

# Here to stay. Recent advances and perspectives about *Acacia* invasion in Mediterranean areas

Pablo Souza-Alonso<sup>1</sup>  · Jonatan Rodríguez<sup>1</sup> · Luís González<sup>1</sup> · Paula Lorenzo<sup>2</sup>

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## Abstract

• **Key message** The above- and belowground impacts due to *Acacia* invasions have been described in detail over the last 25 years. Future research should focus on the early detection and prevention of new *Acacia* introductions and on a cost-effective and sustainable management of the novel ecosystems resulting from invasions.

• **Context** Invasive alien plants (IAPs) strongly alter ecosystems reducing biodiversity, modifying ecosystem services and increasing negative impacts at social and economic level. Among invasive taxa, *Acacia* is a highly problematic genus

worldwide. In fact, almost 500 papers have been published on several aspects of *Acacia* invasions for the last 25 years.

• **Aims** We aim at reviewing the current knowledge on the consequences of the invasion by *Acacia* genus in Mediterranean ecosystems. We also collect and propose different approaches for the management and recovery of invaded areas and suggest future perspectives on *Acacia* research.

• **Methods** We compile, summarise and discuss recent findings on physicochemical, ecological, microbiological and socioeconomic aspects of invasion related to Australian acacias (*Acacia dealbata*, *Acacia longifolia*, *Acacia mearnsii*, *Acacia saligna* and *Acacia melanoxylon*) focusing on Mediterranean areas.

• **Results** *Acacia* invasion generally entails soil physicochemical alterations and changes in microbial function and structure. Consequences such as the decreased biodiversity, altered ecosystem structure, larger seed banks dominated by invasive species, new biotrophic relationships or alterations in water availability and fire regimes suggest that acacias are locally creating novel ecosystems.

• **Conclusions** Forecasting invasions, modelling and managing ecosystems dominated by acacias are challenging tasks that should be addressed in the future, since climatic conditions and intensification in land uses are increasing the likelihood of *Acacia* invasions in Mediterranean areas. Unsuccessful management actions suggest that restoration should be meticulously monitored, but the magnitude of invasion or the inconsistency of economic investment indicate that eradication is often unfeasible. Alternatively, novel integrative and cost-effective solutions including the collaboration of society, politicians and stakeholders are necessary to prevent new introductions and achieve sustainable control of acacias. There is a growing interest in applied research on the valorisation or novel uses for acacias and their residues that result in economic benefits.

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Paula Lorenzo: obtained information, wrote different sections and contributed to correct and organise the manuscript.

Jonatan Rodríguez: obtained information and contributed to correct different sections.

Luís González: contributed to correct and organise the manuscript.

✉ Pablo Souza-Alonso  
souzavigo@gmail.com

Jonatan Rodríguez  
jonatan@uvigo.es

Luís González  
luis@uvigo.es

Paula Lorenzo  
paulalorenzo@uc.pt

<sup>1</sup> Plant Biology and Soil Science Department, University of Vigo, 36310 Vigo, Spain

<sup>2</sup> Centro de Ecologia Funcional - CEF, Departamento de Ciências da Vida, Faculdade de Ciências e Tecnologia, Universidade de Coimbra, 3000-456 Coimbra, Portugal

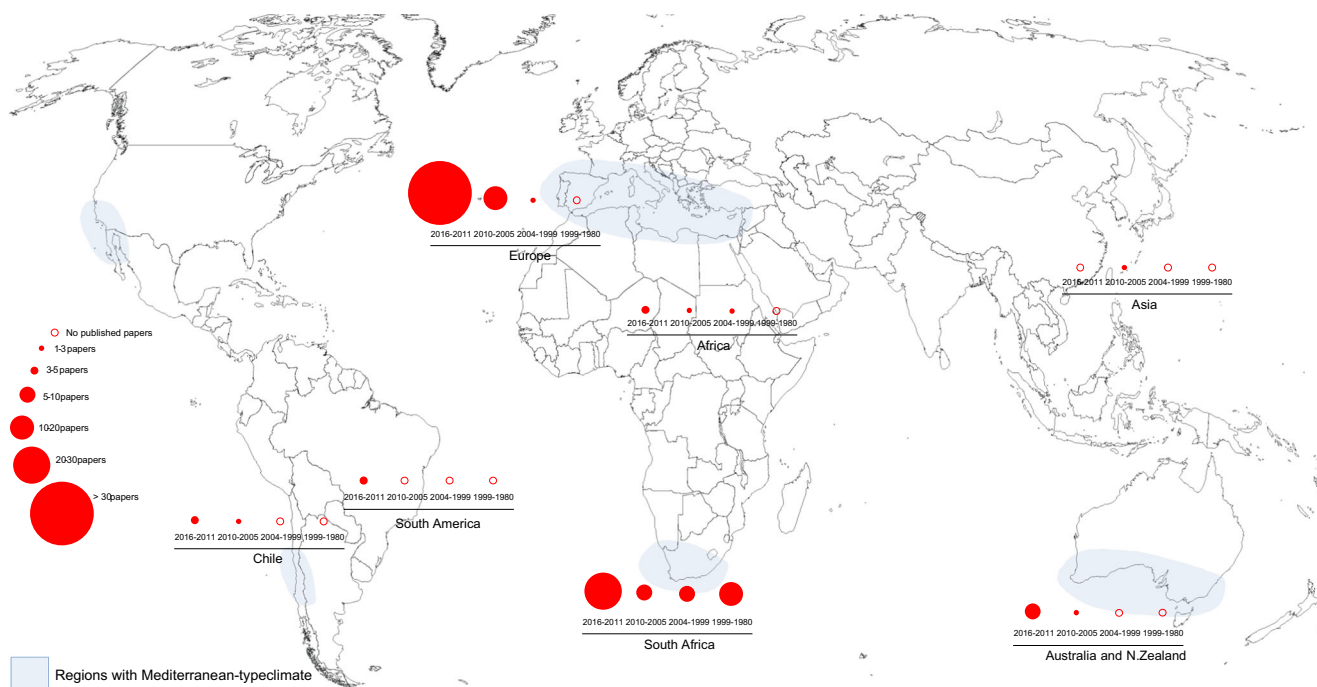
**Keywords** Invasive alien plants · Biodiversity · Ecosystem changes · Seed production · Soil microorganisms · *Acacia* management

## 1 Introduction

Humans induce rapid changes to the environment, including the alteration of major biogeochemical cycles, land surface transformation, changed atmospheric composition and evolution patterns. Such changes are currently taking place at unprecedented rates in the period recently defined as the Anthropocene (Steffen et al. 2007; Lewis and Maslin 2015). Numerous human activities act as driving forces of environmental change by removing physical, biotic and geographical barriers that facilitate plant species movement, which is a main risk factor for biodiversity. Invasive alien plants (IAPs), defined as plant species producing large reproductive progeny that spread over considerable distances from parent plants (Richardson et al. 2000a), are currently a priority research objective of the European Commission (EC Regulation 1143/2014).

Along the wide range of genera containing species classified as invaders, *Acacia* is one of the most controversial and studied genus across the world (Murphy 2008). Currently, 24 *Acacia* species are confirmed as invasive worldwide (Richardson and Rejmánek 2011; Lorenzo and Rodríguez-

Echeverría 2015). *Acacia sensu lato* is a cosmopolitan genus with polyphyletic origin, but in this paper, we exclusively focus on the Australian *Acacia* subgenus *Phyllodineae - Acacia s.s.* (Kyalangalilwa et al. 2013) due to their invasiveness. The movement of acacias to other continents began in the late 1700s (Carruthers et al. 2011), but unprecedented dispersal rates have occurred in the latest two centuries. Albeit Australian acacias are now occurring worldwide, they are more frequently invasive in Mediterranean areas (Fig. 1). Studies on *Acacia* invasions were compiled in a special issue covering not only biological and ecological but also social, economic and ethical perspectives (human-mediated introductions of Australian acacias—a global experiment in biogeography, Diversity and Distributions 2011). At the same time, Lorenzo et al. (2010a) published a review mainly focused on hypotheses explaining the invasive success of *Acacia dealbata* in Europe. These authors suggest that *A. dealbata* not only takes advantage from environmental disturbances, but also possesses high clonal growth and allelopathic ability that reduce native biodiversity in the understory. However, due to the increasing number of studies recently conducted in Mediterranean areas (see also Fig. 1), we consider that an update of the current knowledge on the consequences of *Acacia* invasion at these regions is required. Here, our objective is to not only summarise recent findings (including biological, ecological, physicochemical, microbiological or socioeconomic aspects of invasion) but also to complement



**Fig. 1** Scheme representing the number of papers including highly invasive acacias considered: *Acacia dealbata*, *A. longifolia*, *A. mearnsii*, *A. saligna* and *A. melanoxylon*, through different areas across the world. Map is created based on information ( $n = 214$  manuscripts) after the search in SCOPUS by using the key terms *Acacia* and *plant* and

*invas\** (TITLE-ABS-KEY)+ and “*Acacia dealbata*” or “*Acacia longifolia*” or “*Acacia saligna*” or “*Acacia melanoxylon*” or “*Acacia mearnsii*”. Systematical reviews on the *Acacia* invasive process were not included unless they were strictly focused on a specific area. Note the different scale for the last interval (1999–1980)

and extend previous information related to the most problematic acacias in Mediterranean areas. We also discuss future perspectives on research, management and recovery of invaded areas.

### 1.1 Major problematic acacia species, introduction and current distribution

Although there is an important number of invasive species within *Acacia* genus, we focused on *Acacia dealbata* Link, *Acacia longifolia* (Andrews) Willd., *Acacia mearnsii* De Wild., *Acacia saligna* (Labill) H. L. Wendl. and *Acacia melanoxylon* R. Br. due to their impacts worldwide (Richardson and Rejmánek, 2011; Lorenzo and Rodríguez-Echeverría 2015). *Acacia cyclops*, also considered as an IAP, was not included since available data is almost exclusively based on information from the Cape Region, South Africa (Higgins et al. 1999, 2001).

Specific characteristics of these acacias, such as adaptability to many environmental conditions, easy germination and growth, good survival and rapid growth rates, ornamental value or wood quality, have determined their current distribution (Maslin and McDonald, 2004). In Europe and other Mediterranean areas, some uses of acacias as wood and timber production (Griffin et al. 2011), the perfume industry (Perriot et al. 2010; Kull et al. 2011), stabilisation of dunes and avoidance of sand erosion (Marchante et al. 2003; Cohen et al. 2008; Del Vecchio et al. 2013) or to stabilise slopes derived from the railway construction (Kull et al. 2007), played a significant role in their introduction. Consequently, a wide range of Mediterranean biomes are currently threatened by acacias, such as riparian habitats, shrublands, fynbos, sclerophyllous forests, mixed forests, grasslands and prairies, coastal areas and sand dunes, riverlands and watercourses, islands, agricultural fields or tree plantations (Le Maitre et al. 2000; Marchante et al. 2003; Rodríguez-Echeverría et al. 2009; Lorenzo et al. 2010a, b; Crous et al. 2012; Boudiaf et al. 2013; Hernández et al. 2014; Lazzaro et al. 2014; Celesti-Grapow et al. 2016). In fact, invasive acacias have been also defined as *transformers*, those species that “substantially change the character, condition, form or nature of ecosystems, becoming active agents in region-forming processes” (Richardson et al. 2000a; Marchante et al. 2011a).

### 1.2 Human perception of invasive acacias

“A fascinating story to be told regarding what transpires when an environmental scientist’s problem is a rural community’s livelihood” is how Kull et al. (2011) summarises the contradictory perception of exotic acacias when they represent an economic resource and, at the same time, an ecological threat in the introduced ranges. Human perception of invasive acacias is strongly influenced by biophysical, familiarity, social

variables and socioeconomic circumstances (Tassin et al. 2009a; Kull et al. 2011, 2007). In many countries, large parts of the population have positive perceptions about invasive acacias that are largely cultivated with profitable uses such as construction materials, heat source or medicinal compounds for rural communities (de Neergaard et al. 2005; Wintola et al. 2017). For example, *A. dealbata* is highly valued by local communities of Spain, Portugal and France, where festivals have been celebrated in its honour for almost 50 years (Afonso 2012). In France, some villages such as Mandelieu-la-Napoule or Biot, both at the Côte d’Azur, have celebrations of *A. dealbata* that have continued for more than 80 and 60 years, respectively. On the other hand, when economic activities are affected by *Acacia* invasion, such as forestry or citrus cultivation (Kull et al. 2011), these species are being recognised as problematic.

## 2 New insights into traits that promote invasion

### 2.1 Genetics, phenotype and physiology

The size of the genomic pool has been suggested as a factor promoting invasion (Grotkopp et al. 2004; Kubešová et al. 2010). However, univariate analyses comparing the genome size of 92 acacias introduced outside their native range—21 invasive, 71 non-invasive—did not detect any difference between the genome size based on their invasive character (Gallagher et al. 2011). In addition, low levels of genetic diversity in the introduced areas compared to native areas are not necessarily related to a reduction in the invasion success and vice versa (Harris et al. 2012).

The amplitude of the native range is generally considered as an important predictor of invasiveness as it reveals the adaptation to a wide range of environmental conditions and leads to a large risk of propagation and dispersal by humans (Goodwin et al. 1999). Life history traits, such as tree height and sprouting ability, have an important weight in invasiveness predictive models (Gallagher et al. 2011; Gibson et al. 2011). However, their importance decreases when human factors are included. In fact, human use is one of the most important predictors of *Acacia* invasiveness (Castro-Díez et al. 2011).

Ecophysiological traits can be as important as morphological traits in explaining invasiveness. Once seeds reach the soil, acacias are provided with mechanisms to outcompete native species. For example, in saline water-stressed environments, *A. longifolia* seeds and seedlings present increased intracellular ion concentrations, efficient nitrogen uptake, defence against superoxide radicals and high tolerance to a wide range of salt concentrations compared to native species (Morais et al. 2012; Morais and Freitas 2012). Godoy et al. (2011) indicated that the photosystem II (PSII) activity of

*A. melanoxylon* performs better with higher leaf temperature than that of natives under water stress. This fact could reflect a higher thermostability of the PSII or, on the contrary, a better acclimation and thus, efficiency of the entire photosynthetic process in arid or Mediterranean-type ecosystems. Under experimental conditions, an increase in CO<sub>2</sub> has been related to higher growth rates, final weight and increased N-fixation rates of *A. melanoxylon* (Schortemeyer et al. 2002). Consequently, if N supply is also increased, dry biomass, CO<sub>2</sub> assimilation, foliage thickness and density are significantly enhanced (Schortemeyer et al. 1999). In a expected global warming scenario with higher temperatures and CO<sub>2</sub> levels (IPCC 2013), with acacias growing at higher rates and producing canopies with denser foliage, reducing light availability for understory species, the invasiveness of these species could be severely increased. However, the benefit from new climatic conditions is not clear, at least for *A. dealbata*. González-Muñoz et al. (2014) predicted a decline of its growth in the Iberian Peninsula based on climate-growth patterns and climatic models. Conversely, using species distribution models, habitat connectivity and protected areas layers, Vicente et al. (2016) forecasted an increasing land exposition and connectivity between suitable areas for *A. dealbata* due to climate change.

## 2.2 Reproductive features

Reproduction by sprouting facilitates the establishment of clonal populations (Lorenzo et al. 2010a; Fuentes-Ramírez et al. 2011; Rodríguez et al. 2017). In fact, the proportion of sprouting species is higher among invasive than non-invasive acacias (Gibson et al. 2011). Invasive acacias also reach reproductive maturity earlier (<2 years) than non-invaders (Gibson et al. 2011). *Acacia dealbata* and *A. mearnsii* tend to have higher levels of self-compatibility, suggesting that the ability to self-fertilise may favour its invasiveness (Gibson et al. 2011). Indeed, *A. dealbata* has the capacity to produce progeny by autonomous self-pollination (Rodger and Johnson, 2013). Besides *A. dealbata*, also *A. longifolia* and *A. melanoxylon* showed low level of spontaneous self-pollination allowing them to produce viable offspring in Portugal (Correia et al. 2014). Nevertheless, in the native range of *A. dealbata*, there was little evidence of elevated inbreeding influencing its progeny (Broadhurst et al. 2008). In addition, *A. saligna* has a mixed mating system, preferential outcrossing, but also with a certain level of selfing (George et al. 2008). The ecological function of self-pollination and its role in invasiveness is highly dependent on the trade-off between the benefits of the absence of compatible mates and costs, such as the inbreeding depression (characterised by a reduction in growth and progeny survival). Self-pollination could be a valuable tool to produce offspring under circumstances

that severely constrain plant survival (e.g. isolated areas, absence of pollinators, mate limitation). Interestingly, *A. mearnsii* showed both sexual and asexual reproduction depending on the environmental conditions in the non-native range, showing preference for sprouting in disturbed areas and seed-based reproduction in undisturbed sites (Eilu and Obua 2005).

**Acacias and pollinators** Despite their ability to self-fertilisation, acacias are pollinated by generalist insects and they usually require the presence of pollination vectors to achieve significant seed production (Correia et al. 2014). In fact, low pollen/ovule ratio supports the compatibility with dependence on animal pollen vectors (Gibson et al. 2011). Reproductive success is often maximised by the synchronised and massive opening of flowers both within a single individual and local populations (Stone et al. 2003), which may interfere with the normal relationship between native species and their pollinators. In South Africa, Gibson et al. (2013) indicated that flower visitation to native plants was reduced due to the presence of *A. saligna*. Nevertheless, despite the massive flowering of *A. dealbata* and *A. longifolia*, native plant species attained similar or even higher visitation rates in Portugal (Montesinos et al. 2016). Complementary low temperatures and high relative humidity during winters in the Northern hemisphere favour polyad viability and pollen tube development (Beck-Pay 2012).

**Seed production, dispersal and germination** Seed production is suggested as a factor promoting the invasion of acacias (Castro-Díez et al. 2011). In the introduced range, *A. dealbata* and *A. longifolia* escape pre-dispersal predation and display a higher production of fully developed seeds per fruit (*A. longifolia*) or per tree (*A. dealbata*), accompanied with larger size of individual seeds (Correia et al. 2016). However, rare and widespread acacias have similar levels of seed production (quantitatively and qualitatively), indicating that, in some cases, the level of seed development and release does not necessarily determine plant abundance (Buist 2003). Nevertheless, massive seed production and accumulation is highly variable within acacias (Gibson et al. 2011). Once released, seeds can be dispersed by water or wind, but also through myrmecochory (seeds with elaiosomes) or ornithochory (seeds with arils) (French and Major 2001; Richardson and Kluge 2008; Marchante et al. 2010; Montesinos et al. 2012), remaining viable for up to 150–200 years (Daws et al. 2007; Leino and Edqvist 2010).

Fire stimulates seed germination of several invasive acacias such as *A. melanoxylon*, *A. dealbata* and *A. saligna* (García et al. 2007; Lorenzo et al. 2010a; Wilson et al. 2011). Additionally, butenolide, a chemical compound isolated from smoke, may have a significant positive effect on the post-fire seedling ecology of *A. mearnsii* (Kulkarni et al. 2007). The



stimulating effect of fire has important ecological implications since fire may eliminate native seeds from the surface layer, favouring the germination of resistant acacia seeds and thus, the success of the invasion (Richardson and Kluge 2008; Le Maitre et al. 2011; Hernández et al. 2014). This is particularly relevant for Mediterranean ecosystems that are characterised by frequent fires, which might contribute to explain the success of acacias such as *A. saligna* (Wilson et al. 2011) or *A. melanoxylon* (García et al. 2007). Moreover, under a climate change scenario, extreme and more frequent wildfires are expected in these ecosystems (IPCC 2013), which could effectively expand the distribution area of invasive acacias.

### 2.3 Symbiotic associations

As legumes, acacias are highly reliant on symbiotic associations with compatible microbes. In a new habitat, access to compatible rhizobia is a critical factor conditioning the invasive ability of legumes since mutualisms play a key role during their establishment (Parker 2001). Symbiotic promiscuity—low specificity for building up associations with compatible rhizobia—has been considered a characteristic trait of invasive legumes (Richardson et al. 2000b; Parker 2001). Invasive acacias can associate with a wide range of N-fixing bacteria (Lorenzo and Rodríguez-Echeverría, 2015). The invasive ability of acacias might be primarily determined by the capacity to form nodules profusely and more efficiently than native N-fixing legumes (Rodríguez-Echeverría et al. 2009, 2010). Acacias usually establish symbiotic relationships with the genus *Bradyrhizobium*, more specifically with *Bradyrhizobium japonicum* (Lafay and Burdon 2001; Rodríguez-Echeverría et al. 2007), in both native and non-native ranges (Birbaum et al. 2012; Boudiaf et al. 2014). However, symbiotic interactions with new mutualists have also been reported in non-native ranges for Australian acacias (mainly *Bradyrhizobium* and *Rhizobium*, but also *Mesorhizobium*, *Ochrobactrum* and *Ensifer meliloti*) (Rodríguez-Echeverría et al. 2011; Birbaum et al. 2012). For example, *A. saligna* may effectively associate with different rhizobial communities in non-native and native ranges (Birbaum et al. 2012).

Nevertheless, *A. longifolia*, *A. dealbata* and *A. melanoxylon* preferentially associate with co-introduced symbionts in non-native ranges (Rodríguez-Echeverría et al. 2011; Lorenzo and Rodríguez-Echeverría, 2015), discarding symbiotic promiscuity as an invasive trait. In fact, Le Roux et al. (2016) have recently indicated that native and invasive legumes (*Acacia* within them) interact with distinct rhizobial lineages in South Africa. They found that instead of the classic vision of disrupting invasions, acacias and their symbionts form novel modules which are largely unconnected to highly modular native legume–rhizobium networks. Genetic analysis of symbiotic bacteria from root nodules of *A. saligna* from

Portugal indicated that obtained sequences mainly clustered with Australian sequences, suggesting the co-introduction of symbiotic partners (Crisostomo et al. 2013). Consequently, the rapid expansion and great nodulation ability of *A. longifolia* could enlarge the population and spread of the associated exotic *Bradyrhizobium* through the establishment of positive feedbacks (Rodríguez-Echeverría et al. 2009). The establishment of positive soil feedbacks has been also suggested when *A. dealbata* grows in previously invaded soils (Lorenzo and Rodríguez-Echeverría 2012; Rodríguez-Echeverría et al. 2013). This fact illustrates the ecological risk of the voluntary and involuntary introduction of exotic mutualistic microorganisms in reforestation projects. Invasion by acacia species may be favouring a second invasion by their associated exotic soil microbes. As a consequence, such synergistic interaction could accelerate impacts on ecosystems in the introduced ranges (Invasional meltdown hypothesis, Simberloff and Von Holle, 1999).

### 2.4 A clear role of allelopathy?

The release of allelochemicals by invasive plants has been postulated as a factor influencing the surrounding environment and favouring invasion (Inderjit et al. 2011). Allelopathy occurs because some IAPs bring novel chemicals that affect native species (Callaway and Aschehoug 2000). The allelopathic phenomenon has been broadly studied in *A. dealbata*. In the invaded ranges, extracts of *A. dealbata* containing natural or close to natural concentrations affected germination, seedling growth, net photosynthetic rate, respiration rate and biomass of agricultural and native understory plants (Carballeira and Reigosa 1999; Lorenzo et al. 2010b, 2011, 2012; Aguilera et al. 2015a) and functional diversity of soil microbes (Lorenzo et al. 2013a). Studying the release of allelochemicals along the different phenological stages of *A. dealbata*, Lorenzo et al. (2010c) found that allelopathic interactions were higher during the flowering period and depended on target species. A recent study showed that allelopathic effects mainly take place at root level, causing anomalous growth and morphology and leading to seedling mortality (Aguilera et al. 2015b). Interestingly, in vitro experiments with natural leachates obtained from adult *A. dealbata* plants increase the radicle length of its own seedlings, suggesting self-stimulation (Lorenzo et al. 2010c). However, the stimulatory effect disappeared when *A. dealbata* seedlings were grown on native soils (Lorenzo and Rodríguez-Echeverría 2012). In, volatile organic compounds (VOCs) released by *A. dealbata* flowers reduced germination and growth of its own seedlings (Souza-Alonso et al. 2014a). Despite the evidence of allelopathy under controlled conditions, the allelopathic effect was not detected at field scale, suggesting a negligible role of allelopathy during the invasive process of

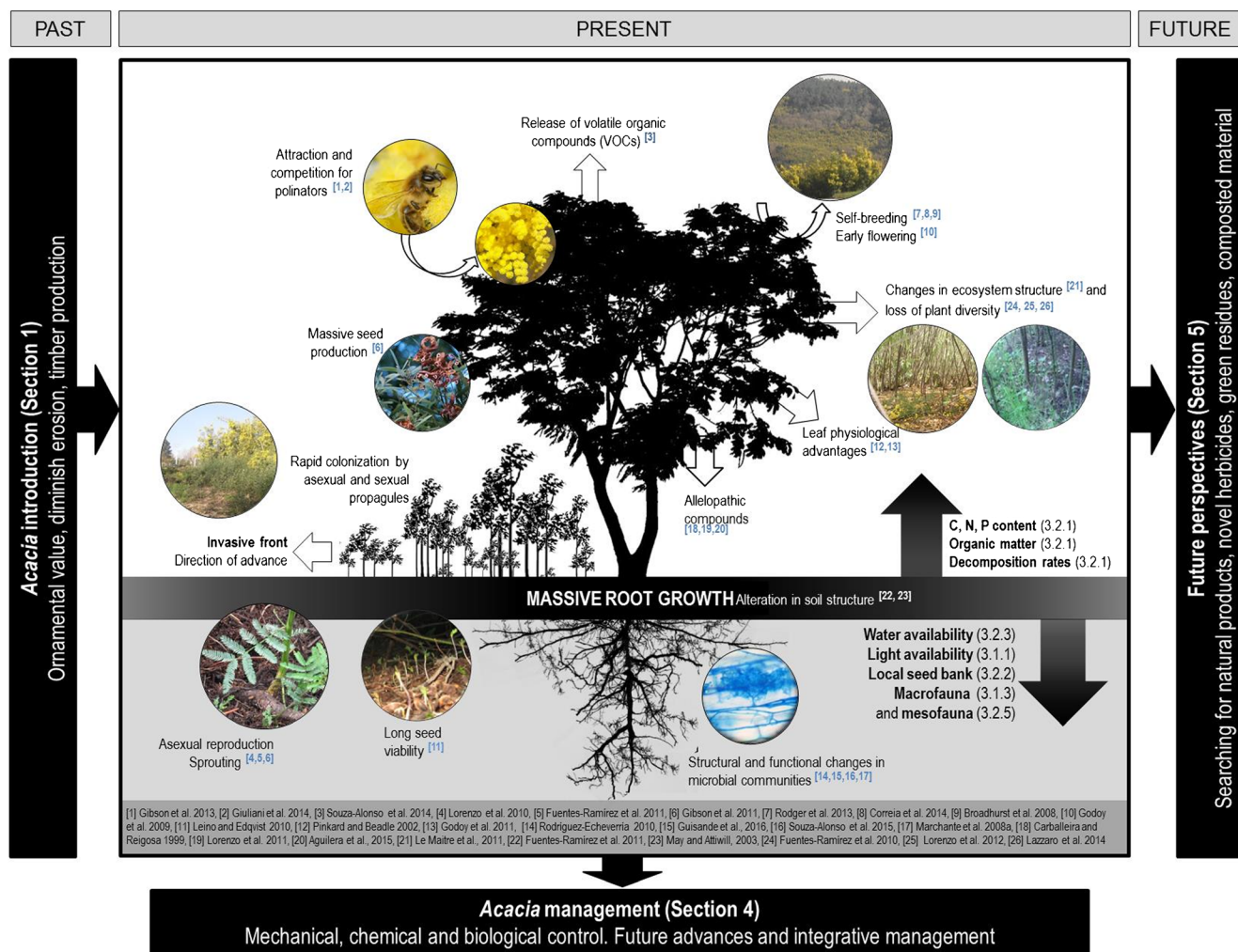
*A. dealbata*, at least in the European range (Lorenzo et al. 2016a; Souza-Alonso et al. under review).

Much less information is available on the allelopathic potential of other acacias. Litter at different stages of decomposition and soils of *A. melanoxylon* have shown negative effects on the germination and growth of native plant species (González et al. 1995; Souto et al. 2001). Stem and bark aqueous extracts of *A. melanoxylon* reduced the growth of the aquatic plant *Lemna aequinoctialis* (Allan and Adkins 2007), whereas extracts from phyllodes and flowers of this species inhibited biometrical and physiological parameters of native and model species (Hussain et al. 2011a, b). Residues of *A. mearnsii* also showed a moderate allelopathic effect on the growth of dicotyledons and grasses (Schumann et al. 1995). Finally, Ens et al. (2009a, b) suggested that allelopathy plays an important role in ecological interactions of *A. longifolia* in their native range. However, these studies only constitute evidence of potential allelopathy since bioassays were conducted under controlled conditions. In fact, the effect of allelopathic compounds depends on bioassay conditions as the

solvent, soil matrix or pH used and the presence/absence of soil microbes (Inderjit and van der Putten 2010; Lorenzo et al. 2016b). Therefore, experiments mimicking natural conditions are necessary to clearly identify the role of allelopathy in the invasive process. Otherwise, the allelopathic picture of the above-mentioned acacias will remain unclear and incomplete.

### 3 Effects on ecosystems

Invasive acacias affect both above- and belowground compartments as well as ecosystem services such as soil formation, water flow, nutrient cycling, wood or fibre production and recreation or educational opportunities that sustain human well-being (Le Maitre et al. 2011). The main characteristics of *Acacia* invasions are represented in Fig. 2. Nevertheless, the invasion of acacias presents geographical differences across Mediterranean regions.



**Fig. 2** Schematic representation of the main processes that take place under *Acacia* invasion and links to the main sections and references included in the manuscript

### 3.1 Aboveground effects

#### 3.1.1 Structural changes

Invasive acacias create homogeneous and dense-vegetation formations (Le Maitre et al. 2011), which drastically decrease light availability for understory plants hindering their establishment (Lorenzo et al. 2010a; Rascher et al. 2011a; Lorenzo et al. 2016a). In fact, Fuentes-Ramírez et al. (2011) found a lower survival of light-demanding native forest species vs. shade-tolerant species under *A. dealbata*. The reduced light availability also leads to lower grass productivity through the reduction of specific leaf area index (LAI) thresholds (Gwate et al. 2016). However, *A. dealbata* did not reduce the light availability in broad-leaf native forests (González-Muñoz et al. 2012). This fact reveals that the influence of *A. dealbata* on light conditions is severe in native open canopies, but with slight effect in closed-canopy ecosystems.

Changes in the dominant tree species entail subsidiary consequences. Dense *Acacia* canopies lead to the accumulation of high quantity of biomass and litter, which increases the occurrence and intensity of fires in invaded ranges. Fires, in turn, stimulate the germination of acacia seeds and reduce the viability of native seeds favouring the invasive process (Richardson and Kluge 2008; Le Maitre et al. 2011). However, this fact has more ecological relevance in ecosystems without dominant species reliant on fire to germinate. In some Mediterranean areas, such as in central Chile, model projections predict the dispersion of *A. dealbata* only in the presence of fire when combined with browsing and/or cutting (Newton et al. 2011).

#### 3.1.2 Plant biodiversity

In general, *Acacia* invasions significantly reduce plant cover, species richness and diversity (Holmes and Cowling 1997; Marchante et al. 2003; Tassin et al. 2009b; Fuentes-Ramírez et al. 2011; Lorenzo et al. 2012; Lazzaro et al. 2014). Biodiversity reduction due to *A. dealbata* invasion results in the replacement of native species by other natives or exotic plants (Fuentes-Ramírez et al., 2011; Lorenzo et al. 2012; Marchante et al. 2011b; González-Muñoz et al. 2012). In comparison with other invasive species, plantations of *A. saligna* have demonstrated a higher capacity to affect plant diversity (Manor et al. 2008). Surprisingly, *A. saligna* selectively increased the presence of ruderal grass species without reducing total richness (Del Vecchio et al. 2013). The identification of changes in plant species composition along invaded areas provides highly valuable information. Nonetheless, to our knowledge, whether modified native communities are accompanied by alterations in functional and phylogenetic diversity of invaded plant communities remains unknown.

#### 3.1.3 Macrofauna

The presence of invasive acacias also modifies habitat suitability for animals and establishes novel ecological networks. Van der Colff et al. (2015) found a different trend of arthropod community composition between native and invaded areas by *A. mearnsii*; arthropods could be using exotic trees as a pathway to reach isolated habitats. In this sense, leaf N content is an important driver of arthropod population dynamics in *A. mearnsii* stands (Maoela et al. 2016a). Nevertheless, arthropod assemblages in the native community can be progressively recovered after the removal of the exotic (Maoela et al. 2016b). On the other hand, Eichhorn et al. (2011) indicated that the artificial damage induced to the leaves of *A. dealbata* activated the production of extra-floral nectaries. After damage, leaves were only visited by the invasive Argentine ant *Linepithema humile*, which could imply an interspecific positive feedback between invasive species. Moreover, larger animals are also affected by acacia invasions. The tree density of *A. saligna* stands, together with other factors such as urban density or vegetation structure, contributed to the decline of birds diversity (Dures and Cummings 2010) and species of small mammals (Manor et al. 2008), linking the decrease in biodiversity with a reduction in habitat quality or ecosystem integrity. Additionally, seeds of *A. mearnsii* are used as a nutrient source by the specialist primate *Cercopithecus albogularis labiatus*, altering its feeding behaviour and probably leading to consequences for *A. mearnsii* dispersion (Wimberger et al. 2017).

### 3.2 Belowground effects

#### 3.2.1 Physicochemical changes and nutrient cycling

The rapid observation of the understory below the canopy of acacias indicates substantial changes in the structure of soil surface, linking *Acacia* invasion with the concept of *niche construction* (Day et al. 2003). The overwhelming surface root development of *Acacia* trees dominates and drastically transforms soil surface. *Acacia dealbata* creates a root net in the upper soil layer due to its extensive creeping rhizomatous system (Fuentes-Ramírez et al. 2011), reducing soil bulk density (May and Attiwill 2003). Similarly, *A. saligna* develops roots reaching 6 m during the first 4 years (Knight et al. 2002). Below the canopy, a thick layer of organic matter is progressively accumulated by the continuous litter fall (Marchante et al. 2004; Castro-Díez et al. 2012). Acacias provide litter with different C-sources composition that can affect nutrient cycling and decomposition, with possible ecological ramifications (Ens et al. 2009a). Nevertheless, decomposed plant material of *A. dealbata* did not produce significant changes in the functional and structural profile of soil microbial communities and soil chemical properties compared to the decomposition



of similar quantities of native plant material (Guisande et al. in preparation).

As  $N_2$  fixers, acacias increase N (Marchante et al. 2008a; Lorenzo et al. 2010b; Souza-Alonso et al. 2014b) or  $NH_4^+$  pools (Castro-Díez et al. 2012). *Acacia saligna* modifies N cycling through the production of higher amounts of litter, resulting in more N being returned to the soil and an increase in the availability of inorganic N (Yelenik et al. 2004). *Acacia longifolia* provides large quantities of N to the surrounding vegetation; however, at the same time, requires substantial amounts of P itself which creates a N/P imbalance at the community level (Ulm et al. 2016). Moreover, acacias substantially and progressively change C content in long-time invaded soils (Yelenik et al. 2004; Marchante et al. 2008a; Souza-Alonso et al. 2015). Other parameters, such as the content of organic matter or interchangeable P, were significantly increased by *A. dealbata* in soils from different ecosystems (Lorenzo et al. 2010b; Souza-Alonso et al. 2014b). However, Castro-Díez et al. (2012) found no differences in pH or organic matter after *A. dealbata* invasion. Souza-Alonso et al. (2014b) suggested that the variation in pH might be highly dependent on the studied ecosystem. *Acacia longifolia* drastically increased the content of C and N, C/N ratio, pH and litter in ecosystems with poor soils, such as sand dunes and coastal areas (Marchante et al. 2008a, c; Rascher et al. 2011a), resulting in differences in the catabolic diversity of microbial communities (Marchante et al. 2008c). Interestingly, these soil changes lead to a positive feedback between acacias and invaded soils. Soils previously invaded by *A. dealbata* favour the growth of its own seedlings and increase the mortality of the co-occurring native *Pinus pinaster* Aiton (Lorenzo and Rodríguez-Echeverría 2012; Rodríguez-Echeverría et al. 2013). This legacy effect—persistent changes in the long term—may continue even after acacia removal (Marchante et al. 2008b, 2011a).

### 3.2.2 Seed bank

The composition of the soil seed bank after acacia invasion is significantly modified by limiting or interrupting native propagule supply. Richness of native seeds was drastically decreased after the increase in *A. longifolia* density, while seeds of the invader were progressively accumulated (Fourie, 2008, Richardson and Kluge 2008; Le Maitre et al. 2011). Similarly, the diversity of the seed bank in understories invaded by *A. saligna* and *A. dealbata* was severely affected (Holmes and Cowling 1997; González-Muñoz et al. 2012), resulting in a diminution and homogenisation in the size of the native seed bank and higher percentages of exotic seeds in invaded ecosystems (Marchante et al. 2011b; González-Muñoz et al. 2012).

### 3.2.3 Water relationships

Water availability is often indicated as one of the main limiting factors of plant growth in Mediterranean areas (Claeys and Inzé 2013; Flexas et al. 2014). Across their range of introduction, invasive acacias are considered as water-consuming species, and their presence leads to a reduction in the quantity and quality of available water in soil and an increase in the evapotranspiration rate (Lorenzo and Rodríguez-Echeverría 2015). In the non-native range, water consumption by *A. melanoxylon* was higher than that measured for highly competitive species such as *Eucalyptus globulus* or *P. pinaster* (Jiménez et al. 2010). In South Africa, besides the use of groundwater, *A. dealbata* and *A. mearnsii* collected an important part of the estimated reduction of the mean annual runoff produced by all invasive plants (Le Maitre et al. 2000). This is particularly relevant in areas that present very low surface runoff, as in coastal arid regions. Novel *A. mearnsii* populations presented higher water losses compared to natives (Dye et al. 2001), whereas *A. longifolia* reduced the water flow on average by 26% in pine forests of coastal dunes in Portugal (Rascher et al. 2011b). At the same time, changes in hydrologic dynamics produced by *A. longifolia* were also associated with decreased C fixation rates of native trees (Rascher et al. 2011b). Interestingly, the high water consumption is generally considered a strategy for individual fast growth. Nevertheless, due to the ability of acacias to sprout, water consumption could be alternatively seen as a community-level strategy promoting the collective rather than individual plants in the long term (Werner et al. 2010).

Acacias can also influence the water availability for surrounding plant communities through other strategies at root level. High molecular weight alkanes exuded from roots by *A. longifolia* can induce water repellence, thereby reducing the accessible water for native seedlings (Ens et al. 2009b). However, under stressful conditions of limited water supply, *A. longifolia* revealed high drought sensitivity in terms of biomass and N-uptake efficiency, which was even more marked when plants grew with intra- or interspecific competition (Werner et al. 2010). Considering the evolutionary link that relates drought-tolerant xylem structure with the capacity to resist lower water potentials (Bhaskar and Ackerly 2006), *A. mearnsii* showed lower water potential at 50% hydraulic conductivity loss ( $P_{50}$ ) compared to native species, suggesting drought-tolerance (Crous et al. 2012). Field xylem water potentials also support that *A. mearnsii* has a significant advantage over some native species under drier conditions (Crous et al. 2012).

The removal of acacias might facilitate the replenishment of water for native vegetation, becoming a key factor to be considered in management operations, particularly in Mediterranean areas. In fact, removal of *A. mearnsii* and *A. longifolia* from riparian habitats increased the streamflow



(Prinsloo and Scott, 1999). Marais and Wannenburg (2008) suggested that the removal of invasive acacias does not immediately imply water availability, but they consider it as an important part of a package of several actions to optimise water supply. Jovanovic et al. (2009) indicated that clearing lands invaded by *A. saligna*, besides the increase in water availability due to the reduction in evapotranspiration, may also reduce the contamination of groundwater by nitrate. Notwithstanding, to be realistic, changes in water regimes attributed to *Acacia* invasions or plantations should also include climatic conditions (rainfall patterns) as a potential source of variability (Rangan et al. 2010).

### 3.2.4 Soil microorganisms

Recent studies found substantial changes in soil microbial communities at structural and functional level produced by *Acacia* invasion (Marchante et al. 2008a, c; Lorenzo et al. 2010b, 2013a; Boudiaf et al. 2013; Souza-Alonso et al. 2014b, 2015). These changes are more pronounced in the long term or in heavily invaded areas and depend on the invaded ecosystem (Marchante et al. 2008a; Lorenzo and Rodríguez-Echeverría 2015). In addition, bacteria seemed to be more affected than fungi (Marchante et al. 2008a; Lorenzo and Rodríguez-Echeverría 2015).

**Bacteria** *Acacia* invasion affects both the structure and functional diversity of soil bacterial communities (Lorenzo and Rodríguez-Echeverría 2015). Particularly, *A. longifolia* and *A. dealbata* alter the structure of bacterial communities from dunes, grasslands and mixed forests (Marchante et al. 2008a, c; Lorenzo et al. 2010b), relating the duration of the invasion with the magnitude of the effect produced (Marchante et al. 2008a; Souza-Alonso et al. 2015). On the other hand, the functional catabolic diversity of soil bacteria also varies after the invasion by *A. longifolia*, *A. dealbata* and *A. mearnsii* (Marchante et al. 2008c; Boudiaf et al. 2013; Lorenzo et al. 2013a).

**Fungi** The effect of invasion on soil fungal communities was mainly studied in soils invaded by *A. dealbata*, which modifies the community structure of generalist fungi in pine forests and shrublands, but the effect depend on the studied ecosystem (Lorenzo et al. 2010b; Souza-Alonso et al. 2014b). Nevertheless, fungal communities seemed to evolve tolerance to invasion since they tended to return to the structure of pre-invaded community after long periods (>25 years) of invasion (Souza-Alonso et al. 2015). *Acacia* invasion also modified specific fungal groups such as arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EM). Structural changes in AMF communities caused by *A. dealbata* were accompanied by a reduced growth of the highly AMF-reliant plant *Plantago lanceolata* (Guisande-Collazo et al. 2016). However,

chemical compounds naturally released by *A. dealbata* did not affect the potential infectivity of AMF in different native soils (Lorenzo et al. 2013b). Similarly, *A. mearnsii* significantly altered the structure and composition of EM which, in consequence, produced a decrease in the early growth of the native tree *Quercus suber* L. (Boudiaf et al. 2013).

### 3.2.5 Mesofauna

The relationships between native plants and the community of decomposers can be also altered due to the presence of acacias. However, despite its fundamental role, studies addressing impacts of acacias on groups implicated in the breakdown of organic matter are scarce. Coetzee et al. (2007) found a significant reduction in richness, abundance and body size of arthropods (Coleoptera) in grasslands invaded by *A. dealbata* compared to non-invaded areas. Additionally, the presence and litter production of *A. mearnsii* in riparian habits altered the structure of invertebrate communities, reducing the abundance of some cobble-dwelling taxa but increasing particle-feeding mayflies and chironomids (Lowe et al. 2008). Below *A. melanoxylon* and *A. mearnsii* canopies, invertebrate richness was reduced compared to that under native species, and this reduction was higher at species level than at family or order level (Samways et al. 1996), indicating that changes in the dominant species has probably lower implications at functional level. Furthermore, qualitative changes in litter composition produced by *A. dealbata* and *A. longifolia* invasion result in poor nutrient material for terrestrial isopods—key components of macro-decomposer communities—leading to smaller individuals (Sousa et al. 1998).

## 4 Control and management

### 4.1 Recent advances in traditional control

Research on *Acacia* management started in South Africa, a pioneer country implementing management policies at national level. First organised efforts to control *A. dealbata*, *A. longifolia* or *A. mearnsii* were carried out mainly through the implementation of the Working for Water program (van Wilgen et al. 2011 and references therein). In general, the management of acacias is an expensive investment and long-time task due to the sprouting ability and their large and resilient seed banks (Richardson and Kluge 2008; Gaertner et al. 2012; van Wilgen et al. 2016).

Potential effective results have been achieved using triclopyr herbicide combined with cutting of *A. dealbata* individuals in a short-term strategy (Campbell and Kluge 1999; Souza-Alonso et al. 2013). Triclopyr was also effective to control *A. mearnsii* seedlings, even at low doses (Viljoen

and Stoltz 2008). Herbicide combined with cutting was useful to reduce *A. saligna* in post-burning control. However, cutting *A. saligna* saplings below the coppicing point produced the best results (Krupek et al. 2016). In other cases, the knowledge of the best phenological stage to manage acacias improves the effectiveness of management actions. For instance, basal cuttings of young *A. mearnsii* individuals ( $\leq 7$  years) should be preferably done in non-growing periods to diminish sprouting (Perrando and Corder 2006). On the other hand, similar management actions may yield different results at different locations due to the specific site conditions and life history traits. In South Africa, the felling and removing of *A. mearnsii* produced both positive and negative results, which could be related to local specific conditions (Blanchard and Holmes 2008). Nevertheless, results obtained during the last decades showed that the successful recovering of invaded areas by using traditional control methods is difficult to achieve due to the extension of invasion invaded areas (van Wilgen et al. 2012).

#### 4.2 Biological control

The biological control of acacias started with the introduction of the bud-galling wasp, *Trichilogaster acaciaelongifoliae*, to control *A. longifolia* in South Africa (Dennill and Donnelly 1991). After several generations, the production of *A. longifolia* pods has been highly reduced. However, the effectiveness of the bud-galling agent was higher in areas with similar atmospheric conditions to native regions of the introduced wasp. In addition, a recent study found that populations of *A. longifolia* showing high genetic variability may differentially respond to the control agent in introduced ranges (Thompson et al. 2015), hampering the success of the biological control and compromising the reproducibility of this method. Similarly, the beetle *Melanterius ventralis* was introduced to feed on seeds of *A. longifolia*, producing seed mortality in a range from 15 to 79.5% (Donnelly and Hoffmann 2004). In Portugal, *T. acaciaelongifoliae* was recently introduced and tested on *A. longifolia* under controlled conditions with positive results (Marchante et al. 2011c). Subsequently, the European Commission (EC), after approval by the EFSA Panel on Plant Health (EFSA 2015; Jeger et al. 2016), authorised field tests that were conducted in late 2015 (Shaw et al. 2016). First reports indicated that *T. acaciaelongifoliae* successfully completed its life cycle in Portugal although the number of detected galls is currently low (Marchante et al. 2017). The flower-galling midge *Dasineura rubiformis* was also effectively introduced to control *A. mearnsii*, exclusively affecting its reproductive capacity (Impson et al. 2008, 2013). During the period of 1991–2005, the introduced rust-fungus *Uromycladium tepperianum* significantly affected *A. saligna* by reducing tree density (between 87 and 98%) and canopy mass, also increasing tree mortality (Wood and Morris 2007).

However, undesirable side effects of biological control may occur (Seymour and Veldtman 2010; Veldtman et al. 2011). In South Africa, the liberation of some control agents such as *T. acaciaelongifoliae*, *Dasineura dielsi* and *M. ventralis* unintentionally damaged the non-target *A. melanoxylon*, *A. longifolia* and *A. melanoxylon*, respectively (Dennill et al. 1993; Post et al. 2010; Donnelly and Hoffmann, 2004). This could be related to the low specificity of biocontrol agents that can lead to affinities for related species (Donnelly and Hoffmann, 2004). In fact, congeneric plants closely related to the target species are more susceptible to be also attacked than distantly related ones (Pemberton, 2000). In these cases, the side effect can be considered “positive” since other invasive congeners (all leading to acacia control) were targeted. Therefore, the use of biological control agents in Europe or North America to control acacias should have presumable low ecological risks due to the absence of native acacias. On the other hand, ecological effects of introduced agents are not completely addressed and unexpected consequences as ecological replacement, compensatory responses or food-web interactions may occur (Pearson and Callaway 2003). In fact, agents introduced to control *A. longifolia* and *A. saligna* in South Africa created complex food webs in the introduced range, similar to those in their native ranges (Veldtman et al. 2011). Main ecological pressures or inconsistencies derived from the introduction of novel agents were identified by Louda et al. (2003) as the susceptibility of related species, host specificity determined by physiological range, increase in the extinction risk of vulnerable species, or the infiltration in natural areas away from targeted agroecosystems.

#### 4.3 Effective recovery of cleaned areas

Theory predicts that management programs are more effective if invaders are rapidly recognised and the time between the introduction and management is as short as possible (Simberloff et al. 2013; Luque et al. 2014; Kimball et al. 2015). The intensity of the required intervention for ecosystem recovery is proportional to the duration (i.e. density) of invasion (Holmes et al. 2000). Furthermore, the early detection of invasive plants also contributes to a cost-effective management. Economic costs of clearing dense invaded areas are 3–20 times higher than those necessary to manage scattered invaded areas (Marais and Wannenburg 2008). In this sense, the current regulation of the European Commission on invasive species foresees three types of interventions: prevention, early detection and rapid eradication and management (EC 2014). However, the success of land restoration after acacia removal is uncertain because of the severe changes in soil physicochemical properties (Marchante et al. 2004, 2011a, b). The transformation of ecosystems invaded by acacias suggests that a return to pre-existing conditions is virtually

impossible. Therefore, the concept of *restoration* should be understood as a synonym of *recovery*.

After the removal of invasive acacias, the ecosystem recovery takes several years before soil nutrients and processes return to similar pre-invasion levels. In fact, the autonomous recovery potential of native vegetation after clearing of dense *Acacia* stands is certainly limited (Mostert et al. 2017). For example, the recuperation of native plant communities in coastal sand dunes is diffculted by the time elapsed from the introduction of *A. longifolia*. Thus, eradication efforts should be maintained in the long term to achieve positive results (Marchante et al. 2008b). To develop efficient recovery programs, secondary effects after the removal on invaders must be also considered. In this line, the enhanced content of N in invaded soils favours the settlement of grasses, forbs and other shrubs, but hinders ericoid or proteoid species (Gaertner et al. 2012). Additionally, the growth rates of the nitrophilous species *Ehrharta calycina* increased in stands where *A. saligna* was removed, suggesting that subsequent invasions by weeds may occur after clearing N<sub>2</sub>-fixing alien species (Yelenik et al. 2004). Consequently, ecosystem recovery can be facilitated by the simultaneous removal of the N-rich litter layer, facilitating the germination of native species in the short term (Marchante et al. 2004, 2008b). Nevertheless, a field study assessing long-term consequences of *Acacia* removal found that the recovery of native vegetation in 15-year-old cleared sites was accompanied by a gradual improvement in soil nutrient levels (Ndou and Ruwanza 2016). Removal without an adequate planning of management can lead to the exposure of infertile subsoil vulnerable to erosion, even more in areas with slow rates of plant colonisation such as hill slopes (Van Der Waal et al. 2012). This fact also restricts the colonisation by indigenous species that could aid in the soil stabilisation (de Neergaard et al. 2005).

The maintenance of the native seed bank is fundamental to successfully recover ecosystems after *Acacia* invasion. Unsuccessful recovering of invaded ecosystems after acacia removal is frequently related to the lack of native seeds or propagule supply (Galatowitsch and Richardson 2005). If the native seed bank is severely depleted after plant invasion, autogenic recovery can be inhibited (Le Maitre et al. 2011). In fact, when the seed bank is exhausted or reaches critical values, the inclusion of native seeds in restoration programs could be essential to achieve pre-existing conditions. For example, the re-introduction of riparian species is required in highly transformed river basins to promote recovery and prevent re-invasion (Holmes et al. 2005). In addition, native species with low nutrient requirements and strong competitive ability that can outcompete invasive acacias at the early seedling stage are particularly valuable (Werner et al. 2010), which may facilitate ecosystem recovery.

At the same time, massive seed banks of acacias are difficult to manage after the removal of acacias (Richardson and

Kluge 2008). In some cases, fire was used to manage the acacia seed bank in dense invaded stands (Krupek et al. 2016). The application of fire after tree removal reduces the content of N in soil, causes a mass germination of *Acacia* seeds and occasionally stimulates the indigenous seed bank, as in fire-prone ecosystems (Le Maitre et al. 2011). Nevertheless, fire has negative consequences, and prescribed burns are only recommended under specific circumstances, as steep slopes or inaccessible areas (Fill et al. 2017). In general, fire should be used judiciously, combined with other methods or discarded in situations where conservation of indigenous biological diversity is of central consideration (Richardson and Kluge 2008). Soil surface temperature can be modified without the use of fire. In the case of small invaded areas, the dormancy of *Acacia* seeds might be artificially removed through soil solarisation. For example, Cohen et al. (2008) achieved a complete exhaustion of buried seeds of *A. saligna* using polyethylene mulches to impede the photosynthetic process and produce hydrothermal stress.

However, active restoration actions are rarely implemented after clearing invaded areas, unless the cost/benefit ratios are deemed acceptable (Fill et al. 2017). Active restoration can be effective and even financially feasible when compared to passive restoration. The density of exotic tress generally determines whether the economic balance of restoration is positive or negative (Gaertner et al. 2012). There is increasing evidence that, in some cases, the restoration of invaded areas is feasible and can provide multiple social and economic benefits (Murcia et al. 2014).

#### 4.4 Towards an integral management

Experience obtained in the management of acacias has shown that successful projects require clear and time-based goals, adequate resources and actual and in-kind support from the stakeholders (Forsyth et al. 2012). An improved management strategy based on recently developed frameworks (Kumschick et al. 2012, 2015; Blackburn et al. 2014; Hawkins et al. 2015) should focus on priority areas and species, assuming trade-offs between preserving biodiversity and avoiding the expansion of the invasion; otherwise, money allocated to control actions will be wasted (van Wilgen et al. 2016).

However, until now, management actions conducted in priority areas showed little progress in reducing total infestation (van Wilgen et al. 2012; Gwate et al. 2016). Even in South Africa where public funds were periodically invested and maintained to control invasive acacias, the economic resources were clearly insufficient to eradicate the invasive acacias (van Wilgen et al. 2012). Combining management techniques such as the integrated use of fire and active re-seeding of cleared areas with indigenous shrubs would substantially increase the effectiveness of ecosystem restoration (Fill et al. 2017). Profitable land uses, selective thinning of invasive

aboveground biomass or grazing could enhance multi-benefits in invaded landscapes (Seastedt et al. 2008; Gwate et al. 2016).

Spatiotemporal modelling approaches, such as individual-based models (IBMs), stochastic dynamic methodology (StDM), or species distribution models (SDMs) are being developed to anticipate *Acacia* invasions and manage their impacts in Mediterranean areas (Thompson et al. 2011; Santos et al. 2015). However, SDMs combined with phylogeographic approaches were not totally effective in predicting the occurrence of the two subspecies of *A. dealbata* (*A. dealbata* ssp. *dealbata* and ssp. *subalpina*) in South Africa (Hirsch et al., 2017). Recently, hierarchical framework that combines SDMs, scenario analysis and cost analyses to improve the assessment of *Acacia* invasions at regional and local scales has also been developed (Vicente et al. 2016). In addition to previous approaches, impacts of acacias in a specific area can be initially assessed by using the generic impact scoring system (GISS), a novel and feasible tool to easily quantify ecosystem impacts (Nentwig et al. 2016).

In our opinion, the current vision of *Acacia* management by scientists is mainly focused on the ecological perspective, avoiding socioeconomic implications. Generally, management actions are carried out with public sources, resulting in an unavoidable necessity of social and scientific alliances. Public perception of IAPs is a key part in the assessment of management strategies, therefore providing a favourable social and political environment which is essential to achieve successful results. The engagement of public perception in management actions is more efficient and accepted by both parts (Panetta and Timmins 2004). In this sense, the use of inquiries is currently gaining interest as an informative and feedback tool in decision-making processes (Verbrugge et al. 2014; Liu and Cook 2016). Otherwise, eradication efforts are useless when administration and social actions do not pursue similar interests, suggesting that local communities need to be actively involved in the control of IAP and management programs (Mukwada and Manatsa 2017).

After several years of observation, we are also certain that socioeconomic aspects such as the forced human migration from rural to urban areas leads to land neglect and misuse and this movement is favouring the invasion by *Acacia*—and also other IAPs. Facilitating the settlement of population in rural areas would help to quickly identify and avoid the dispersal of acacia propagules, preserving rural native vegetation. In fact, increase access to land use for farming purposes could result in a greater concern, care and, ultimately, a better management of acacias (de Neergaard et al., 2005). Unfortunately, unworked or unprotected lands do not represent a significant value for the society. To us, government policies exclusively focused on the control of IAPs, but avoiding the problem of land misuse, cannot be totally effective.

Moreover, in many areas worldwide, the governmental actions to control acacias rely on workers that are seasonally

recruited and do not necessarily return the following season (Fill et al. 2017). In other cases, as in the Working for Water program, the objective of maximising employment (reducing cost/person day) limits the effective monitoring and evaluation of outcomes due to poorly trained workforce (van Wilgen and Wannenburg 2016). Alternatively, operational models that extend monitoring units throughout the year would lead to a better IAP management, saving economic funds (e.g., training costs) and ameliorating decision-making processes (Fill et al. 2017). In our point of view, an effective and sustainable control of acacias should include not only management actions and continuous monitoring, but also the maintenance of population in rural areas, thereby facilitating the surveillance and stability of ecosystems. Further actions to include the participation of society should also be a motivational challenge for those social agents involved in controlling IAPs (Le Maitre et al. 2011). Idealistically, in the current context of a changeable economic scenario and unsustainable consumption of resources, policies adopting long-term initiatives to ameliorate human life conditions, reorganising our concepts of human progress, sustainable society and land development, are required.

## 5 Future research and perspectives

Here to stay? Was a rhetorical question proposed by Richardson et al. (2011) exploring the human dimension—historical, scientific, social—of introduced acacias. In our opinion, *Acacia* invasions are far from being fully understood and foreseeable, becoming a challenging task for the next decades. In a context of climate change and land use alterations, Mediterranean ecosystems are under the pressure of new invasions by *Acacia* species. Wilson et al. (2011) recommended key topics of short- and long-term research to understand and manage potential invasiveness of invasive acacias, highlighting the importance of seed bank dynamics and seed dispersal, biogeographical comparisons to understand successful introductions, control and responsible actions (including public awareness). In this sense, emerging tools such as modelling, genomics, remote sensing and new imaging tools, the elaboration of improved ecological databases or the application and amelioration of allometric equations for biomass estimation based on larger forestry datasets will contribute to answer past and future questions regarding *Acacia* invasions. According to our experience, acacia stands should be considered as an *entity* instead of a group of individuals due to the massive vegetative reproduction. Thus, the clonality, physiological integration or resource allocation are topics that remain poorly understood for invasive acacias.

Acacias are catalogued as undesirable plants while, at the same time, their cultivation also provides profitable resources in different countries. It is therefore fundamental to determine



the trade-off between the commercial value and related environmental problems. To avoid the undesirable impacts without interfering with industry purposes, the implementation of sterile lineages of acacias is under investigation (Beck and Fossey 2007; Beck-Pay 2013). We also suggest that forest managers, industries or land owners that benefit from the cultivation of exotic acacias should be economically responsible for the problems derived from their plantations. Law reinforcement to unify forest regulations, especially among countries in the Mediterranean basin such as Spain, Portugal or Italy, is necessary to avoid further introduction of invasive acacias.

Current socioeconomic conditions are unstable in many countries, which imply that cost-effective management investments should be preferred instead of those which uniquely imply costs. Large management actions are probably unsustainable in the long term, whether they are entirely dependent on external funding (de Neergaard et al. 2005). In this line, we suggest that obtaining benefits of residues obtained from the management of acacias could alleviate the cost of the management. Therefore, we compiled several incipient research areas where acacias could be useful:

1. *Agriculture*: according to the directive on the sustainable use of pesticides proposed by the European Commission (2009/128/EC), the excessive use of synthetic herbicides should be reduced. In this sense, phytotoxicity compounds of invasive acacias could be used as a base to develop new bio-herbicides, bio-pesticides or phytotoxic mulches to control weeds or plagues in crops (Narwal 2010; Jabran et al. 2015). In fact, studies to identify the phytotoxic activity of chemical compounds from different *A. dealbata* material (Lorenzo et al. 2016b) and the use of green manures from *A. dealbata* and *A. longifolia* as bio-herbicides in agricultural soils (Souza-Alonso et al. under review) are currently in progress. Similar to other legume species (Narwal 2010), acacias pose nutrient-enriched leaves that could be used as fertilisers and a source of nutrients for crops. After full compost maturation, *A. longifolia* and *A. melanoxydon* provide agricultural amendments, biocomposts, with high organic matter content and low electrical conductivity (Brito et al. 2013, 2015). Composting residues of *A. dealbata* with sewage sludge also improves soil biochemical and chemical properties (Tejada et al. 2014). The use of acacia residues can be included into the current idea of changing towards a green economy, in the framework of the bioeconomy strategy (H2020 Program).
2. *Industry*: the high polysaccharide content of *A. dealbata* is a valuable resource for biorefineries, providing a way of upgrading underused renewable feedstocks (Yañez et al. 2009, 2013). New cationic polymeric coagulants for water and different types of industrial effluent treatments were synthesised with tannin extracted from *A. mearnsii*

(Beltrán-Heredia et al. 2010, Sánchez-Martín et al. 2012; Soares et al. 2012), having also potential as phytoextractor in the remediation of heavy metal contaminated biosolids (Mok et al. 2013). Similarly, Kumari and Ravindhranath (2012) successfully employed *A. melanoxydon* as biosorbent in the extraction of  $Al^{+3}$  ions from waste waters collected from industrial effluents and polluted lakes. In addition, extracts from *A. mearnsii* showed positive results to control blue algal blooms (Zhou et al. 2012).

3. *Health purposes*: acacias can also be a chemistry source of chemical components with medical and health purposes. In example, bark of *A. mearnsii* is traditionally used in the treatment of stomach diseases (Wintola et al. 2017). Crude extracts from this species also exhibited significant antimicrobial activity, becoming a potential source of bioactive compounds (Olajuyigbe and Afolayan 2012). Phenolic, flavonoid and alkaloid contents of raw extracts from *A. dealbata* and *A. melanoxydon* showed stronger antioxidant activities (Luis et al. 2012). Preliminary results also indicate that water-soluble compounds present in extracts of *A. melanoxydon* exhibited anthelmintic activity against larval development of horse parasites (Payne et al. 2013). Acacia honey induces the expression of cytokines and a metalloproteinase that degrades collagen IV involved in the disorganisation of basal membrane during the re-epithelialisation process of wounds (Burlando and Cornara 2013).
4. *Cosmetics*: Absolute oils from *A. dealbata* have been used in cosmetic industries, especially in the production of perfumes, due to the presence of odorant compounds (Perriot et al. 2010).

## 6 Conclusions

Substantial efforts have been carried out during the last years to address the consequences of the invasion of Mediterranean ecosystems by acacias. Nowadays, having left behind the consideration of emerging threats, acacias are recognised as severe menaces to Mediterranean ecosystems and the reinforcement of transnational regulations, together with the development of crossing-information platforms, seems crucial to prevent novel *Acacia* introductions. Under a future scenario of climate change, these ecosystems are expected to be largely occupied by invasive acacias due to their increased growth under higher  $CO_2$  conditions, seed production and fire resistance. Changes in hydrological dynamics by acacia invasions may also exacerbate droughts in Mediterranean areas under expected extreme climatic events.

Invasions by acacias usually lead to changes in ecosystem services as water and fire regimes, reduction in plant biodiversity and alteration in soil physicochemical properties and

function. Modified soil microbial communities may have negative implications for nutrient cycling, ecosystem processes and native vegetation that rely on them, which, in turn, might favour acacia invasion and increase the vulnerability of affected ecosystems. In terms of the assessment of native plant communities, a deeper knowledge of the functional and phylogenetic diversity, rather than the use of classic diversity indices, should be considered to evaluate the extent of the ecological impacts produced. Further work is also needed to elucidate the proportion of sexual vs. vegetative reproduction during the invasion process to design adequate control strategies.

We consider that the management of acacias should be focused on prioritising the preservation of non-invaded habitats and the identification of areas with potential to host invasive acacias. Risk assessment studies, based on recently developed frameworks and more focused on forecasting and preventing future introductions rather than evaluate changes in already invaded areas, are also desirable. It is also time to communicate and to engage social, politician and stakeholder perceptions to provide integrative, sustainable and adapted solutions to *Acacia* invasion, since high economic investments do not necessarily assure the success in the control of *Acacia* invasions. The search of potential uses for acacia residues could possibly bring solutions to partially alleviate the economic resources allocated to their management and, at the same time, reduce the extension of invasive populations. Therefore, applied research on profitable uses for acacia residues seems to be highly relevant in the future.

After two centuries of introduction, rapid evolutionary processes could be occurring and should be an interesting point of future works. Ecologists and evolutionary biologists are at the forefront of a model group, with challenging research possibilities. In the same line, novel relationships between plant pollinators, plant-seed dispersers or plant herbivores and acacias can produce novel ecological interactions that could alter or displace well-established ecological networks. In this sense, the rhetorical question raised 6 years ago *here to stay?* should be currently transformed—as the title of our review indicates—into an affirmative sentence. The emerging assumption that the complete eradication of acacias seems, in some cases, unfeasible provides a new context in which the study of the ecological role of *Acacia* formations—as novel ecosystems—emerges relevant.

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