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The cost of being specialized: Pollinator limitation in the endangered geophyte *Brunsvigia litoralis* (Amaryllidaceae) in the Cape Floristic Region of South Africa

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Abstract

The impacts of habitat fragmentation and reduced population sizes on ecological processes deserve more attention. In this study we examine pollination in rural and urban populations of *Brunsvigia litoralis* (Amaryllidaceae), an endangered endemic and a flagship species for plant conservation in South Africa. *B. litoralis* has flowers conforming to the bird-pollination syndrome, but the only flower visitor at the urban sites, the Greater Double-collared Sunbird (*Cinnyris afra*) (1.6 visits/flower/hour), is unable to access the nectar in the usual way due to a long perianth tube (38.8 mm) and resorts to robbing. Supplemental hand pollination was used to test for pollen limitation of seed set at the urban sites flowers were pollen-supplemented. Seed set in supplemented plants increased by more than an order of magnitude relative to controls. The longer-billed Malachite Sunbird (*Nectarinia famosa*) was observed as the sole pollinator of *B. litoralis* at the rural site where seed set was significantly higher. Although *B. litoralis* plants are long lived, the absence of pollinators in these urban fragments might place populations at an extinction risk.

Keywords: Flower robbing; Malachite Sunbird; Mutualism disruption; Plant–pollinator interactions; Pollen limitation; Specialized pollination

1. Introduction

South Africa is renowned for its large number of red-listed plant species with small population sizes on the one hand (Raimondo et al., 2009) and for its highly specialized pollination systems on the other (Johnson and Steiner, 2000; Johnson et al., 2009). Specialized pollination systems are predicted to be sensitive to anthropogenic disruption (Bond, 1994), while small population size is a frequent cause of reduced fecundity (Lamont et al., 1993; Agren, 1996; Groom, 1998; Ward and Johnson, 2005). Nevertheless, few studies have addressed the question of whether endangered South African plants, which occur in small populations, suffer high levels of pollinator-limited seed set. This question has important management implications: if pollinators are indeed limiting seed set in these endangered plants, fecundity can be enhanced by pollinator conservation or hand pollination.

Birds are important pollinators of many rare South African plants (Rebelo, 1987), but are also particularly sensitive to environmental degradation, and are among the first species to be lost from human impacted ecosystems (Turner, 1989; Saunders et al., 1991; Lamont et al., 1993; Turner, 1996; Debinski and Holt, 2000). Within the Cape Floristic Region avian nectarivores are negatively affected by human structures like roads (Geerts and Pauw, 2010) and demonstrate lower species richness and density in very small fragments compared to larger natural areas (Pauw, 2004; Fox and Hockey, 2007). Within this avian nectar feeding guild, the Malachite Sunbird, *Nectarinia famosa* (Linnaeus), is particularly sensitive to anthropogenic influences and is seldom found in small

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conservation areas (when in a highly transformed matrix) or penetrating deep into urban areas (Pauw, 2004). However, Malachite Sunbirds are ecologically irreplaceable pollinators, acting as the sole pollinator for a group of deep-flowered plant species within the Cape flora (Geerts and Pauw, 2009). This high degree of specialization among plants could potentially increase the risk of pollination disruption in fragmented habitats (Bond, 1994; Johnson and Steiner, 2000).

Natural habitats in the lowlands of the Cape Floristic Region are highly fragmented by agriculture and urbanisation, but effects on ecological processes have rarely been studied (but see Donaldson et al., 2002; Pauw, 2007; Pauw and Bond, (2011)). An important consequence of habitat fragmentation, which has received relatively little attention, is the potential erosion of biodiversity through the breakdown of pollination mutualisms (Aizen and Feinsinger, 1994a,b; Steffan-Dewenter and Tscharntke, 1999; Murren, 2002). Small populations of plants are less attractive to pollinators and unable to support viable populations of pollinating animals thereby reducing the chances of pollination (Collins et al., 1984; Sih and Baltus, 1987; Jennersten, 1988; Johnson, 1992; Lamont et al., 1993; Morgan, 1999). These effects are likely to be exacerbated in self-incompatible animal-pollinated plant species dependent on a pollen vector for seed set (Kearns et al., 1998; Cunningham, 2000; Wilcock and Neiland, 2002; Aguilar et al., 2006).

Brunsvigia litoralis R.A. Dyer is a narrow endemic to the coastal lowlands of the Eastern Cape Province of South Africa and is listed as Endangered according to the IUCN Red List categories. Most of the remaining populations occur in small fragments of coastal vegetation, often in a residential setting and are threatened by urban expansion (Raimondo et al., 2009). A spectacular inflorescence is produced in autumn (from February to April) while the plant is in a leafless state. The flowers show all the features indicative of bird pollination: flowers are scentless, red, robust and tubular, and contain large volumes of nectar with a low concentration (Faegri and Van der Pijl, 1979; Proctor et al., 1996). Furthermore, the floral tube length of *B. litoralis* suggests membership of the Malachite Sunbird pollination guild (Geerts and Pauw, 2009), but this hypothesis remains untested. In this study we test: (1) whether *B. litoralis* is pollinated by Malachite Sunbirds, and (2) whether pollinator specialization in this species is associated with pollinator-limited seed set in small populations.

2. Methods

2.1. Study species

B. litoralis R.A.Dyer (Amaryllidaceae) occurs on coastal sands from Cape St. Francis to Port Elizabeth (Eastern Cape, South Africa) (Doutt, 1994; Snijman, 2002). Leaves are present during the wet winter (May–September) and plants are leafless during the dry summer (October–April). When flowering (March–April), the umbellate inflorescences are easily seen above the grasses in open fields among the low coastal shrubs of the genera *Sideroxylon*, *Searsia*, and *Cassine* (Fig. 1a). Flower morphology is similar to *Brunsvigia orientalis* (L.) Aiton ex Eckl. (Pauw, 2004) and *Brunsvigia josephinae* (Redouté) Ker Gawl (pers. obs.). *B. litoralis* is a long-lived bulbous plant that is unable to reproduce vegetatively belowground and therefore depends entirely on seeds for reproduction (G. Duncan pers. comm.). Seed set, in turn, is dependent on cross-pollination because the plants are self-incompatible (Koopowitz, 1986; cited in Doutt, 1994).

2.2. Study sites

We studied fragmented sites consisting of "habitat islands" within expanding human settlements. In the flowering seasons of 2006 and 2007 three sites located in a residential area at Cape St Francis and two within the city of Port Elizabeth were studied (henceforth "urban sites"). In 2007 we added an undisturbed site in a large area of natural vegetation (henceforth "rural site"). This is the largest known population and occurs within an untransformed area (about 20 km^2) at Rowallan Park on the western outskirts of Port Elizabeth.

To determine the proportion of plants flowering, plants in one fragment were marked with painted sticks in two previous years. Only 16% of the marked plants flowered in 2006 (B. Logie pers. com.), and this fraction is likely to be an overestimate because small individuals are difficult to locate. Population size of flowering plants (for 2006) were 11, 42 and 10 plants for Cape St Francis, 25 and 30 for the two urban populations within Port Elizabeth, and an estimated 100–120 flowering plants for the rural population at Port Elizabeth.

2.3. Flower morphology and nectar

Tube length was measured in young flowers using a steel ruler (n = 20 flowers). Although tube length is the distance from the base of the nectary to where the nectar chamber is sealed (Fig. 1b), the perianth tube experienced by flower visitors is effectively longer. Tube length was therefore measured from the top of the ovary to where the petals no longer overlap. Nectar was extracted early in the morning in the field (~9:00 AM) with 40 μl capillary tubes and the sugar concentration determined with a Bellingham and Stanley 0–50% handheld refractometer (n = 5). The sample size is low because all other flowers were robbed (see below).

2.4. Flower visitation and robbing rate

Detailed observations of the behaviour of flower visitors were made at five urban populations (three at Cape St Francis; two at Port Elizabeth) and one larger rural population (near Port Elizabeth). This was done from a distance of ~10 m aided by close focusing 8 × 40 binoculars. Flower visitors were only recorded in the morning. At the urban sites in Cape St Francis 12 h of observations was conducted (7 h, 16–18 March 2006; 4 h, 9–10 March 2007; 1 h, 10 March 2007, relocation site). At the urban sites in Port Elizabeth 2 h of observation were conducted (7 March 2007); while at the nearby rural site 8 h of observations (8, 9 March 2007) were made.