



Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (*Myrtus communis*)

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ABSTRACT

Pollinator assemblages may shift as a consequence of the destruction and fragmentation of natural habitats. The scarcity of mates and pollinators can lead plant populations to suffer from pollen limitation and a decrease in reproductive performance within fragmented areas. We studied the shift in pollinator assemblages along with pollen limitation and seed production patterns in the Mediterranean shrub *Myrtus communis*. Our study included six populations contrasting in patch and population size (Large vs. Small) within a fragmented landscape characterized by ~1% of potential forest coverage. The breeding system in *Myrtus communis* was self-compatible, but compared with natural pollination, fruit set increased with pollen addition (quantity limited), and seed set (brood size) increased with outcross pollen addition (quality limited). While the pollinator assemblage in Large patches was taxonomically diverse, it was almost monopolized by honeybees in Small patches, where visitation rates were highest and wild bee species were almost absent. In general, Small populations were less pollen limited for fruit set than Large populations, particularly those that received the highest rates of honeybee visits. However, despite differences in fragmentation and pollinators between Large and Small populations, seed production patterns (brood size and seed mass) were rather similar among them, in agreement with similar pollen limitation levels found for brood size. A higher susceptibility of native pollinators to the presence of honeybee hives was found in Small patches, suggesting that the pollinator assemblage may be severely altered when fragmentation occurs in combination with beekeeping. We discuss its implications and effects on plant reproduction in fragmented areas.

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1. Introduction

Habitat fragmentation is one of the main results of current global change and thus is considered a major threat for biodiversity of terrestrial ecosystems, compromising the long-term persistence of species in small and isolated patches (Fahrig, 2003; Lindenmayer and Fischer, 2006). Plants, as sessile organisms, are prone to suffer these threats because of the spatial arrangement of habitat patches, which affects the ecological processes occurring within them, such as genetic bottlenecks, alteration of biotic interactions and biological invasions (Hobbs and Yates, 2003).

One of the main threats to plant reproduction within fragmented habitats is pollination failure (Wilcock and Neiland, 2002). Fragmentation usually leads to a correlated decrease in plant population size, and plant species occurring at low population size or density are more sensitive to pollen limitation, defined as a lower fruit and seed production caused by a scarce pollen receipt (Burd, 1994). Generally, pollen limitation is a consequence of

reduction in quantity and/or quality, e.g., self- or cross-pollination, of pollen deposited on stigmas, which provokes lower ovule fertilization and seed production or less vigorous offspring (Knight et al., 2005; Aizen and Harder, 2007). Thus, pollen-limited plant populations have been documented to experience disruptions in seed production (e.g., Aizen and Feinsinger, 1994a), which, in an extreme case, may compromise their long-term viability (Lamont et al., 1993; Groom, 1998).

Besides the scarcity of mates for cross-pollination, in animal-pollinated plants, pollen limitation is also caused by low pollinator visitation rates (Cunningham, 2000). Pollinators are also vulnerable to habitat fragmentation, and the pollinator assemblage may be shifted because different pollinator species may respond differently to landscape changes (Steffan-Dewenter et al., 2002; Aizen and Feinsinger, 2003; Ashworth et al., 2004). In consequence, fragmentation may reduce the abundance of pollinators (e.g., Steffan-Dewenter and Tschardtke, 1999), shift the pollinator guilds (e.g., Donaldson et al., 2002) and facilitate non-native species to access floral resources (e.g., Aizen and Feinsinger, 1994b).

However, despite numerous studies over the last two decades, results do not show clear patterns on the effects of fragmentation on pollination failure (reviewed in Hobbs and Yates, 2003; Aguilar

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et al., 2006; for pollinators see Steffan-Dewenter and Westphal, 2008). In general, self-incompatible plants are more likely to show lower fecundity than self-compatible ones (Aguilar et al., 2006), although most studies were biased to self-incompatible herbs and tree species in tropical or temperate ecosystems. Therefore, results of particular studies are a consequence of the several possible combinations of plant traits, e.g., breeding systems, degree of specialization in pollinators, rarity, and ecosystem properties (evolutionary setting of the biota, history of anthropogenic disturbance, sensitivity of pollinator fauna).

Despite the long-standing process of habitat fragmentation in the Mediterranean (Grove and Rackham, 2001), its effects on ecological processes, in general, and plant reproduction, in particular, have received little attention (but see Santos et al., 1999 for studies on seed dispersal by vertebrates). Additionally, the Mediterranean region has been recognized as likely to have more intense climate change in the near future (IPCC, 2007), which may foster reduction of suitable habitats and increasing fragmentation. Thus, there is a need for more empirical studies to detect the effects of habitat fragmentation on critical ecological processes such as the reproductive performance of plant species, particularly if these are important components of the natural vegetation. These studies will provide a sound basis for establishing conservation guidelines in regions prone to deforestation and fragmentation, such as those in the Mediterranean.

We investigated these issues in Mediterranean myrtle (*Myrtus communis* L., Myrtaceae), an insect-pollinated shrub, which has the typical traits of sclerophyllous Mediterranean plants and is a main component in many oak woodland understoreys and late successional shrublands across the Mediterranean Basin. The study was carried out in the Guadalquivir River Valley (SW Spain), a large and fertile lowland area devoted to intensive agriculture, where forest vegetation was virtually eliminated by humans several centuries ago. Nowadays, the landscape in this area can be considered of 'relictual' type (*sensu* McIntyre and Hobbs, 1999), where overall patch area is very low and spatial connectivity among patches is mostly lacking (Aparicio, 2008). Among them, small, isolated patches supporting small myrtle populations (<50 inds.) are frequent.

In this study, we addressed pollinator assemblage, pollen limitation and seed production in myrtle populations with contrasting levels of habitat and population size. Because fruit and seed set may depend on abiotic factors and resources, we performed a pollen supplementation experiment to ascertain the degree to which differences in fruit and seed set are caused by pollen limitation (Knight et al., 2005). Specifically, we aimed to answer the following questions: (1) are the pollinator assemblages and the visitation rates different among Large and Small patches?; (2) are Small myrtle populations more pollen limited than Large populations?; (3) is there any relationship between local pollinator assemblages and pollen limitation?; and (4) are seed production patterns influenced by population size (Large or Small) or pollinator visitation rate?

For a correct understanding and interpretation of the effects of variation in pollinator assemblages on myrtle fecundity, we determined the breeding system of the species, which had not been previously reported.

2. Methods

2.1. Study species

The myrtle is a common sclerophyllous shrub and the sole representative of the Myrtaceae in the flora of the Mediterranean Basin. It grows up to 4 m in height in fertile soils in low and warm habitats. In southern Spain, it is a main component of late succes-

sional woodland understoreys, blooming massively during late June–early July. The flowers are hermaphrodite, with a white open dish corolla up to 3 cm in diameter with a life span of 1–3 days (Fig. 1), have one style and many stamens (>50) and contain a mean (\pm SD) of 72 ± 12 ovules ($n = 150$ flowers from 15 plants). Fruits are ellipsoidal berries, dark blue when ripe from November, with a mean diameter (\pm SD) of 8.8 ± 1.1 mm, containing 5.6 ± 3.2 seeds (González-Varo et al., 2009) that account for an average natural seed set of $7 \pm 2\%$ ($n = 15$). The number of seeds per fruit (hereafter, brood size) is not significantly correlated with the number of ovules per flower ($r = 0.28$, $P = 0.32$, $n = 15$ plants), and given the large number of ovules per flower and their low level of variation among plants (CV = 16%), brood size may be considered a useful surrogate for seed set as shown by the highly positive correlation among both variables ($r = 0.84$, $P < 0.001$, $n = 15$ plants).

Self-compatibility in myrtle has been inferred by means of bagged pollinations in cultivar clones (Mulas and Fadda, 2004). A mating system analysis using isozyme markers has revealed a mixed-mating system in large and dense populations (González-Varo et al., 2009). Endozoochorous seed dispersal is carried out by frugivorous passerine birds and carnivorous mammals (Traveset et al., 2001). However, many aspects of the pre-dispersal reproductive biology of the species, such as its breeding system and pollinators (but see Herrera, 1988), remain unknown to date.

2.2. Study area and populations

The Guadalquivir River Valley is a large lowland area of ca. 21,000 km² located in south-western Spain and long devoted to intensive agriculture, where 535 natural or semi-natural (holm-oak, cork-oak and stone-pine) forest patches covering about 1% of the valley area can be found (see Aparicio, 2008, for a detailed description). Myrtle is known to occur in 162 of these patches, and during its late flowering peak (early summer) is virtually the only dominant species in full bloom (see González-Varo et al., 2009). We selected six patches contrasting in both area and population size: three large patches (>90 ha) supporting large myrtle populations (>2000 inds.) and three small patches (<30 ha) supporting small populations (<70 inds.) (hereafter Large and Small patches/populations, respectively; see Table 1). None of selected patches had animal-pollinated co-flowering crops in their surroundings (spring flowering olive and orange orchards, and cereal and cotton fields). The number of reproductive adult myrtles in each patch was estimated by extrapolating myrtle density to the patch area in Large populations and by direct counting in Small

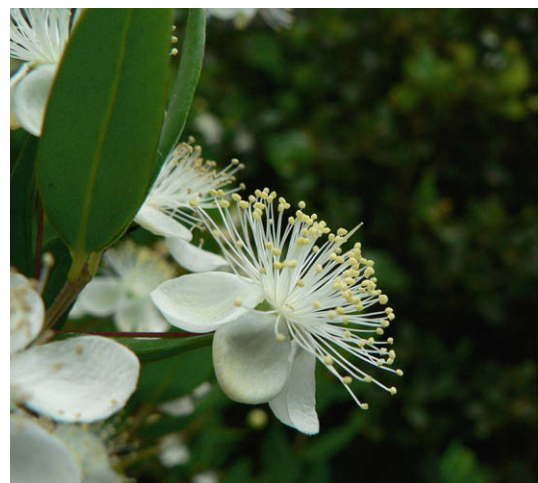


Fig. 1. Flower of Mediterranean myrtle (*Myrtus communis*).

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