., 2011). *Acacia longifolia* success in low-resource environments has been associated with high nutrient acquisition rates even under drought conditions (Werner et al., 2010). Although legumes may have difficulties in encountering compatible rhizobia (Parker, 2001), some invasive *Acacia* species show symbiotic promiscuity (Parker, 2001; Rodríguez-Echeverría, 2010; Rodríguez-Echeverría et al., 2011). For example, in low-nutrient dune soils in Portugal, *A. longifolia* can be more efficient at associating with rhizobia than native species are; this has been proposed as an important factor in invasion success (Rodríguez-Echeverría et al., 2009). Nevertheless, a high symbiotic promiscuity has also been reported for the N₂-fixing Iberian *Cytisus*, *Genista* and *Retama* shrubs (Rodríguez-Echeverría et al., 2003), a trait that would help to explain the invasive ability of *Cytisus scoparius* (L.) Link in North America, Australia and New Zealand, despite this species being displaced by some Australian acacias in western Iberia.

3.2.2 Reproductive traits

Acacias' high colonization capacity is related to their vegetative reproduction (Lorenzo et al., 2010a; Fuentes-Ramírez et al., 2011) and their high investment in flower production, especially for *A. dealbata* (Correia et al., 2014). Mixed pollination (through honeybees and wind) in *A. longifolia* has been proposed as a strategy the species uses to succeed in Portugal coastal ecosystems (Giovanetti et al., 2018). Moreover, invasive *Acacia* species are able to rapidly build a massive and persistent seed bank (Gibson et al., 2011; Le Maitre et al., 2011; Vazquez-de-la-Cueva, 2014) owing to a short generation time, long fruiting period, large seed number, small seed size, and prolonged and high seed viability (Alpert et al., 2000; Table 5). Propagule pressure after disturbances is an important facilitator of invasion for some exotic species (Catford et al., 2012). Nevertheless, it must be highlighted that, despite being displaced by *Acacia* spp. in western Iberia, several Iberian Fabaceae shrubs, such as *Cytisus scoparius* and *Ulex europaeus* L., share all these reproductive traits, which have been considered important factors for their high invasiveness in North America, Australia and New Zealand (Richardson and Hill, 1998; Bossard, 2000; Clements et al., 2001; Hill et al., 2001).

Long-distance endozoochory of seeds by birds has been found in South Africa for *A. cyclops* (Mokotjomela et al., 2015) and *A. melanoxylon* (Global Invasive Species Database, 2016) and for the latter species also in Portugal (Heleno et al., 2011). However, zoochory in acacia species is mostly associated with ants (Marchante et al., 2010; Wandrag et al., 2013; Pascov et al., 2015), and, consequently, few *A. longifolia* seeds have been seen to disperse over long distances in Portugal (Marchante et al., 2010). Dispersion can also be facilitated by habitat properties such as connectivity (Saad et al., 2009; Vicente et al., 2013; see Hernández et al., 2014, for *A. dealbata* and *A. melanoxylon*).

3.2.3 Enemy release

Invasive species success has been associated in some cases with enemy release, because in the invaded area their specialist enemies are not present, which gives them a competitive advantage over native species (Keane and Crawley, 2002; Lorenzo et al., 2010a). Evidence of enemy release has been found comparing invasive (Portugal) and native (Australia) populations of *A. dealbata* and *A. longifolia*, as Portuguese populations showed less pre-dispersal predation and higher production of fully developed seeds per fruit and bigger seeds (Correia et al., 2016). Another study comparing native and invaded areas in Australia of several acacia species (including *A. longifolia* and *A. melanoxylon*) did not find evidence of enemy release in soil microbial communities, which the authors attributed predominantly to the high homogeneity of vegetation and to the dominance of shrubby leguminous plants throughout Australia (Birnbaum and Leish-

Table 5. Reproductive traits of the most widespread *Acacia* species in southern Europe and two abundant native legumes (*Ulex europaeus* and *Cytisus scoparius*) in western Iberia.

	Age of maturity (years)	Seed bank (seeds m ⁻²)	Seed viability (%)	Seed persistence (years)
<i>Acacia dealbata</i>	4–5 ^a	10 000–22 500 ^c	30–90 ^c	> 5 ^b
<i>Acacia longifolia</i>	2 ^b	500–34 000 ^c	88–99 ³	> 10 ^b
<i>Acacia melanoxylon</i>	2 ^a	~ 50 000 ^c	70–91 ^c	> 50 ^a
<i>Ulex europaeus</i>	3 ^d	650–1050 (native) ^f 2500–16 000 (invasive) ^g	25 ^j	26 ^l
<i>Cytisus scoparius</i>	2–5 ^e	30–10 000 (native) ^h 30 000 (exotic) ⁱ	69–98 ^k	5–30 ^m

^a WorldWideWattle (2016). ^b Brown and Bettink (2009). ^c Gibson et al. (2011). ^d CABI (2016b). ^e Sheppard et al. (2006). ^f Puentes et al. (1988). ^g Moore et al. (2006). ^h Rees and Paynter (1997). ⁱ Downey (2001). ^j Ivens (1982). ^k CABI (2016a). ^l Moss (1959).

^m Maryland Department of Agriculture (2015).

man, 2013). On the other hand, the enemy release hypothesis has been used to explain the invasiveness of some western Iberia autochthonous shrubby legumes (*Ulex europaeus*, *Cytisus scoparius*) outside their native range (Memmott et al., 2000; Hornoy et al., 2011). The fact that some Australian acacias and Iberian shrub legumes reciprocally outcompete each other outside their native range arises as a supporting argument for the enemy release hypothesis.

3.2.4 Empty niche

Native legumes in western Iberia are shrubs, so the fact that *A. dealbata* and *A. melanoxylon* are the unique leguminous trees in the invaded areas could partly explain their establishment as they would be filling an empty niche. In the case of *A. longifolia*, it is considered a shrub or small tree due to its low height. The empty niche hypothesis has been recurrently used to explain invasiveness (Hierro et al., 2005). At an intermediate successional stage, *A. dealbata* and *A. melanoxylon* might have, as wooded trees, a competitive advantage over native shrubs. However, it must be highlighted that some native legumes (*Ulex europaeus*, *Cytisus striatus*) which are frequent in western Iberia can easily reach up to 2.5–3 m height and that in many areas, due to high fire recurrence, the invasive acacias do not exceed that height.

3.2.5 Human-mediated factors

Acacia species dispersal can be enhanced through their economic exploitation (Castro-Díez et al., 2011) and due to the movement of soil as a result of human activities (Hodkinson and Thompson, 1997). In fact, all acacia species widely used in forestry have become invasive (Richardson et al., 2015), likely thanks to the existence of disturbed areas along infrastructures (forest tracks, roads) which can act as dispersal corridors, as well as to involuntary transport and dispersal of seeds during forest management activities. Propagule pressure has also been enhanced in coastal ecosystems through

acacia use for dune stabilization (Marchante et al., 2003) or on roads and in human-disturbed areas due to their deliberately introduction as ornamental trees (Fuentes-Ramírez et al., 2010). Propagule pressure has been considered, jointly with residence times, one of the major drivers of acacia invasiveness (Richardson et al., 2015) and in some cases may have been confused with acacia invasiveness traits due to their overlap with traits associated with human usefulness (Richardson et al., 2011). Land abandonment and misuse in rural areas can also favour acacia invasion (Souza-Alonso et al., 2017). Cultural perception of these species can also play in their favour. For example, in Spain and Portugal, *Acacia dealbata* has been greatly appreciated in rural areas for the last 50 years (Souza-Alonso et al., 2017), and acacias provide different benefits such as timber or honey production (Vaz et al., 2019). *Eucalyptus globulus* Labill. plantations can favour acacias through facilitative interactions (Forrester et al., 2011, although see also Rodríguez-Echeverría et al., 2013); these mixtures are common in both NW Spain (Hernández et al., 2014) and Portugal (Martins et al., 2016).

4 Effects of acacias on the invaded soil–plant system

4.1 Effects on biodiversity

Acacia species can lead to a biotic homogenization of ecosystems (Lorenzo et al., 2010a; Lorenzo and Rodríguez-Echeverría, 2012) and to the decrease in biodiversity of soil bacteria (Slabbert et al., 2014), invertebrates (as found for Coleoptera in *A. dealbata* by Coetzee et al., 2007) and plants (for *A. longifolia* see Marchante et al., 2003, 2015; Hellmann et al., 2011; for *A. dealbata* see Fuentes-Ramírez et al., 2010; González-Muñoz et al., 2012; Lorenzo et al., 2012; Lazzaro et al., 2014).

Acacias are often able to exclude native plants (Fuentes-Ramírez et al., 2011; Le Maitre et al., 2011) through (a) high competition capacity in resource-poor environments (Bro-

dribb and Hill, 1993; Marchante et al., 2003; Werner et al., 2010; Morris et al., 2011; Belay et al., 2013), (b) a tendency to form monospecific stands (Lorenzo et al., 2010b; Werner et al., 2010; Vazquez-de-la-Cueva, 2014) and (c) the depletion of native seed banks derived from the suppression of native plant species (Marchante et al., 2003; Lorenzo et al., 2010a; Le Maitre et al., 2011).

Other exclusion factors are their allelopathic ability (as found in *A. dealbata* – Carballeira and Reigosa, 1999; Lorenzo et al., 2010a, 2011; Aguilera et al., 2015 – and in *A. melanoxylon* – Hussain et al., 2011) and the formation of a thick litter layer (Lorenzo et al., 2010b; Le Maitre et al., 2011; González-Muñoz et al., 2012) which can inhibit the germination and establishment of plants with small seeds (Marchante et al., 2011a). Allelopathy in *A. dealbata* is related to flowers (Carballeira and Reigosa, 1999; Aguilera et al., 2015), and, in Iberia, its flowering coincides with the germination period of most native species, increasing the allelopathic effects of the invasive species (Lorenzo et al., 2010a). Allelopathy can be presumed to be a novel weapon that increases the competitiveness of *A. dealbata* (Lorenzo et al., 2011), in accordance with the “novel weapon hypothesis”, which states that root exudates of invasive species can be highly damaging to native plants or soil microorganisms because invasive and native species have not co-evolved (Callaway and Ridenour, 2004; Weidenhamer and Callaway, 2010). However, some Fabaceae shrubs native to western Iberia, where they are being displaced by some *Acacia* species, also have allelopathic potential, as reported for *Cytisus scoparius* (Nemoto et al., 1993), and also share with acacias many of the other aforementioned traits (high competition capacity, monospecific stands, thick litter layer; CABI, 2016a, b).

4.2 Alteration of ecosystem functioning

4.2.1 Fire regime

In South African fynbos invasive *Acacia* species provide more fuel load than native species (Van Wilgen and Richardson, 1985); they can alter the fire regime and characteristics, and, consequently, a relation between more frequent fires and diminishing soil nutrient concentration in the long term could be anticipated (Ehrenfeld, 2010). If this is also the case in western Iberia, which already has the highest wildfire incidence in Europe (Borrelli et al., 2016), a worrying scenario with a fire–invasion positive feedback could arise. However, due to the meaningful ecological and environmental differences between both areas, studies on the effect of these invaders on the fire regime of western Iberia are needed. Contrastingly, in fynbos, the higher humidity of *A. saligna* tissues has resulted in a decrease in fire intensity (Van Wilgen and Richardson, 1985).

4.2.2 Water regime

In South African fynbos, *Acacia* species decrease stream flows through higher water use and evapotranspiration (Le Maitre et al., 2002, 2011; Morris et al., 2011) and even change water quality (Chamier et al., 2012). In this habitat, *Acacia* species invasions have resulted in increased soil erosion of riverbanks because the *Acacia* invaders are not adapted to floods (D’Antonio and Meyerson, 2002). In Iberia, some of the most invasive acacias (*A. dealbata*, *A. longifolia*) widely colonize the river margins (Marchante et al., 2005; Fagúndez and Beiras, 2007; Lorenzo et al., 2010a), especially those that have been channelized (Aguilar et al., 2001). However, still little is known about their effects on the hydrological cycle, although *A. longifolia* has been seen to alter the ecosystem water balance in a semi-arid region (Rascher et al., 2011).

4.2.3 Soil

Acacia spp. can modify soil properties (Ehrenfeld et al., 2001; Marchante et al., 2008; Lorenzo et al., 2010b; Souza-Alonso et al., 2014), for instance through their recalcitrant phylloides and N₂-fixing capacity (Lorenzo et al., 2010a; Morris et al., 2011; Castro-Díez et al., 2012). Owing to its ability to fix N₂, *A. dealbata* produces a high amount of nutrient-rich litter that decomposes quickly (Witkowski, 1991; Souza-Alonso et al., 2014, 2015a) although the presence of secondary metabolites may cause the opposite effect (Castro-Díez et al., 2012). Consequently, its invasion commonly results in lower pH (except in very acidic soils) and higher contents of C, total N, inorganic N and P in the topsoil (May and Attiwill, 2003; Lorenzo et al., 2010b; González-Muñoz et al., 2012; Lazzaro et al., 2014; Souza-Alonso et al., 2014, 2015a). Similar patterns have also been found for other *Acacia* species, namely increased soil organic matter and N content (*A. longifolia* – Marchante et al., 2008; Rodríguez-Echeverría et al., 2009; Hellmann et al., 2011; *A. saligna* – Yelenik et al., 2004, 2007). The increase in soil N concentration has been seen to expand beyond the invaded area for *A. longifolia* (Rascher et al., 2012). Soil C, N and P enzymatic activities (β -glucosidase, N-acetylglucosaminidase, urease, acid phosphatase) also increased after the invasion (Souza-Alonso et al., 2014, 2015a). Nevertheless, there is still a lack of knowledge about the effects of acacias on the net and gross N fluxes of the invaded ecosystems. Moreover, in the bibliographic search we could not find sound comparisons of soil N pools between acacia-invaded sites and mature stands of native Fabaceae, namely *Ulex europaeus* or *Cytisus scoparius*.

Soil base cations (Na, K, Mg, Ca) under *A. dealbata* have been less studied and show different responses, variable with time (Souza-Alonso et al., 2014, 2015a), which underlines the importance of the time elapsed after invasion for soil property variations (Strayer et al., 2006; Marchante et al.,

2008; Souza-Alonso et al., 2015a). However, as found in *A. longifolia* (Marchante et al., 2008; Hellmann et al., 2011) and *A. saligna* (Yelenik et al., 2007), an increase in exchangeable base cation concentration due to the uplift of nutrients to shallower soil layers and to the higher cation exchange capacity derived from the increment in organic matter content would be expected (Dassonville et al., 2008). We found a lack of studies about the effect of invasive acacias on soil-available micronutrients, despite their importance in plant survival and development when present in limiting or deleterious concentrations (Williams and Fraústo da Silva, 2000). As for soil N, no sound comparisons of soil nutrients between *Acacia* spp.-invaded sites and mature stands of native Fabaceae species were found.

Acacia dealbata can also affect the structure and function of soil bacterial and fungal communities (Lorenzo et al., 2010b; Rodríguez-Echeverría, 2010; Lorenzo et al., 2013; Souza-Alonso et al., 2015a) that vary with the ecosystems invaded (Lorenzo et al., 2010b). Allelopathy affects soil microorganisms differently depending on the ecosystem (Lorenzo et al., 2013). In the long term, by changing soil properties and microbiota composition, *A. dealbata* and *A. longifolia* seem to favour (a) their own invasion, as they benefit from the increased nutrient soil content and compatible N₂-fixing bacteria availability (Marchante et al., 2008; Lorenzo and Rodríguez-Echeverría, 2012; Rodríguez-Echeverría et al., 2013), and (b) the proliferation of nitrophilous species, which can result in secondary invasions (Le Maitre et al., 2011; González-Muñoz et al., 2012; Lazarro et al., 2014; Marchante et al., 2015).

Consequently, the above-mentioned *Acacia* invasive species can be considered “ecosystem transformers” (Richardson et al., 2000) as they act at least as donors of limiting nutrients (N in low-resource ecosystems) and also as fire promoters, sand stabilizers and litter accumulators.

5 *Acacia* species control and subsequent restoration of the soil–plant system

5.1 Physical and chemical control

In the case of *Acacia* species, a very common control technique is cutting, which should be accompanied by herbicide application in the case of vigorous resprouting species (Le Maitre et al., 2011; Souza-Alonso et al., 2013). The use of the herbicide triclopyr in *A. dealbata* is effective and not detrimental to soil microorganism activity in the long term according to results obtained in NW Spain (Souza-Alonso et al., 2013), although it has been associated with structural variations in soil bacteria communities during the first year after the herbicide application (Souza-Alonso et al., 2015b). Basal cutting has been employed for *A. longifolia* control in Portugal, sometimes followed by herbicide use to avoid resprouting; however, a low success rate was obtained due to the high contribution of seed germination to the reinvasion

(see Marchante et al., 2011a, and references therein). Also, in many localities the herbicide is only applied several hours or days after cutting, which reduces its success (Ana S. Vaz, personal communication, 30 March 2020). Controlling species (e.g. *A. dealbata*, *A. melanoxylon*, *A. mearnsii*) with trunk debarking of all trees from waist height down to the soil surface, when the vascular cambium is active, is being carried out in Portugal (Silva and Marchante, 2012). There are alternatives to the complete elimination of the invasive plant by using the aforementioned control methods: lowering their density, in order to reduce the cost of a subsequent control, or hindering their spread if the available budget is not enough for applying a control technique (Myers et al., 2000). Moreover, the persistent seed bank of acacias can be decreased with prescribed burning or solarization; the combination of both methods can be highly effective for *A. saligna* (Cohen et al., 2018).

5.2 Biological control

As highlighted previously (see “Enemy release” subsection), the absence of specialized predators or parasites can be a decisive competitive advantage for invasive *Acacia* species in western Iberia. Therefore, biological control by introducing natural enemies arises as a promising technique for *Acacia* species control in this region.

In South Africa, seed predator *Melanterius* beetles have been introduced to control *A. baileyana* F. Muell., *A. dealbata*, *A. mearnsii* and *A. pycnantha* (*M. maculatus* Lea); *A. saligna* (*M. compactus* Lea); *A. longifolia* (*M. ventralis* Lea); *A. cyclops* (*M. servulus* Pascoe); and *A. melanoxylon* (*M. acaciae* Lea), the introduction being successful for the three latter cases (Sheppard et al., 2006; Wilson et al., 2011). *Trichilogaster* hymenopterans (bud-galling wasps) have also been successfully employed to control *A. longifolia* (*T. acaciaelongifoliae* (Froggatt)) and *A. pycnantha* (*T. signiventris* (Girault); Hoffmann et al., 2002; Sheppard et al., 2006). Besides, the flies *Dasineura dielsi* Rübsaamen and *D. rubiformis* Kolesik have been tested for *A. cyclops* and *A. mearnsii* control, respectively (Wilson et al., 2011). Among fungi, the basidiomycete *Uromycladium tepperianum* (Sacc.) McAlpine, which causes gall rust, extensively damages *A. saligna* (Sheppard et al., 2006; Wilson et al., 2011).

Among the six natural enemies of acacias successfully employed to control acacias invasions in South Africa, only *T. acaciaelongifoliae* has been released in western Iberia to control *A. longifolia* after the study of Marchante et al. (2011b) and the approval of the EFSA PLH Panel (2015). This agent can largely reduce seed production, decreasing the capacity of dispersal and reinvasion of *A. longifolia* (Invasive Plants in Portugal, 2019). Regarding *A. dealbata*, biological control techniques have not yet been used, despite this species being one of the invasive plants most prioritized as a potential biocontrol target in western Europe (Sheppard et al., 2006). However, the administrative and scientific pro-

cedures to introduce two potential agents – *Melanterius acaciae* Lea and *Melanterius maculatus* Lea – have been initiated in Portugal for the control of *A. melanoxylon* and *A. dealbata*, respectively (Carrapeto Gil, 2017).

5.3 Ecosystem restoration

After *Acacia* species removal, in order to recover ecosystem composition and function (Le Maitre et al., 2011; González-Muñoz et al., 2012) and to avoid side effects such as re-invasion or erosion (Enright, 2000; Marchante et al., 2011a), proactive restoration may be needed. Restoration efficiency depends on the understanding of the processes by which invasive acacias alter the environment (Le Maitre et al., 2011). In order to facilitate the recovery of the ecosystem, eradication should be accompanied by the elimination through physical removal or burning of acacia litter (Marchante et al., 2004, 2009; Le Maitre et al., 2011), which affects soil properties and can enhance secondary invasions through increased N (Yelenik et al., 2004; Marchante et al., 2009; Le Maitre et al., 2011). Corbin and D'Antonio (2004) suggest that invasive species not only affect soil N fluxes but also N pools, making restoration efforts increasingly difficult. In some cases, removal of the exotic species might not be enough due to the legacy effects produced in the ecosystem (D'Antonio and Meyerson, 2002), for example when N₂-fixing species lead to a persistent increase in N concentration that can hinder restoration efforts (Yelenik et al., 2007). *Acacia* species leave persistent alterations in soil that can hamper restoration efforts and create a need for complementary actions such as reducing N availability (as is the case for *A. longifolia*; Marchante et al., 2009) in naturally N-poor ecosystems. The addition of a C-rich source that leads to N immobilization can counteract the decreased C : N ratio through N₂ fixing, thereby avoiding secondary invasions by N-demanding species (Yelenik et al., 2004). However, lowering resource availability would not be an effective strategy with species that invade low-resource environments (Funk and Vitousek, 2007).

Regeneration with native species by active planting or sowing can be considered after the eradication of invasive species (Richardson et al., 2007). This is especially important for species such as *A. dealbata* and *A. longifolia* that deplete the native soil seed bank and reduce plant diversity (Marchante et al., 2011a; González-Muñoz et al., 2012). In order to avoid future invasions, Funk et al. (2008) propose revegetating with native species with similar attributes to invaders but ones that do not modify their environment in a similar way, with the objective of filling ecological niches. Although this is not possible when invaders occupy an empty ecological niche, as happens with Australian *Acacia* spp. that invade low-nutrient coastal dunes in Portugal (Rodríguez-Echeverría et al., 2009), it can be feasible in forest or shrubland areas which are usually colonized by native legumes (*Ulex*, *Cytisus*, *Pterospartum*). When the invasion has been

triggered by changes in disturbance regimes, the control of exotic plant populations and regeneration with natives could be ineffective; thus management should focus on reverting environmental changes (Catford et al., 2012).

5.4 Constraints on control and restoration

Several reproductive characteristics of invaders that may restrict their control success, such as large and persistent seed banks (Wilson et al., 2011), vigorous resprouting and high propagule dispersal capacity (Myers et al., 2000; Panetta, 2009), are common traits in *Acacia* spp. (Lorenzo et al., 2010a; Fuentes-Ramírez et al., 2011; Gibson et al., 2011; Le Maitre et al., 2011; Vazquez-de-la-Cueva, 2014). As a consequence, the management of this genus is difficult and control actions can have strong side effects. For example, using fire to stimulate germination (and by that, deplete the seed bank; Wilson et al., 2011) may affect the native seed bank, favour secondary invasions (Nsikani et al., 2019) and induce *Acacia* spp. sprouting (Le Maitre et al., 2011), which is one of the main factors that makes the control of these invaders very difficult in post-fire situations (Silva and Marchante, 2012). If litter removal, earth covering or soil inversion are used to avoid germination (Wilson et al., 2011), they can increase erosion risk and expose soil to higher N mineralization which can hamper native species recolonization (Yelenik et al., 2004), as also occurs after tree removal (D'Antonio and Meyerson, 2002). Moreover, restoration efforts that cause disturbances in the invaded areas can enhance secondary invasions by other species (Le Maitre et al., 2011).

Other examples of side effects on native species include (a) the use of herbicides to prevent resprouting of *Acacia* species, which could indirectly affect natives through effects on symbiotic microorganisms (Weidenhamer and Callaway, 2010); (b) the use of biological control, which can lead to unexpected impacts on non-target species (Cory and Myers, 2000); and (c) the addition of a C source to counteract the decline in the litter and soil C : N ratio triggered by *Acacia* spp. invasions, which can affect native species (Haubensak et al., 2004).

Increased time after invasion exacerbates all these constraints, as acacias' seed banks become larger (Marchante et al., 2010), changes in soil properties and microbial communities become more pronounced (Marchante et al., 2008; Souza-Alonso et al., 2015a), and distribution widens (Myers et al., 2000). Consequently, as for other species (Myers et al., 2000; Catford et al., 2012; Monaco and Genovesi, 2014), a preventive approach should prevail over a reactive one in acacia invasion control (Sanz-Elorza et al., 2004; Wilson et al., 2011). For instance, fire prevention and control are strongly recommended to preclude *A. dealbata* spread in Spain (Sanz-Elorza et al., 2004). However, once the species is introduced, the possibility of restoring the affected area must be considered (Myers et al., 2000), and, due to the high cost of restoration, it is necessary to select areas that are most af-

fects or where management has the highest probability of success (D'Antonio and Meyerson, 2002). For example, in the case of *A. longifolia*, recently invaded areas should be prioritized (Marchante et al., 2011b).

As management outcomes cannot be accurately predicted, an adaptive approach is needed through continuous monitoring and assessment of the restoration actions (Van Wilgen et al., 2011). Also, regional strategies should be implemented for dealing with invasive acacia species. The coordination of efforts from national to municipal levels, with clear lines of responsibilities, and involvement of the private sector can effectively achieve restoration goals (Van Wilgen et al., 2011).

Another challenge in acacia control and restoration is the delay in the implementation of European laws. EU regulation was implemented in 2015 (European Parliament and Council, 2014), setting guidelines for the management of invasive species and highlighting the need for prevention, early detection, and rapid eradication and management. However, it was not until 2019 that this European regulation was implemented in Portugal (Decree-Law 92/2019) and Spain (Real Decreto 216/2019). The reinforcement of transnational forest regulations for the southern European countries could help to prevent introductions of new acacia species (Souza-Alonso et al., 2017).

6 Conclusions

Due to their high invasiveness, *Acacia dealbata*, *A. melanoxylon* and *A. longifolia* are at present the most prolific invader acacias in western Iberia, the European region where acacia invasions are most widespread. This is likely due to the combination of several factors: (a) greater introduction effort, (b) acidic soils, (c) a temperate and humid climate, and (d) the highest wildfire incidence in Europe. Because of the strong changes they induce in the soil–plant system, these species are highly damaging to the environment, which is particularly worrying for the protected areas where they are present. Besides these species, other congeners are widening their distributions in Iberia and can emerge as dangerous future invaders. Therefore, more research is needed on the least known *Acacia* species to prevent new invasions and to predict which areas are the most vulnerable to their invasion.

Further studies are also needed on how *Acacia* species became so invasive in ecosystems where native species with similar ecological traits (N_2 fixing, resprouters, pyrophytes, able to form monospecific stands, allelopathic potential) are already abundant and widespread. Moreover, for European ecosystems there is no available information about the effects of invasive acacias on fuel load and fire risk, despite the fact that acacia expansion in burnt areas is a cause of great concern. This knowledge would enable the use of more efficient preventive, control and restoration practices. If it is confirmed that some Australian acacias and Iberian Fabaceae

shrubs outcompete each other outside their native range due to enemy release, the introduction of specific enemies, as recently carried out in Portugal for *A. longifolia*, can be a promising tool to control their invasions.

Besides sound comparative studies on the availability of macronutrients between *Acacia* spp.-invaded sites and mature stands of native Fabaceae species, another research gap is the lack of knowledge about the effects of acacias on net and gross N fluxes, as well as on available micronutrients, in the invaded ecosystems. Moreover, integrated studies on the effects of CO_2 increase and changes in temperature, frost risk and water availability could provide a more reliable understanding of the effect of climate change on these invasive species.

In addition to reactive actions, such as eradication, the proactive restoration of areas invaded by these *Acacia* species must be carefully planned to recover the ecosystem composition and function without side effects. However, the complexity of controlling both invasion and restoration side effects highlights the importance of taking a preventive approach.

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