



Original article

Comparative studies on plant range size: Linking reproductive and regenerative traits in two *Ipomoea* speciesJulia Astegiano^{a,*}, Guillermo Funes^{a,b}, Leonardo Galetto^a^a Instituto Multidisciplinario de Biología Vegetal (IMBIV), Universidad Nacional de Córdoba, Argentina, Consejo Nacional de Investigaciones Científicas y Técnicas, CC 495, CP 5000, Córdoba, Argentina^b Cátedra de Biogeografía, FCEyN, UNC, Argentina

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ABSTRACT

Reproductive and regenerative traits associated with colonization and persistence ability may determine plant range size. However, few comparative studies on plant distribution have assessed these traits simultaneously. Pollinator richness and frequency of visits, autonomous self-pollination ability, reproductive output (i.e., reproductive traits), seed bank strategy and seedling density (i.e., regenerative traits) were compared between the narrowly distributed *Ipomoea rubriflora* O'Donnell (Convolvulaceae) and its widespread congener *Ipomoea purpurea* (L.) Roth. The narrowly distributed species showed higher ecological specialization to pollinators and lower autonomous self-pollination ability. Frequency of visits, natural seed/ovule ratio and fruit set, and total fruit production did not differ between species. However, the number of seeds produced per fruit was lower in the narrowly distributed species, translating into lower total seed production per plant. Indeed, *I. rubriflora* formed smaller transient and persistent seed banks and showed lower seedling density than the widespread *I. purpurea*. These reproductive and regenerative trait results suggest that the narrowly distributed species may have lower colonization and persistence ability than its widespread congener. They further suggest that the negative effects of lower fecundity in the narrowly distributed species might persist in time through the long-lasting effects of total seed production on seed bank size, reducing the species' ability to buffered environmental stochasticity. However, other regenerative traits, such as seed size, and processes such as pre- and post-dispersal seed predation, might modulate the effects of plant fecundity on plant colonization and persistence ability and thus range size.

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1. Introduction

A fundamental question for ecologists and biogeographers is why most of the world's species have relatively small range sizes while a few related species are geographically widespread (Gaston, 2003). Among plant ecologists, the wide interest in the causes of species distribution has recently focused on differences in biological traits between geographically restricted species and their widespread congeners (e.g., Laverne et al., 2004; Young et al., 2007; Kristiansen et al., 2009). Traits associated with the persistence and colonization ability of plants may determine plant distribution, and so these may be found to differ among species with contrasting distributions (Gaston, 2003).

Seed production determines both the number of seeds available for dispersal and the contribution of the species to the local seed bank, and is thus a key trait determining colonization and persistence ability in plants (Ehrlén and van Groenendael, 1998; Dupré and Ehrlén, 2002). Indeed, several authors have reported that plants with smaller ranges tend to have lower annual seed production than more widespread congeners (studies reviewed in Murray et al., 2002; Laverne et al., 2004). However, it remains uncertain which reproductive traits associated with seed production differ between narrowly distributed plants and widespread congeners (Murray et al., 2002; but see Laverne et al., 2005; Rymer et al., 2005). Furthermore, since studies simultaneously assessing reproductive and regenerative traits are still scarce, little is known about how differences in seed production may translate into differences in local persistence (e.g., Walck et al., 2001; Münzbergová, 2005).

The seed production of flowering plants is commonly limited by inadequate pollen deposition, i.e., pollen quantity and/or quality (Knight et al., 2005). In biotically-pollinated flowering plants, the frequency of visits of pollinators to plant species has been shown to

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be positively associated with pollen deposition on stigmas (e.g., Price et al., 2005), and thus pollinator visits may affect the reproductive success of plants (e.g., Ghazoul, 2005). Also, given that the degree of ecological specialization or generalization of plants to pollinators can be related to the probability of seed production being pollen limited (Knight et al., 2005; Hegland and Totland, 2008), the number of pollinator species that interact with a plant species may also determine seed production (Klein et al., 2003; Gómez et al., 2007). Thus, if the seed production of pollinator-specialist plants is more likely to be pollen limited (Knight et al., 2005 but see Larson and Barrett, 2000; Hegland and Totland, 2008), then lower seed production can be expected of pollinator-specialist plants than of pollinator-generalist species growing in the same site. Therefore, by affecting seed production, both the degree of specialization or generalization of plants to pollinators and the frequency of visits received by plants may influence the levels of recruitment from seeds and may thus affect the local persistence of plants (Wilcock and Neiland, 2002; Price et al., 2005).

Seed production may also be associated with the plant's breeding system because the latter determines the degree of dependence of plants on pollinators for pollen deposition (Bond, 1994). For instance, in contrast to self-incompatible and self-compatible non-autogamous plants, species capable of autonomous self-pollination can alleviate the pollen limitation generated by insufficient pollinator service through self-pollen deposition (Kaliz et al., 2004; Kennedy and Elle, 2007). Therefore, by decreasing the probability of seed production being pollen limited (e.g., Larson and Barrett, 2000), autonomous self-pollination may increase the probability of local persistence of plants under unfavourable pollination conditions, such as those found near the limits of the geographic distribution of the species (Herrera et al., 2001). Moreover, plants capable of autonomous self-pollination are more likely to be successful as colonists, as was proposed by Baker (1955) and recently supported by the high incidence of autogamy found among invasive species (e.g., Rambuda and Johnson, 2004) and the wider distribution of autogamous invasive species (e.g., Van Kleunen and Johnson, 2007).

However, how differences in seed production may lead to differences in persistence ability between narrowly distributed and widespread plants may also be related to their demographic dependence on annual seed production. For instance, species with persistent seed banks can decrease the impact of annual variation of seed production on seedling establishment (Masaki et al., 1998; Maron and Kauffman, 2006), and this may have an important positive demographic effect on population growth in years of low reproductive output (e.g., Kaliz and Mc Peek, 1993; Adams et al., 2005). Therefore, the local persistence of species forming persistent seed banks is expected to be less affected by reproductive failure or a decrease in annual seed production (Bond, 1994; Wilcock and Neiland, 2002). Moreover, in the case of reproductive or establishment failure in annual plants, persistent seed banks may ensure that annual species can locally persist with a low colonization rate or even without immigration (Baskin and Baskin, 1998; Fenner and Thompson, 2005). In fact, the long-term local persistence of annual species has been reported to completely depend on the ability of these species to form persistent seed banks (e.g., Aikio et al., 2002).

Although it is widely accepted that, in biotically-pollinated plants, seed production depends on pollinator service as well as on the plant's ability to self-pollinate, comparative studies of plant distribution have generally considered these reproductive traits separately, yielding opposite results (Murray et al., 2002; but see Lavergne et al., 2005; Rymer et al., 2005). On the other hand, these comparative studies generally fail to evaluate the demographic dependence on annual seed production of the species (e.g., seed

bank formation and size), leading to an incomplete understanding of the role of differences in seed production in determining differences in persistence ability between narrowly distributed and widespread species (but see Van der Veken et al., 2007).

In this study, we evaluated differences in reproductive (i.e., from pollinators to seed production) and regenerative traits (i.e., seed bank strategy and seedling density) commonly associated with colonization and persistence ability, between the narrowly distributed annual *Ipomoea rubriflora* O'Donnell (Convolvulaceae) and its widespread co-occurring congener, the annual *Ipomoea purpurea* (L.) Roth. Specifically, we aimed to answer the following question: does the narrowly distributed species present reproductive and regenerative traits indicative of lower colonization and persistence ability than its widespread congener? Comparisons between closely related congeners are encouraged because they minimize the confounding effects of disparate phylogenetic histories (Walck et al., 2001). In addition, the study of rare and common congeners sharing the same habitat has recently been highlighted, because differences between species resulting from their growing in different habitat conditions are controlled (Münzbergová, 2005). As our objective was to determine differences between species in regenerative traits associated with plant persistence ability, we were interested in comparing species of similar longevity, especially annuals – i.e., plants highly dependent on regeneration success to persist locally. Although *I. rubriflora* and *I. purpurea* probably belong to different clades (Miller et al., 2004), these species are the only two annual *Ipomoea* with contrasting range sizes present in the Chaco Serrano Woodland of central Argentina (Chiarini and Ariza Espinar, 2006).

Given that traits associated with the persistence and colonization ability of species may differ among species with contrasting distributions (Gaston, 2003), we expected lower pollinator richness and frequency of visits, higher dependence on pollinators and lower reproductive output in the narrowly distributed *I. rubriflora*. In addition, we expected the absence of persistent seed banks or smaller-sized seed banks in the narrowly distributed species.

2. Materials and methods

2.1. Study species and sites

I. rubriflora O'Donnell (*Ipomoea* subg. *Quamoclit* section *Mina*) occurs in Paraguay, Bolivia and from north to central Argentina; in contrast, *I. purpurea* (L.) Roth (*Ipomoea* subg. *Ipomoea* or *Quamoclit*, section *Pharbitis*) is a geographically widespread species, originally from the Americas but with a cosmopolitan distribution nowadays (Austin and Huáman, 1996). These two species commonly co-occur in the Chaco woodland and can grow in disturbed areas such as gardens, roadsides and abandoned crop fields (J. Astegiano, personal observation). However, *I. rubriflora* is less frequent than *I. purpurea* in the study region (Cagnolo, 2007). *I. rubriflora* flowered from mid-March to mid-April while *I. purpurea* flowered from early March to mid-May at the study sites in 2006. Both species are annual vines, with showy flowers of ca. 30 mm of corolla length (Galetto and Bernardello, 2004). Flowers last ca. 10 h and offer nectar as reward, with the nectar of *I. rubriflora* being less concentrated than that of *I. purpurea* (Galetto and Bernardello, 2004). *I. rubriflora* has red tubular flowers whereas *I. purpurea* has tubular flowers of different colours, with dark blue, pink, white and purple morphs present at the study sites. *I. rubriflora* generally presents four ovules per flower while *I. purpurea* presents six ovules (Chiarini and Ariza Espinar, 2006). *I. purpurea* has been reported as a self-compatible species capable of autonomous self-pollination in the study region (Galetto et al., 2002). Different species of Hymenoptera have been reported as pollinators

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