



Original article

Pollination ecology of a plant in its native and introduced areas

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ABSTRACT

Entomophilous and obligate out-crossing non-native plants need to become well integrated in the resident plant–pollinator network to set seeds and become established. However, it is largely unknown how pollination patterns differ between native ranges and those where plants have been introduced.

We compared the identity, abundance and visitation rates of pollinators, insect pollen loads, pollen deposition on stigmas, and fruit and seed sets of *Hedysarum coronarium*, an entomophilous short lived N-fixing perennial, in populations from native and introduced ranges in Spain (South of mainland Spain and Menorca Island, respectively).

In both areas, *Hedysarum* was visited by a similar number of species, mainly hymenopterans; seven species were common between native and introduced areas. However, pollinator richness, abundance, and visits per flower were greater in the native than in the introduced range, as were fruit and seed sets. *Hedysarum* pollen loads on stigmas and on *Apis mellifera*, the most common pollinator, did not differ between areas. Lower abundance of pollinators might be causing lower visitation rates, and to some extent reducing *Hedysarum* fruit and seed sets in the introduced area.

Our biogeographical approach shows that integration of a non-native plant in a resident pollinator network does not prevent pollen limitation in the introduced area. Therefore, despite being necessary, pollination mutualistic relationships might not be the key for non-native plant establishment success in the introduced area.

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1. Introduction

The success of many non-native plants in the range where introduced depends on the mutualistic relationships they establish with the resident biota (Richardson et al., 2000). For instance, entomophilous and obligate out-crossing non-native plant species require resident pollinators in order to reproduce and to eventually invade (Parker, 1997; Chittka and Schürkens, 2001; Vanparys et al., 2008; Rodger et al., 2010; Goodell et al., 2010; Gross et al., 2010). However, most research on the pollination of non-native plant species has focussed on their impact on the pollination and subsequent reproductive success of co-flowering native species (Traveset and Richardson, 2006; Bjerknes et al., 2007), rather than on the role of pollination in facilitating or constraining their naturalization and/or invasion (but see Parker, 1997; Parker and Haubensak, 2002; Stout et al., 2002; Simpson et al., 2005; Gross et al., 2010; Rodger et al., 2010).

Generalization in pollination is more often the rule than the exception (Jordano, 1987; Waser et al., 1996), enabling non-native plants to quickly integrate into resident plant–pollinator networks (Memmott and Waser, 2002; Vilà et al., 2009). In many cases, super-generalist pollinators such as the honeybee *Apis mellifera* and bumblebees *Bombus* spp., which have been introduced worldwide and often massively, play a key role in such integration (Stout et al., 2002; Simpson et al., 2005; Jesse et al., 2006; Gross et al., 2010).

It is not only non-native plants with generalist pollination systems that integrate into resident plant–pollinator communities, but specialist species can also be integrated in different ways. Some may find specialist pollinators if these have wide distribution ranges or have also been introduced there (i.e. “alien complexes” *sensu* Olesen et al., 2002). Other non-native plants may generalize their specialist pollination behaviour, as in the case of *Fuchsia magellanica*, which in its native range in South America is mainly visited by a hummingbird (*Sephanoides galericus*) (Traveset et al., 1998) while in its area of introduction in Britain is visited by several generalist insects (Valentine, 1977). Even self-pollinated plant species may be included in resident plant–pollinator communities, promoting their naturalization and eventual invasion

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through increased out-crossing and seed sets, if autonomous self-pollination does not result in the fertilization of all ovules (Aizen and Harder, 2007).

In addition to non-native plants being integrated into the resident plant–pollinator community, their pollination success requires pollinator visits to be efficient in terms of quantity and quality of pollen loads transported among conspecific plant individuals (Feinsinger, 1987; Aizen and Harder, 2007; Mitchell et al., 2009). Pollination efficiency is context dependent (Potts et al., 2001; Ne'eman et al., 2010). Moreover, subsequent reproductive success of non-native plants also depends on plant variables (requirement of a minimum threshold of pollen deposition for fruit and seed production, etc.) (Ne'eman et al., 2010). Therefore, in some cases, as it has been observed for the invasive *Lonicera maackii*, high visitation rates do not prevent pollen limitation (Goodell et al., 2010); while in other cases visitation rates can constitute a good surrogate of reproductive success (Parker, 1997; Vázquez et al., 2005). Furthermore, pollinator communities show high inter-annual variability (Roubik, 2001; Petanidou et al., 2008). Therefore, although this is rarely done (but see Parker, 1997; Brown et al., 2002; Moragues and Traveset, 2005; Jesse et al., 2006; Dietzsch et al., 2011), studies should contemplate more than one season in order to attribute the invasion process of a plant species with the relationships it establishes with the resident pollinator community (Petanidou et al., 2008).

Most studies on the role of insect mediated pollination of introduced plants have been conducted solely in the introduced range, often with little knowledge of the pollination ecology in the native range. A biogeographical approach comparing native and introduced areas would help to disentangle the processes that enable non-natives to succeed in their new ranges (Hierro et al., 2005; van Kleunen et al., 2010). Information on the pollination ecology and reproductive success in native and introduced areas of some plant species is available from different studies; e.g. *Cytisus scoparius* (see Parker, 1997; Parker and Haubensak, 2002; Suzuki, 2003; Simpson et al., 2005; Galloni et al., 2008; Paynter et al., 2010) and *Nicotiana glauca* (compiled in Ollerton et al., 2012). But, to our knowledge, only the pollination interactions of *Rhododendron ponticum* have been studied from this biogeographical perspective by following a standard field sampling protocols both in the native and introduced areas (Stout et al., 2006).

In this study we apply this biogeographical approach to the pollination ecology and reproductive success of an entomophilous plant species whose native and introduced areas have a close regional proximity. Our main questions are: a) Do the identity of pollinators and generalization degree of plant populations differ between native and introduced areas? b) Do pollinator richness, abundance, and visitation rates differ between the two areas? c) Do pollen loads on the main pollinator species and on stigmas differ between the two areas? and finally d) Do fruit and seed sets differ between areas? Our hypothesis is that an entomophilous non-native plant species which has become naturalized in a new area might have similar pollination patterns as in the native area. We expect resident pollinators to provide non-native plants a pollination service preventing pollen limitation and allowing for similar seed sets than in their native area.

2. Materials and methods

2.1. Study species

Hedysarum coronarium L. (Fabaceae; hereafter *Hedysarum*) is a short-lived N-fixing and sexually reproduced perennial (Sulas et al., 2000; Bullitta et al., 2000) that can reach 1.5 m tall when erect in growth habit, but can also be prostrate (Montes, 1993/94;

Bustamante et al., 1998). Its inflorescences are racemes with up to 30 pink flowers with 1 cm long corollas, rich in pollen and nectar that bloom during April and May. Its flowers need to be tripped and are pollinated mainly by bees (Louati-Namouchi et al., 2000a,b; Satta et al., 2000) and are self-compatible but present high out-crossing rates (Yagoubi and Chriki, 2000; Louati-Namouchi et al., 2000a). *Hedysarum* is native of the south-western Mediterranean basin (Talavera et al., 1988), where it grows from sea level to low frost-free altitudes (Gutiérrez, 1982). It has been introduced as a forage plant in other semiarid regions of the Mediterranean basin because of its high feed value for cattle (Yagoubi and Chriki, 2000). It is also used for erosion control, re-vegetation, and high-quality honey production (Flores et al., 1997; Satta et al., 2000). Currently, whether naturally or due to human intervention, it grows in many Mediterranean basin countries, from Turkey to Spain (Flores et al., 1997).

2.2. Study sites

The study was conducted in two areas of Spain. The native area was located in the province of Cádiz, S Spain, while the introduced area was the NE of Menorca, the northernmost of the Balearic Islands (Fig. 1). These areas have a close regional proximity and share a Mediterranean climate with similar average monthly temperatures around 17 °C, and an average annual precipitation of 600 mm (AEMET). We are aware that, as the introduced area is an island, description of patterns of pollination between native mainland areas and introduced insular areas cannot disentangle nativity from insular differences. However, in insular areas the introduction and potential invasion of species from mainland is a highly common phenomenon (Kueffer et al., 2010) that deserves exploration even if causality cannot be inferred. Furthermore, the close geographic proximity between the native and the introduced allows for comparing highly similar ecological settings (i.e. climate, vegetation type, species assemblages, landscape configuration), reducing the influence of major confounding factors that preclude any causality.

In Menorca, *Hedysarum* was introduced between the end of the 18th and the beginning of the 19th centuries (Ortells and Campos, 1983). Since 1860 it has been used in a traditional cyclical agro-farming system, which consists of growing crops of *Hedysarum* for two consecutive years, followed by cereal cropping the third year and leaving the land fallow in the fourth year (Bustamante et al., 2007). To some extent, this traditional system is still used on the island with minor modifications. Today, *Hedysarum* has escaped from crops and is well established (i.e. naturalized *sensu* Pysek et al., 2004) in natural and semi-natural areas (Fraga et al., 2004) such as ditches, old-fields, field edges, and ruderal areas.

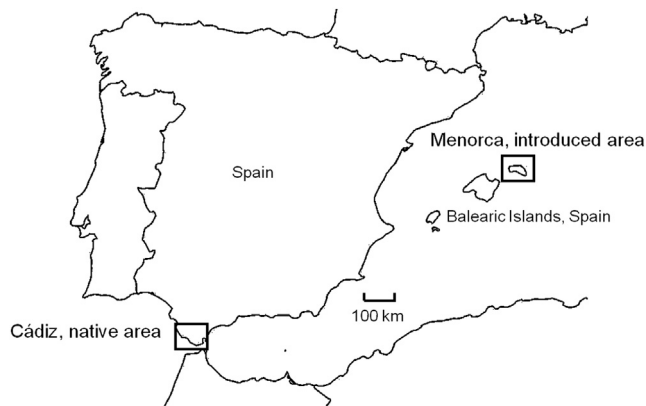


Fig. 1. Location of the study areas.

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