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Original article

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ABSTRACT

In plants, narrow geographic distributions are generally associated with low colonization and persistence abilities, therefore narrowly distributed plants are expected to have lower plant recruitment success than widespread species. Determining the association between recruitment success and range size requires the comparison of the success in multiple life-history stages among narrowly distributed and widespread congeners sharing the same habitat, an integrated approach rarely considered. We compared transition probabilities from ovule to reproductive adult between the narrowly distributed annual vine *Ipomoea rubriflora* O'Donnell (Convolvulaceae) and the widespread *Ipomoea purpurea* (L.) Roth at sites in Chaco woodland where they co-occur. *I. rubriflora* had marginally lower ovule fertilization success, a lower probability of seed maturation and lower seedling establishment than *I. purpurea*. The lowest transition probability for both species was seedling emergence. Seedling establishment in *I. rubriflora* was similar to seedling emergence. Plant recruitment success in *I. rubriflora* was an order of magnitude lower than that of *I. purpurea*. Indeed, *I. rubriflora* had lower total seed production per plant and smaller seed mass. Our results suggest that understanding processes determining regeneration (i.e., seedling emergence and establishment) may be of high importance for understanding narrow distributions in annual plants. The results also suggest that the narrowly distributed species is not only at a “numerical disadvantage” for colonizing new sites—i.e., lower total seed production per plant—but it also has a lower per-seed probability of establishing and thus to persist. However, as lower establishment success in this species seemed to be associated with the lower ability to survive adverse conditions of seedlings from smaller-seeded species, a narrower regeneration niche might also explain its narrow distribution.

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1. Introduction

Understanding how narrowly distributed plants differ from geographically widespread species in biological and ecological attributes can provide valuable information for the conservation of species with narrow distributions, one of the key issues for

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conservation biologists (Gaston, 2009). Although the study of the causes of plant range size has long history (Stebbins, 1942; Rabinowitz et al., 1987; Gaston, 2003; Lavergne et al., 2004; Van der Veeken et al., 2007; Luna and Moreno, 2010), a general explanation for narrow distributions in plants has yet to emerge and thus more comparative studies are still needed (Murray et al., 2002; Gaston, 2009). In this sense, studies considering several pairs of closely related species with contrasting distributions may be particularly valuable (e.g., Lavergne et al., 2004; Van der Veeken et al., 2007). However, studies that consider only one pair of species allow the measurement of several attributes and by including standardized traits may also contribute to an overall understanding of rarity via future meta-analyses (Young et al., 2007).

Given that a species' range size can be viewed as the result of the establishment of new populations—i.e., colonization ability—and the persistence of extant populations (Gaston, 2003), plant recruitment success may differ among narrowly distributed and geographically widespread species. Plant recruitment success depends on the success of individuals at different life-history stages (e.g., ovule, seed, seedling, adults) (Rey and Alcántara, 2000; Traveset et al., 2003). The need to studying those different life-history stages when looking for the demographic causes of narrow distributions has been recognized (Bevill et al., 1999) because it allows the identification of the stages where the mortality of potentially reproductive individuals is the highest, and thus of processes that might determine the colonization and persistence abilities of species. In this sense, although it has been reported that narrowly distributed species have lower total seed production than their widespread congeners (Murray et al., 2002; Lavergne et al., 2004; Van der Veeken et al., 2007), studies that simultaneously compare the success of these species in pre-dispersal (pollination success, seed abortion and survival of pre-dispersal predation) and post-dispersal stages (seedling emergence, seedling establishment, and plant survival to reproductive maturity) are still scarce (Fiedler, 1987; Byers and Meagher, 1997; Münzbergová, 2005) and to our knowledge no demographic study included annual species—i.e., species more dependent on annual recruitment success to persist. Moreover, few studies controlled for differences between narrowly distributed and geographically widespread species that may arise from their growing in different habitat conditions by focusing in species sharing the same habitat (Buckley and Kelly, 2003; Münzbergová, 2005; Miller et al., 2007). As a consequence, the importance of plant recruitment success in determining narrow distributions remains poorly understood.

In annuals, plant fecundity may be critical for population growth rate (Kaliz and Mc Peek, 1993; Dostal, 2007; Levine et al., 2008). Therefore, recruitment success in pre-dispersal stages may play a central role in determining species persistence. In this sense, narrowly distributed species may be more ecologically specialized on pollinators and more dependent on pollinator service to produce seeds, which may increase the probability of pollen limitation occurrence in these species (Rymer et al., 2005; Carrió et al., 2009; Astegiano et al., 2010; Fernández et al., 2012). On the other hand, narrowly distributed species may suffer from higher levels of inbreeding depression due to small population sizes (Barret and Kohn, 1991; Lavergne et al., 2004), which may cause higher levels of seed abortion. Moreover, lower seed production may reflect higher seed abortion due to lower resource availability for plant reproduction in narrowly distributed plants (Lavergne et al., 2004).

Pre-dispersal seed predation has been found to be a key process determining plant recruitment success (Ehrlén, 2002; studies reviewed in Maron and Crone, 2006; Kolb et al., 2007) and narrow geographic distributions (Hegazy and Eesa, 1991; Bevill et al., 1999; Münzbergová, 2005). Because of the influence of seed predation on population dynamics will depend on the sensitivity of overall plant performance to changes in seed production (Horvitz et al., 2005; Kolb et al., 2007), annual plants would be expected to be particularly sensitive. However, the importance of seed predation levels for plant recruitment would also depend on seed bank strategy since in species showing a persistent seed bank population growth was showed to be less sensitive to seed predation levels (Maron and Crone, 2006). Moreover, a reduction in seed production caused by seed predators will negatively influence plant recruitment only when subsequent density dependent population responses do not compensate for seed losses (e.g. seedling survival can be enhanced through reduced intraspecific competition) (Maron and Crone, 2006).

The period between seed emergence and seedling establishment is one of the most vulnerable in the life cycle of plants (Fenner and Thompson, 2005; Moles and Westoby, 2006) and has been shown to be critical for the population growth of annual species (Griffith and Forpeth, 2005; Quintana Ascencio et al., 2011). Mortality during this period may be caused by biotic (e.g., competition among plants, herbivory, fungal attack, etc.) or abiotic factors (e.g., physical damage due to the fall of branches, water stress, etc.; Boege and Marquis, 2005; Fenner and Thompson, 2005). Seedlings from larger-seeded species may be more likely to become established under adverse conditions (e.g., soil drought, deep shade, herbivory) because of proportionally higher reserves (Westoby et al., 2002), and have higher seedling recruitment success. Thus survival in these life-history stages may differ between species with contrasting seed masses (Leishman et al., 2000). However, this advantage of larger-seeded species may be temporary and disappear in subsequent life-history stages (Moles and Westoby, 2006; but see Metz et al., 2010). On the other hand, in species reaching higher seedling densities due to higher seed production or seedling establishment success, processes like intra-specific competition or herbivory could be enhanced resulting in a decrease in the number of plants becoming reproductive adults (Harms et al., 2000; Goldberg et al., 2001; Maron and Crone, 2006).

In this study, by means of transition probability analyses we compare the plant recruitment success of the narrowly distributed *Ipomoea rubriflora* and its widespread congener *Ipomoea purpurea* at sites in Chaco woodland where these species grow in sympatry. These two species are particularly interesting to study because it has been reported that they have contrasting patterns of seed production and seedling density (Astegiano et al., 2010), in accordance with the idea that narrow geographic distributions in plants are associated with lower seed production, and thus with lower colonization and persistence abilities. However, differences in seed production between these two *Ipomoea* species could be lower than differences in seedling density (Astegiano et al., 2010), suggesting that not only pollination or resources can be limiting final recruitment success (via seed production) in the narrowly distributed species, but also seed predation and seedling establishment success among other factors.

Specifically, we addressed the following questions: (1) How does the narrowly distributed species differ from its widespread congener in their success in stages prior to seed dispersal (i.e., ovule fertilization, seed maturation and surviving predation), and post-dispersal stages (i.e., seedling emergence, seedling establishment and plant survival to reproductive maturity)? and (2) In which stage does the narrowly distributed species show the lowest transition probability (i.e., which stage might potentially be critical to plant recruitment)? We also compared total seed production per plant and seed mass as these traits also contributed to the understanding of the relative importance of differences in the success in pre- and post-dispersal stages in determining differences in colonization and persistence abilities between these species with contrasting range sizes.

2. Materials and methods

2.1. Study species and sites

I. rubriflora O'Donnell (*Ipomoea* subg. *Quamoelit* section *Mina*) occurs in Paraguay, Bolivia and from north to central Argentina; in contrast, *I. purpurea* (L.) Roth (*Ipomoea* subg. *Ipomoea* or *Quamoelit*, section *Pharbitis*) is a geographically widespread species, originally from the Americas but currently with a cosmopolitan distribution (Austin and Huaman, 1996). The actual geographic distribution of *I. purpurea* includes the distribution of *I. rubriflora*. These two

species commonly grow in disturbed areas such as abandoned crop fields, roadsides and gardens (J. Astegiano, personal observation). Both species are annual vines, with showy flowers (Galetto and Bernardello, 2004). *I. rubriflora* generally has four ovules per flower while *I. purpurea* has six ovules (Chiarini and Ariza Espinar, 2006). Both species are capable of autonomous self-pollination (Astegiano et al., 2010). However, *I. rubriflora* presents a smaller fruit set than *I. purpurea* after autonomous self-pollination and in comparison with natural pollination levels (Astegiano et al., 2010). Different species of Hymenoptera have been reported as pollinators of *I. purpurea* in the study sites, whereas only one hummingbird has been reported to pollinate *I. rubriflora* (Astegiano et al., 2010). Both species produce a dehiscent capsule; that of *I. rubriflora* with 2–4 seeds and that of *I. purpurea* with 4–6 seeds. Two morphospecies of bruchids (Bruchidae, Coleoptera) were identified as seed predators on the *I. rubriflora*, and only one morphospecies of weevil (Curculionidae, Coleoptera) was observed in *I. purpurea* (Astegiano, 2010). When present, these three seed predators produce severe damage to the seeds (J. Astegiano, personal observation). Both species can form persistent seed banks (Astegiano et al., 2010).

This study was done in communities of Chaco woodland of central Argentina where *I. rubriflora* and *I. purpurea* coexist, even at the microsite scale. The Chaco woodland is a dry forest currently restricted to isolated patches surrounded by intensively managed matrices (Zak et al., 2004). Data were obtained from March 2008 to April 2009 from two sites: the CONAE site (from its name in Spanish: Comisión Nacional de Actividades Espaciales, the National Commission for Space Activity; 31°31'28"S, 64°27'30"W) which is a 3.5-ha natural reserve surrounded by soybean and maize fields; and the Santo Domingo site (31°10'59"S, 64°15'29"W) which is a continuous 1000-ha forest, surrounded by soybean and maize fields. The CONAE site is 43 km from the Santo Domingo site.

2.2. Total seed production per plant, seed mass and pre-dispersal recruitment success: ovule fertilization, seed maturation and surviving pre-dispersal seed predation

We quantified total seed production, seed mass and success in pre-dispersal stages of *I. rubriflora* and *I. purpurea* for ten randomly chosen individuals of each species at each site ($n = 20$). These variables were evaluated in 10 individuals per species per site because of the natural low local abundance of *I. rubriflora* observed in March 2008 at those sites (11 and 15 individuals of *I. rubriflora* at the CONAE and the Santo Domingo sites, respectively; J. Astegiano, unpublished data).

Total fruit production per plant was obtained by directly counting fruits and dispersed capsules in plants. Then, ten randomly chosen mature fruits were harvested from each individual after fruit dispersal began. The number of aborted, predated and undamaged mature seeds per fruit was obtained. The number of initiated seeds per fruit was calculated as the sum of aborted, predated and undamaged mature seeds. Then, the mean values of each of these seed types per plant were calculated to characterize individuals. The total number of seeds per plant was estimated by multiplying the total number of fruits produced per plant by the mean number of undamaged mature seeds per fruit. Although the number of seeds per fruit, total fruit and seed production per plant has been evaluated in these species in a previous study performed during the 2006 reproductive season (Astegiano et al., 2010), we decided to include them in the present study because of the high among years variation that reproductive output can show in flowering plants (e.g., Price et al., 2005). Seed mass was obtained from 200 undamaged seeds from each species (10 seeds from each individual from each site).

We calculated three transition probabilities (TP) for the stages prior to seed dispersal, on a per individual basis:

1. TP₁, the probability of an ovule being fertilized, i.e. the number of initiated seeds relative to the number of ovules per flower. Since ovule number is relatively constant in both *Ipomoea* species (F. Chiarini, pers. comm.), we used the number of ovules reported in a previous study of *Ipomoea* species in this study region (Chiarini and Ariza Espinar, 2006).
2. TP₂, the probability of an initiated seed reaching maturity (estimated as 1- the number of aborted seeds relative to the number of initiated seeds).
3. TP₃, the probability of an initiated seed surviving pre-dispersal predation (estimated as the number of undamaged seeds –i.e., those not preyed upon–relative to the number of initiated seeds, but excluding aborted seeds).

The pre-dispersal cumulative probability of each species was calculated as the product of TP₁, TP₂ and TP₃ (see Rey and Alcántara, 2000).

2.3. Post-dispersal recruitment success: seedling emergence, seedling establishment and plant survival to reproductive maturity

Transition probabilities from seed arrival to reproductive adults were evaluated in permanent plots established at each study site. Mature seeds were harvested from at least ten randomly chosen individuals per species per site between April and June 2008, and stored in paper bags.

Seeds were sown at the beginning of December 2008, when the natural emergence of seedlings of both species begins. Seeds sowed at each site had come from that site. The number of permanent plots at each site ($n_{\text{CONAE}} = 17$; $n_{\text{Santo Domingo}} = 20$) was determined by the number of seeds of *I. rubriflora* previously harvested. Three permanent plots of 30 × 30 cm were set up at each station: *I. rubriflora*, and *I. purpurea*, along with a control plot (no seeds sown) to estimate the number of seedlings of each *Ipomoea* species that emerge naturally from sowed plots. Ten scarified seeds of each species were sown at each corresponding plot, nine in a matrix of three rows and three columns separated by 8 cm, and one seed was placed at random. Seeds were scarified mechanically with a piece of sandpaper because these two species of *Ipomoea* exhibit physical dormancy (Baskin and Baskin, 1998; J. Astegiano, unpublished data). After the first rain (8 days after sowing) each site was visited approximately every 3 days when newly emerged seedlings were labeled with tags of different colors according to their date of emergence. Plots were visited until no new seedlings had emerged. Twenty days after the first seedling was labeled, each plot was visited approximately every 3 days to determine the number of established seedlings, defined as those that had survived more than 20 days. This criterion was adopted based on a previous study of *Ipomoea* seedlings (Astegiano et al., 2010). The apparent cause of seedling death (e.g., presence of herbivory, fungal attack, water stress, etc.) was also recorded. In March, 2009 (ten weeks later), each study site was visited and the number of plants that had survived to reproductive maturity (plants with flowers or fruits) at each plot was recorded.

We calculated three transition probabilities from seed arrival to reproductive adults, on a per plot basis:

1. TP₄, seedling emergence probability (i.e. the number of seedlings that emerged in each sowed plot relative to the sum of the number of seeds sowed in that plot and the number of seedlings of the species that emerged in the control plot).

2. TP₅, seedling establishment probability (i.e. the number of seedlings that survived more than 20 days relative to the number of emerged seedlings)
3. TP₆, probability of reaching reproductive maturity (i.e. the number of reproductive plants relative to the number of established seedlings).

The cumulative probability of regeneration was obtained as the product of TP₄ and TP₅. The cumulative probability of final recruitment was calculated as the product of all the probabilities previously calculated, from TP₁ to TP₆ (see Rey and Alcántara, 2000).

2.4. Data analyses

Differences in the number of seeds per fruit, seed mass and the total number of fruits and seeds per plant, between the narrowly distributed *I. rubriflora* and the widespread *I. purpurea* were determined using an analysis of variance (ANOVA) done with the SPSS 15.0 statistical package (2006). Species was considered a fixed factor and sites were blocks. Replicates of each species were represented by individuals. Assumptions of normality and homogeneity of variances were tested using standard techniques.

To analyze differences between species in transition probabilities, different analyses were performed, depending on the error distribution of each response variable. Since TP₁ was normally distributed, differences between species in this variable were determined using ANOVA, with species as a fixed factor and sites as blocks. To determine differences between species in TP₂, TP₃, TP₄ and TP₅ generalized linear mixed models were generated (GLMM; Pinheiro and Bates, 2004) using the lme4 package in R (3.0 release, R Development Core Team, 2008). We constructed a GLMM model for each transition probability (except TP₆), using a binomial error distribution and a logit link function. In each model, species was considered a fixed factor and site was a random factor (i.e., a block). The Laplace criterion was used to fit the models (Pinheiro and Bates, 2004). The fixed effect of species on each transition probability was determined with the Likelihood Ratio Test, which analyzes significant changes in deviance after the removal of the factor species through Chi-square tests (Pinheiro and Bates, 2004). As seedlings only became established at one study site (CONAE), we analyzed differences between species in TP₆ with a generalized linear model (GLM), using a binomial error distribution and a logit link function.

3. Results

3.1. Total seed production per plant, seed mass and pre-dispersal recruitment success

The narrowly distributed *I. rubriflora* produced significantly fewer seeds per fruit ($F_{(1, 33)} = 187.57, P = 0.0001$; Fig. 1) and a lower total number of fruit ($F_{(1, 33)} = 21.77, P = 0.0001$; Fig. 1) and seeds per plant than its widespread congener *I. purpurea* ($F_{(1, 33)} = 31.58, P = 0.0001$; Fig. 1). Seed mass was also smaller in *I. rubriflora* than in *I. purpurea* ($F_{(1, 33)} = 29.33, P = 0.0001$; Fig. 1).

I. rubriflora had a marginally lower probability of ovule fertilization ($F_{(1, 33)} TP_1 = 4.06, P = 0.052$; Fig. 2) and the probability of an initiated seed reaching maturity (i.e., to not be aborted) was also lower for this species ($\chi^2_{TP_2} = 116.1, df = 1, P = 0.0001$; Fig. 2). The probability of an initiated seed of surviving pre-dispersal predation was not significantly different between species ($\chi^2 = 1.69, df = 1, P = 0.19$; Fig. 2).

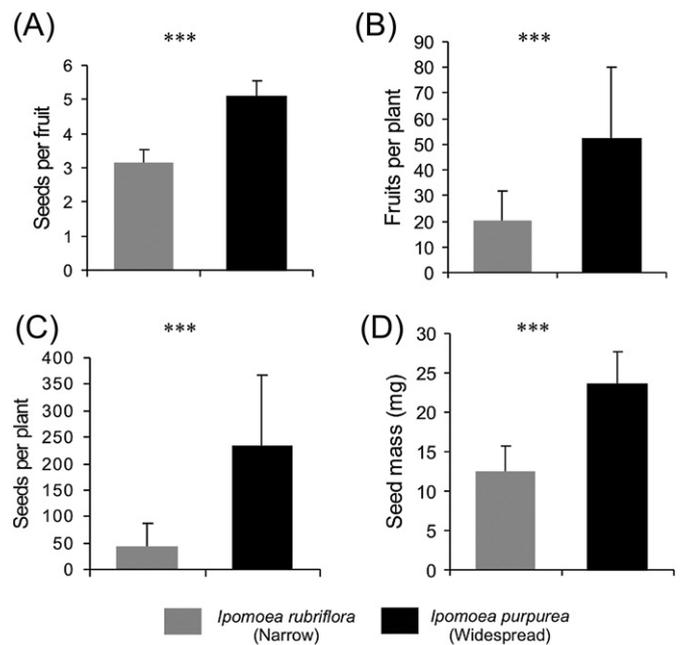


Fig. 1. (A) Seeds per fruit (B) Total number of fruits per plant, (C) Total number of seeds per plant and (D) Seed mass of the narrowly distributed *I. rubriflora* and its geographically widespread congener *I. purpurea*. Mean values \pm SD are shown. Significance levels: *** $p < 0.0001$.

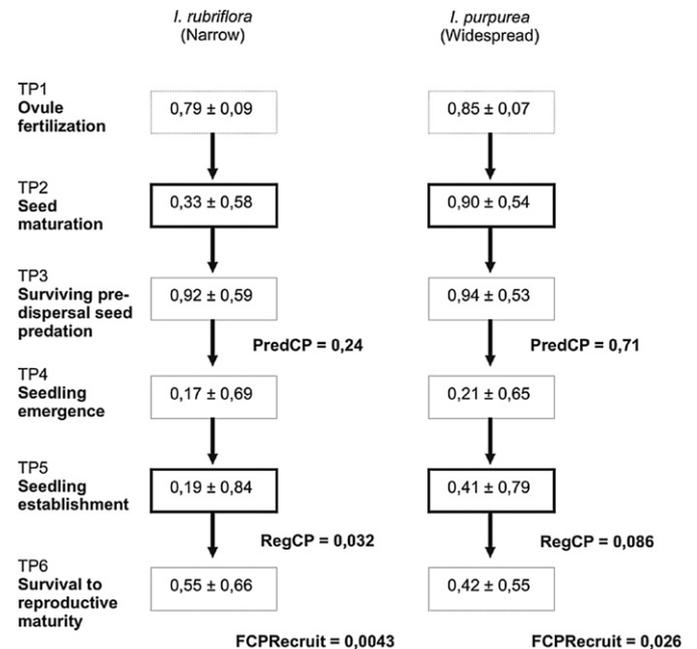


Fig. 2. Diagram of the recruitment success of the narrowly distributed *I. rubriflora* and its geographically widespread congener *I. purpurea*. Mean values \pm standard errors estimated from GLMM (TP2-TP5) and GLM (TP6) of the evaluated transition probabilities are shown. For TP1 (Ovule fertilization) observed mean values \pm SD are shown (see section 2.4. Data analysis for details). Pre-dispersal (TP₁ \times TP₂ \times TP₃), regeneration (TP₄ \times TP₅) and final (TP₁ \times TP₂ \times TP₃ \times TP₄ \times TP₅ \times TP₆) cumulative probability are also shown. Thick lines around boxes represent statistically significant differences between species at $P < 0.05$ and dashed lines represent tendencies; i.e., $0.10 > P > 0.05$. Abbreviations: PredCP = cumulative pre-dispersal probability, RegCP = cumulative regeneration probability, FCPRecruit = final cumulative probability of recruitment.

3.2. Post-dispersal recruitment success

The probability of seedling emergence did not differ significantly between species ($\chi^2 = 2.13$; $df = 1$; $P = 0.14$; Fig. 2). However, the probability of seedling establishment in *I. rubriflora* was significantly lower than it was in *I. purpurea* ($\chi^2 = 8$; $df = 1$; $P = 0.004$; Fig. 2). No seedling of either species established at the Santo Domingo site, thus TP₆ was evaluated only at the CONAE site. The probability of an established seedling becoming a reproductive adult did not differ significantly between species ($\chi^2 = 1.42$; $df = 1$; $P = 0.232$; Fig. 2).

3.3. Cumulative transition probabilities: pre-dispersal, regeneration and final plant recruitment success

There was a larger decrease in the number of potential individuals prior to dispersal for *I. rubriflora* than for *I. purpurea*: cumulative pre-dispersal transition probabilities indicated that 24 percent and 71 percent of these individuals reached the mature seed stage undamaged in these species, respectively (Fig. 2). However, the most disadvantageous phase for both species was regeneration, as evidenced by this phase having the lowest cumulative transition probability (Fig. 2). The lowest transition probability for both species was seedling emergence (Fig. 2). In *I. rubriflora* seedling establishment showed a probability similar to that of seedling emergence (Fig. 2). *I. rubriflora* had a final cumulative probability of plant recruitment (from ovule to reproductive adult) an order of magnitude lower than that observed for *I. purpurea* (Fig. 2).

4. Discussion

Narrowly distributed plant species are expected to have lower fecundity than widespread congeners (studies reviewed in Murray et al., 2002; Lavergne et al., 2004; Young et al., 2007), and this may be associated with greater pollen (Rymer et al., 2005; Carrió et al., 2009) or resource (Lavergne et al., 2005; but see Lavergne et al., 2004) limitation. In accordance with the general results reported in those studies we found that the narrowly distributed *I. rubriflora* produced fewer seeds per plant than its widespread congener *I. purpurea*. Moreover, as revealed by transition probabilities analyses, the lower fecundity observed in the narrowly distributed species may be associated not only with its lower ovule production (Astegiano et al., 2010) but also with its greater pollen and resource limitation. The lower probability of an ovule being fertilized may support the idea of higher pollen limitation whereas the lower probability of a seed reaching maturity and the lower total fruit production per plant may be indicative of greater resource limitation in *I. rubriflora* than in *I. purpurea*.

Greater resource limitation in the reproduction of narrowly distributed species has commonly been associated with the idea of lower competitive ability in these species compared to their more widespread congeners (Lavergne et al., 2004). However, seed production by narrowly distributed species has generally been evaluated for sites different from the site where the widespread congeners are found, thus the demographic causes of rarity might be confounded with the effects of growing in more stressful habitats (Münzbergová, 2005). As this study was performed at sites where these *Ipomoea* species coexist, even at the microsite scale, the higher seed abortion and consequently the lower seed production of *I. rubriflora* might be associated with lower competitive ability. *I. purpurea* has been reported as a superior competitor in recent studies (Chaney and Baucom, 2012). Moreover, the smaller size of individuals of *I. rubriflora* than that of *I. purpurea* at the study sites (J. Astegiano, personal observation) might support the idea of lower competitive ability in *I. rubriflora*. However, the possibility of the

lower seed maturation of *I. rubriflora* being the result of higher inbreeding depression cannot be dismissed, as recognized in a previous study (Astegiano et al., 2010). Since fecundity in “good” years may be critical for plant population growth in annuals (Kaliz and Mc Peek, 1993; Dostal, 2007; Levine et al., 2008) experimental studies combining fertilizer addition and pollen supplementation with different pollen sources would certainly improve our understanding of the mechanisms determining the narrow distribution of *I. rubriflora*.

Seed survival to pre-dispersal predation did not differ between *I. rubriflora* and *I. purpurea*, and was higher than the other pre-dispersal probabilities evaluated in this study (i.e., ovule fertilization and seed maturation). These were unexpected results, since pre-dispersal seed predation by insects is one of the main processes that can affect plant recruitment (Ehrlén, 2002; Maron and Crone, 2006; Kolb et al., 2007) and several studies have highlighted the importance of this process in limiting the local, regional and global distribution of plants (Hegazy and Eesa, 1991; Bevill et al., 1999; Maron and Crone, 2006). However, when compared with widespread congeners (i.e., controls), narrowly distributed plants showed opposite trends in pre-dispersal seed predation levels (Lavergne et al., 2004, 2005; Münzbergová, 2005; Young et al., 2007; Boieiro et al., 2010). On the other hand, since individuals of *I. rubriflora* showed less than half of the seed production of its widespread congener, their initiated seeds would be expected to show lower seed predation levels. Similar degree of specialization by seed predators to these *Ipomoea* species might explain these results (Boieiro et al., 2010). However, as seed predation levels were relatively low (10% of total seed production in both species), seed predators might also be making use of other plant species also present at the study sites or these predators might naturally have low local abundances. Although seed predation can present high variation among-years (Kolb et al., 2007) and its effects on seed output can be accumulated into seed banks (Maron and Gardner, 2000), the population growth rate of species with a persistent seed bank strategy, as is the case of these *Ipomoea* (Astegiano et al., 2010), may be less sensitive to variations on seed predation levels (Maron and Crone, 2006). Consequently, the negative impact of pre-dispersal seed predators on recruitment success might be generally low and less important than other processes in determining the difference in range size between these *Ipomoea*.

In both species, seedling emergence had the lowest transition probability. This was another unexpected result since for these species the germination success of scarified seeds in germination chambers can be high (83% in *I. rubriflora* and 94% in *I. purpurea*; J. Astegiano, unpublished data). On the other hand, since species differ in seed mass and larger-seeded species may produce larger seedlings that may be able to emerge from deeper soil levels or more developed litter layers (Jurado and Westoby, 1992; Molofsky and Augspurger, 1992; Pearson et al., 2003), we expected higher probability of emergence in *I. purpurea*. We propose that the generally negative effect of litter on plant regeneration, by either preventing germination or suppressing seedling growth and which may be independent of seed size (Dalling and Hubbell, 2002; Fenner and Thompson, 2005), might explain the similar probability of emergence recorded for these two species of *Ipomoea*. Moreover, negative density-dependent effects diminishing emergence probability in *I. purpurea* (Goldberg et al., 2001) might also explain this result, as in a previous study we found that this species presented higher seed density in the seed bank (Astegiano et al., 2010). Future experimental studies focused on the effects of litter and seed density on seedling emergence success in these *Ipomoea* species would provide valuable data on processes determining the geographic distribution of these species. Indeed, as seedling emergence can be critical for annual species population growth

(Griffith and Forpeth, 2005; Quintana Ascencio et al., 2011), understanding which processes limit the emergence of seedlings of *I. purpurea* may provide some clues about how *I. rubriflora* can coexist, even at the microsite scale, with its widespread congener (Chesson, 2000).

Seedling establishment success was similar to seedling emergence in *I. rubriflora*, showing a significantly lower probability than in *I. purpurea*. This difference between species could explain previous results of significantly lower natural seedling density in *I. rubriflora* (Astegiano et al., 2010). Herbivory is one of the main causes of seedling mortality in plant communities (Hanley, 1998) and experimental studies have indicated that seedlings from large seeds tolerate herbivory better than seedlings from small seeds (Armstrong and Westoby, 1993; Harms and Dalling, 1997). Seedling mortality in *I. rubriflora* and *I. purpurea* seemed to be associated with cotyledon and foliar herbivory, and also with water stress (J. Astegiano, personal observation). Thus, lower establishment success in *I. rubriflora* might be related to the production of seedlings with proportionally fewer reserves that are therefore less likely to survive adverse conditions such as herbivory, or that have a less developed root system (Leishman et al., 2000). However, this recruitment advantage of the widespread *I. purpurea* may be temporary and may not carry through to the adult phase in accordance with the hypotheses of a temporal advantage of large-seeded species due to proportionally higher reserves (Moles and Westoby, 2006; but see Metz et al., 2010). Herbivory on adult plants of *I. purpurea* can be high at the study region—up to 90 percent of leaf area—while adult plants of *I. rubriflora* are rarely attacked (J. Astegiano, personal observation) and this may explain the lower (though not significantly so) transition probability to the reproductive adult phase in this geographically widespread species. In this sense but contrary to our results, studies on the tolerance of *I. purpurea* to herbivory have showed that herbivore damage can be more detrimental for plants in the seedling stage and in adult plants producing fruits, being plants in intermediate states—i.e., previous to the production of flowers—more tolerant (Tiffin, 2002). However, high competition environments may diminish plant tolerance to herbivory (Tiffin, 2002). Thus we hypothesize that the apparently beneficial higher seedling survival of *I. purpurea* might result in higher plant abundance and thus higher competitive environments resulting in lower plant tolerance to herbivory, which may lead to lower survival to reproductive adults. On the other hand, changes in resource allocation to plant defense with ontogeny might explain the survival of individuals of *I. rubriflora* to the reproductive adult phase (Boege and Marquis, 2005). Understanding how these species respond to plant herbivory may be also an important avenue of research for understanding both plant distribution and coexistence (Hulme, 1996; Chesson, 2000).

In this sense, we cannot discard the possibility that our studies on these species may correspond, in a broad sense, to bad years for the narrowly distributed species and good years for its widespread congener. If this is the case, a stable coexistence via a storage effect (*sensu* Chesson, 2000) might be expected. However, previous results on long-term persistent seed bank density (Astegiano et al., 2010) may support the idea of a general lower performance of *I. rubriflora*, and not simply that our studies reflect bad years for this narrowly distributed species. Moreover, since in a recent study it has been reported that *I. purpurea* exhibits at least nine of Baker's 12 ideal weed traits (Chaney and Baucom, 2012) the idea that they might represent just good years for the widespread species seems even less likely. In this context, the results of our comparative study suggest that differences in density-dependent mechanisms acting at post-dispersal stages might explain how *I. purpurea* and *I. rubriflora* coexist, as suggested for the results obtained for seedling emergence, establishment and individual survival to reproductive adults.

5. Conclusions

The evaluation of transition probabilities from ovule to reproductive adults in two sympatric congeners with contrasting geographic range sizes showed that the narrowly distributed species had lower plant recruitment success. This result may support the idea of lower capacity for colonization and persistence in narrowly distributed species (e.g., Van der Veecken et al., 2007). On the other hand, our results suggest that understanding plant regeneration (i.e., seedling emergence and establishment) may be central for understanding plant recruitment success and thus differences in geographic ranges between these annual species as well as their coexistence. As regeneration can be critical for plant population maintenance in annuals, processes acting at these plant stages may be considered key for understanding narrow distributions.

Overall, our results may highlight the importance of evaluating the success of individuals at different life-history stages when looking for the demographic causes of rarity (Münzbergová, 2005): with its lower total seed production per plant and its lower seed mass, *I. rubriflora* is not only at a numerical disadvantage for reaching local microsites that are favorable for regeneration or colonizing new sites, but also has a lower per-seed probability of becoming established which might be critical for the local persistence of this annual species. Indeed, as the lower probability of successfully establishing in narrowly distributed species may be related to narrower regeneration niches (e.g., Brändle et al., 2003; Luna and Moreno, 2010), future experimental studies of the regeneration niche of these *Ipomoea* species (*sensu* Grubb, 1977) might be of particular importance to disentangling the mechanisms limiting the distribution of *I. rubriflora*. The lower local abundance of *I. rubriflora* at the study sites seems to support the idea of a lower regeneration niche, as hypothesized for narrowly distributed species (Gaston, 2003). However, the fact that this narrowly distributed species coexists even at the microsite scale with its widespread congener might suggest that they differ in some resource requirements (Chesson, 2000). Otherwise, coexistence will not be stable and *I. rubriflora* will be going to extinction (Chesson, 2000).

Finally, if differential survival until reproductive maturity in these *Ipomoea* species is associated with differences in resource allocation to plant defenses or tolerance to herbivory, then differences in pre-dispersal recruitment success and reproductive output might also be explained by differences in resource allocation to plant functions (Obeso, 2002). As 66% of the potential individuals can be lost before seed dispersal occurs and seed production seems to be limited by resources available to mature seeds in *I. rubriflora*, the study of the association between range size and resource allocation strategy might also offer an important avenue of research.

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