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Original article

Two invasive acacia species secure generalist pollinators in invaded communities

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ABSTRACT

Exotic entomophilous plants need to establish effective pollinator interactions in order to succeed after being introduced into a new community, particularly if they are obligatory outbreeders. By establishing these novel interactions in the new non-native range, invasive plants are hypothesised to drive changes in the composition and functioning of the native pollinator community, with potential impacts on the pollination biology of native co-flowering plants. We used two different sites in Portugal, each invaded by a different acacia species, to assess whether two native Australian trees, *Acacia dealbata* and *Acacia longifolia*, were able to recruit pollinators in Portugal, and whether the pollinator community visiting acacia trees differed from the pollinator communities interacting with native co-flowering plants. Our results indicate that in the invaded range of Portugal both acacia species were able to establish novel mutualistic interactions, predominantly with generalist pollinators. For each of the two studied sites, only two other co-occurring native plant species presented partially overlapping phenologies. We observed significant differences in pollinator richness and visitation rates among native and non-native plant species, although the study of β diversity indicated that only the native plant *Lithodora fruticosa* presented a differentiated set of pollinator species. Acacias experienced a large *number* of visits by numerous pollinator species, but massive acacia flowering resulted in flower visitation *rates* frequently lower than those of the native co-flowering species. We conclude that the establishment of mutualisms in Portugal likely contributes to the effective and profuse production of acacia seeds in Portugal. Despite the massive flowering of *A. dealbata* and *A. longifolia*, native plant species attained similar or higher visitation rates than acacias.

1. Introduction

Once an exotic plant is introduced into a new community, it typically needs to engage in a number of mutualistic interactions in order to successfully establish into the new area (Richardson et al., 2000; Traveset and Richardson, 2006). For entomophilous plants, one key mutualism for the effective production of offspring is the interaction with pollinators, which is of particular importance for obligatory outbreeders (Gibson et al., 2011). Invasive plants tend to be pollinated by generalist insects both in their native and non-native ranges (Chrobock et al., 2013; Gibson et al., 2011; Gotlieb et al., 2011; Lopezaraiza-Mikel et al., 2007; Padrón et al., 2009), and often offer large floral displays and floral rewards which can influence pollinator behaviour and preferences and thus affect the surrounding plant community either positively, by attracting shared pollinators to the site, neutrally, or negatively, by competing for pollination services (Moragues and Traveset, 2005; Larson et al., 2006; Bartomeus et al., 2008). Such effects are often species-specific, and invasive plants can benefit some native species while harming others in the same community (Ferrero et al., 2013; Moragues and Traveset, 2005). In any case, the presence of invasive species has the potential to influence pollinator species composition and relative abundance, influencing pollination efficiency and reproductive success of native plants (Ferrero et al., 2013; Gibson et al., 2012; Gotlieb et al., 2011; Lopezaraiza-Mikel et al., 2007).

Nevertheless, the potential impact of invasive species on the reproductive success of natives should be strongly related to their phenological synchrony. Because flowering phenology is an essential factor of pollination success, the degree of synchrony between the flowering period of the exotic species and the native flora has important implications both for the success of exotic species and for the native plant species (Traveset and Richardson,

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2006). Invasive species tend to present high phenological plasticity (Munguía-Rosas et al., 2013) and because flowering phenology has important fitness implications, phenology is usually under strong selection (Munguía-Rosas et al., 2011). Phenological asynchrony between native and invasive plants is frequent at invaded communities (Godoy et al., 2009a, b) and although it has been scarcely studied, the available literature suggests that asynchrony with native plant species is mostly beneficial to invasives, which have the opportunity to benefit from an at least partially empty niche (Godoy et al., 2009a, b; Wandrag, 2012). Pollinators tend to favour early flowering, particularly if it involves extending the pollination season (Elzinga et al., 2007; Munguía-Rosas et al., 2011; Rafferty and Ives, 2011). Unsurprisingly, the exploitation of new temporal niches with reduced competition for biotic and abiotic resources has been found to benefit invasive species (Godoy et al., 2009a, b; Lediuk et al., 2014) and is believed to benefit invasive acacias (Gibson et al., 2011) although experimental data is not yet available for this group of plants.

Acacia dealbata Link and *Acacia longifolia* (Andrews) Willd. [*Acacia* subgenus *Phyllodineae* (DC.) Ser. = *Acacia s.s.*], are two native Australian trees which have become invasive in several parts of the world, including Portugal where they are considered the most problematic and widespread invasive species in the country (Almeida and Freitas, 2012; 2006). Although both acacia species have the ability to successfully self-fertilize, the efficiency of self-pollination is low (below 0.5% of seed:ovule ratio), thus both species require pollination vectors to produce significant seed yields, and both are considered predominantly outcrossing species (Correia et al., 2014). In their native range both species sustain mutualistic interactions essential for the successful maintenance of populations and for the colonization of new areas (Berg, 1975; Gibson et al., 2011; O'Dowd and Gill, 1986; Rodríguez-Echeverría et al., 2011). In Australia they are predominantly pollinated by bees, beetles and flies, and are occasionally visited also by birds, butterflies and bee flies (Bombylidae) (Lorenzo et al., 2010; Stone et al., 2003). Previous studies found that acacias introduced into New Zealand and South Africa successfully established mutualistic interactions with pollinators, where *Apis mellifera* played an important role (Rodger, 2012; Wandrag, 2012). However, pollination mutualisms for these two invasive species are poorly known in other invaded ranges. Previous studies on the reproductive biology of *A. dealbata* and *A. longifolia* in Portugal showed that supplementary pollination significantly increased fruit set, suggesting pollen limitation (Correia et al., 2014). *Acacia* species produce massive and long-lasting floral displays but flowering occurs during the winter, when pollinators are less active and have to face floral resource scarcity (Gibson et al., 2011; Godoy et al., 2009a, b). In the present study, we studied *A. dealbata* and *A. longifolia*, pollination ecology and networks in Portugal, as well as that of the co-occurring native species with overlapping flowering phenologies. Specifically, we aimed to assess if the two invasive acacias were able to (1) effectively guarantee pollination services in their invaded range of Portugal, and (2) whether the pollinator community visiting acacia trees differed from the pollinator communities interacting with native co-flowering plants.

2. Materials and methods

2.1. Study species

Acacia dealbata and *A. longifolia* are perennial trees native to Australia with a lifespan of 20–50 and 30 years, respectively (Richardson et al., 2011). Both species were introduced in Portugal in the beginning of the 20th century as forestry species, as ornamental trees, and for soil stabilization (Almeida and Freitas, 2006; Lorenzo et al., 2010). They have expanded out of their introduction sites, particularly during the last ten years, and nowadays are dominant in many areas, being among the most aggressive invasive species in Portugal (Gibson et al., 2011; Lorenzo et al., 2010; Marchante et al., 2010). Each species has different habitat requirements and consequently thrives in different regions of Portugal, similarly to what is observed in the native area in Australia. *Acacia dealbata* inhabits Portuguese mountain ranges and road sides of continental regions, whereas *A. longifolia* inhabits coastal sand dunes across most of the Portuguese coast (Almeida and Freitas, 2006; Buscardo et al., 2010; Lorenzo et al., 2010; Rodríguez-Echeverría et al., 2009). *Acacia dealbata* and *A. longifolia* produce many small flowers that are organized in, respectively, spherical or elongated cylindrical flower heads (Correia et al., 2014). The flower heads are considered the unit with which pollinators interact, and thus, all interactions were recorded as visits per flower head and we will refer to them as "flowers" hereafter. Both acacia species present winter flowering both in their native Australia (July–September) and in the invaded Portugal (January–March), while the native co-occurring plant species start flowering in January and extend their flowering period until April (*Ulex europaeus*) or as far as June (*Erica australis*; *Lithordora fruticosa*) (Castroviejo, 2012, Vols. 4,7,11; www.flora-on.pt [last accessed 2016-01-04]).

2.2. Study sites

The pollination network was studied in the secondary dunes of Tocha for *A. longifolia* (40.328420,-8.807237, datum WSG84); and in the mountainous area of Lousã for *A. dealbata* (40.102568,-8.233698). Both sites have a Mediterranean climate with Atlantic influence. Tocha is a coastal dune system in central Portugal; the mean annual precipitation is 948 mm and mean monthly temperature ranges from 10.2 °C in January to 20.2 °C in June, with the annual mean being 16.2 °C. It consists on a well-preserved dune system with foredunes, primary dunes, inter-dune slacks and secondary dunes. The study was performed on the secondary dunes area. Vegetation is composed by trees (*Pinus pinaster* and *A. longifolia*) and characteristic sand dune species of herbs and small shrub such as *Corema album, Halimium halimifolium, Cistus salviifolius, Cytisus grandifolius, Cytisus striatus, Euphorbia paralias, Ulex europaeus,* and *Erica australis*. Lousã mountains are located 70 km inland from Tocha; the mean annual precipitation is 752 mm and mean monthly temperatures range from 3.0 °C in January to 17.6 °C in August, with an annual mean of 9.2 °C. Vegetation is composed by a mixed oak forest dominated by *Quercus canariensis, Castanea sativa, P. pinaster,* and *A. dealbata;* with an understory dominated by *E. australis, Erica arborea*, *Pterospartum tridentatum* and *L. fruticosa.*

2.3. Pollinator observations

Within each site, we selected and marked several observation plots, at least 20 m from each other, for each of the species flowering simultaneously with acacia trees. We only considered visits to flowers occupying a volume of up to one cubic meter even when the individual plant to be observed was larger (typically acacias) to guarantee the correct monitoring of all visits. For *A. dealbata* (in Lousã), we selected 13 acacia plots and seven native species observation plots: four for *E. australis* and three for *L. fruticosa*; the only two co-occurring species flowering at the time of the study. For *A. longifolia* (in Tocha), we selected 14 acacia plots and 20 native species plots: ten for *E. australis,* and ten *U. europaeus*; the only co-occurring flowering species at the time. Since we were only at the beginning of the native plant species flowering time, it was