Depressed pollination of *Lapageria rosea* Ruiz et Pav. (Philesiaceae) in the fragmented temperate rainforest of southern South America

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Abstract. We studied the pollination and reproductive success in continuous and fragmented populations of *Lapageria rosea*, a self-compatible plant endemic to temperate forests of Chile. Pollinator abundance, visitation rates, flower abundance, nectar volume and concentration, pollen germination and fruit and seed production, were compared between continuous forest of 145 ha and four forest fragments of 6, 3, 3, and 1 ha respectively, surrounded by mature pine plantations of *Pinus radiata*. Flower abundance was lower in three out of four forest fragments relative to continuous forest. Nectar volume and sugar concentration did not differ between flowers in the two habitats. Pollinators of *L. rosea*, the hummingbird *Sephanoides sephaniodes* and bumblebee *Bombus dahlbomii* were less abundant and visited flowers of *L. rosea* at lower rates in fragments than in continuous forest. In addition, *in vitro* rates of pollen germination were lower for flowers in forest fragments. The number of seeds per fruit was also lower in forest fragments. We suggest that fragmentation affects the reproductive success of *L. rosea*, lowering the total numbers of seeds produced and possibly compromising long term persistence of fragmented populations.

Introduction

Habitat fragmentation can have profound effects on pollination with negative consequences for plant reproduction (Murcia 1996; Aizen 1998). The reduction in habitat size and increment in isolation can reduce the diversity and abundance of the remaining pollinators (Jennersten 1988; Aizen and Feinsinger 1994a). Such reductions may in turn lead to a reduction in the frequency of visits to the flowers, triggering a reduction in seed production (Jennersten 1988; Aizen and Feinsinger 1994b; Ghazoul and McLeish 2001).

At the same time, small patches of flowering plants may be less attractive to pollinators, reducing the amount of pollen received by the stigmas (Sih and Baltus 1987). Since nectar characteristics are dependent on environmental conditions (Zimmerman 1988; Rathcke 1992), forest fragmentation might also affect the attractiveness of plants to pollinators, through modifications in nectar production rates and sugar concentration. In fact, sugar concentration usually increases under low humidity through evaporation of water, as a trade-off with nectar volume. Hummingbirds prefer concentrated nectar up to

30% of sugar concentration (Tamm and Gass 1986; López-Calleja et al. 1997). Therefore, high concentrated nectar, might in turn translate into an increased frequency of visits by pollinators (Southwick et al. 1981; Pleasants 1983). Because habitat fragmentation can reduce atmospheric humidity (Kapos 1989; Matlack 1993; Camargo and Kapos 1995), the attractiveness of flowers, in terms of nectar traits, might be higher in fragmented populations. Hence, habitat fragmentation could lead to one of two opposite trends, a diminution in the frequency of pollinator visits, because small and isolated patches are less attractive; or an increment in visitation rates, because flowers in fragments might produce more concentrated nectar. Higher nectar sugar concentration in flowers from fragments might compensate for the reduction in the size of flower patches in fragments, resulting in similar visitation rates of pollinators to plants, and as a result, similar rates of seed production.

The reduction in plant population size and increment in isolation in a fragmented landscape can trigger an increase in mating among close relative, and consequently can produce inbreeding depression (Barrett and Kohn 1991; Ellstrand and Elam 1993; Young et al. 1996). Pollen produced by individuals with higher levels of inbreeding may show lower germination rates, affecting seed production (Johannsson et al. 1998). Inbreeding depression can also express an increase in fruit and seed abortion and, consequently, a reduction in seed set (Ramsey and Vaughton 1996; Hauser and Siegismund 2000).

In temperate forests of central Chile, pollination by animals is highly important. Here, up to 85% of genera of woody plants are visited, and probably pollinated by animals (Aizen et al. 2002). Forest from central Chile has been severely fragmented, and contains high levels of endemism in both animal and plant species (Armesto et al. 1996; San Martín and Donoso 1996; Bustamante and Castor 1998). To date, native forests in central Chile are reduced to numerous small fragments, most of them surrounded by plantations of the exotic tree, *Pinus radiata* L (Bustamante and Castor 1998). Thus, study of the effects of habitat fragmentation on pollination, and its consequences to plant reproduction is of great importance for conservation.

In this work we investigate the interaction of copihue (*Lapageria rosea* Ruiz et Pav. Philesiaceae) with their pollinators in a fragmented landscape, and how fragmentation of forests affect its reproductive success. *Lapageria rosea* is a vine, endemic to these forests and it has lower population size and density in forest fragments than in continuous forest (Henríquez 2002). This self-compatible plant depends mostly on two animal species for pollination, the green-backed fire crown *Sephanoides sephaniodes* Lesson (Trochilidae), and the giant bumblebee *Bombus dahlbomii* Güer. (Apidae) (Humaña and Riveros 1994). Blooming peak occurs in autumn, time at which is also flowering the mistletoe *Tristerix corymbosus* (L.) Kuijt, being both plants pollinated by *S. sephaniodes* (Smith-Ramírez 1993; Henríquez 2002).

If abundance of hummingbirds and bumblebees is reduced in a fragmented landscape, we expect lower visitation rates to *L. rosea* in smaller forest fragments. Consequently, plants in forest fragments might exhibit lower

pollination success, expressed as a lower proportion of flowers fertilized, fruit and seed sets. Lower quality of the transported pollen might also increases fruit and seed abortions. However, if reduction in air humidity increases nectar concentration in smaller fragments, we expect a compensatory effect on visitation rates in these fragments, and probably, a null effect on seed production.

Methods

Study site

We studied fragmented and non-fragmented populations of *L. rosea* in the coastal range of central Chile (35°59′ S, 72°41′ W) during one reproductive season, from May 2001 to June 2002. The zone comprised Maulino forest, a rich forest in deciduous and evergreen trees, currently severely fragmented due to forestry (San Martín and Donoso 1996; Bustamante and Castor 1998). Specifically, we worked in a continuous forest, at Los Queules National Reserve (a protected area of 145 ha embedded in a forest track of 600 ha), and four fragments of native forest of small size (from 1 to 6 ha), all of them surrounded by *Pinus radiata* plantations. Forest fragments are less humid than continuous forest, all year around (Henríquez 2002).

Flower density and nectar volume and concentration

We estimated flower density as the number of flowers in 25 m^2 plots. Plots were randomly distributed across sites. Flower density was assessed during the peak of flowering season of *L. rosea*, in May 2002 (Henríquez 2002). We measured nectar volume in bagged ripe flowers during 24 h ($n = 35$ in continuous forest, $n = 35$ in forest fragments) inserting repeatedly a 60 μl microcapillary tube, in the six nectaries of each flower until no further nectar could be extracted. Bags were made with tulle mesh for diminishing possible temperature and humidity differences within the flower and the environment, thus avoiding biases in the assessment of nectar volume and sugar concentration. Measurements were made every 2 h throughout the day, from 8:30 to 18:30 h, between March and May 2002. At the same time of nectar volume measures, we estimated sugar concentration in the nectar, expressed in % w/w units. Measurements were made with a temperature-compensated hand refractometer.

Pollinator abundance

Pollinator abundance was estimated as the number of individuals of *S. sephaniodes* and *B. dahlbomii* recorded through visual records at 48 fixed stations in continuous forest and 48 in fragments. Each station had 10 m radius, and they were separated by 30 m approximately. Observations were made at 10 min

intervals from 8:00 to 12:00 h. This time corresponds to the peak of activity for both pollinators (Smith-Ramírez and Armesto 1998)

Frequency of visits and pollen load

We assessed the frequency of visits by pollinators to randomly selected flowers, during 10 min periods of observation, along a day from 8:00 to 17:00 h, between March and June 2001 (Kearns and Inouye 1993). Sampling was performed over twenty 10 min period per day and 4 days per month at the continuous forest and two 3 days at forest fragments. Total number of observations corresponded to 253 periods in continuous forest, and 153 in forest fragments. To test whether *S. sephaniodes* and *B. dahlbomii* were effectively transporting pollen grains from *L. rosea*, we counted the number of pollen grains of *L. rosea* among pollen from other species carried on the animal bodies. Extraction of pollen from hummingbirds ($n = 3$) was made capturing the birds with mist nets, and putting a sticky transparent adhesive tape applied to the head and bill of each bird. Then, the adhesive tapes were analyzed directly under microscopy. To obtain pollen grains from bumblebees, we captured the animals with an entomological net ($n = 17$), which were washed with 5 ml of ethanol solution at 50% (Kearns and Inouye 1993). Finally, we counted the number of pollen grains of *L. rosea* in six aliquots by using a hemacytometer under microscopy. Pollen load per bumblebee was assessed as the average number from the six aliquots extrapolated to whole volume of the sample.

Pollen quality

We estimated pollen quality, obtaining pollen from flowers from continuous forest and fragments (one flower per plant, $n = 34$ in continuous forest and $n = 37$ in fragments). Pollen germination was estimated as the percentage of pollen germinated *in vitro*, in a Brewbaker-Kwack medium at 20% of sucrose (Kearns and Inouye 1993). Pollen grains were considered germinated when the pollinic tube was developed. The optimal sucrose solution concentration was previously determined by germination trials at six different sucrose concentrations (1, 2.5, 5, 10, 20 and 30% w/w). From each sample, we counted the number of pollen grains germinated in six aliquots by using a hemacytometer under microscopy. The number of pollen grains germinated per flower was estimated as the average of the six aliquots.

Seed and fruit set

To estimate seed and fruit set, we tagged 46 mature flowers in the continuous forest, and 44 in forest fragments, one flower per plant, following them

throughout the year. We estimated the proportion of fertilized flowers, fruits aborted and fruits preyed, and finally, the proportion of flower successfully setting fruits at each site. We also estimated the number of seeds per fruit.

Results

Flowers density and nectar production

Flower abundance was 1.4 times lower in forest fragments than in continuous forest (0.6 ± 0.2 flowers / 25 m^2 in the fragments, and 0.9 ± 0.2 flowers / 25 m^2 in continuous forest, average ± SE Mann-Whitney Test, U = 4036, $p = 0.002$). Within fragments, three out of four forest fragments had flower abundance lower than the continuous forest (range: 0.16 ± 0.08–1.04 ± 0.31 flowers / 25 m^2 in the fragments). Consequently, the total offer of flowers to pollinators is lower in fragments than in continuous forest. Nectar volume and concentration per flower was similar between fragments and continuous forest, ranging from 22 μl to 38 μl along a day in continuous forest and fragments (Figure 1, ANOVA repeated measured, $F_{1,5} = 0.69$, $p = 0.63$). Sucrose concentration in nectar was also similar between continuous forest and fragments ($t = -1.51$, df = 127, $p = 0.14$), being 17.01 ± 4.72%. w/w in forest fragments, and 18.33 ± 4.75% w/w in continuous forest (average ± SE).

Pollinator abundance

Overall, pollinator abundance was approximately 1.4 times lower in forest fragments than in continuous forest (Mann-Whitney Test, U = 603,

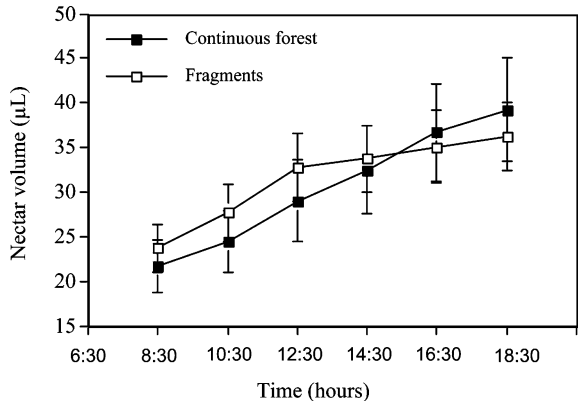

Figure 1. Volume of nectar of *Lapageria rosea* in continuous and fragmented forest (average ± SE).

$p < 0.001$. Figure 2a). No fragment exhibited a pollinator abundance higher than the continuous forest (range: 0.13 ± 0.07–1.38 ± 0.25 pollinators / station in the fragments). *Sephanoides sephaniodes* was 35% less abundant in fragments than in continuous forest (Mann-Whitney Test, U = 519, $p < 0.001$. Figure 2b), while the abundance *B. dahlbomii* did not differ between forest fragments and continuous forest (Mann-Whitney Test, U = 961.5, $p = 0.12$. Figure 2c).

Frequency of visits and pollen load

Only *S. sephaniodes* and *B. dahlbomii* visited flowers of *L. rosea* at both, fragments and continuous forest. Flowers were visited approximately three times less frequently by both pollinators in forest fragments than in continuous forest (Mann-Whitney Test, U = 409, $p \ll 0.001$. Figure 3a). No fragment presented visits per flower higher than the continuous forest (range: 0.06 ± 0.04–0.24 ± 0.06 visits / flower / 10 min). The major difference in frequency of visits was given by *B. dahlbomii*. In fact, the relative importance of visits of *B. dahlbomii* in continuous forest was 57.5% of the total number of visits (Figure 3c), while in forest fragments represented 35.0% of the total number of visits. *Sephanoides sephaniodes* had 60% less visits in fragments than continuous forest (Mann-Whitney Test, U = 5394, $p = 0.03$, Figure 3b), while *B. dahlbomii* had 80% less visits in fragments than continuous forest (Mann-Whitney Test, U = 4960, $p = 0.003$, Figure 3c).

Two out of three individuals of *S. sephaniodes*, and fifteen out of seventeen individuals of *B. dahlbomii*, carried pollen of *L. rosea*. Eighty five percent of the pollen grains transported by *S. sephaniodes* (29.7 ± 25.7 pollen grains / bird, average ± SE), and 96% of the pollen transported by *B. dahlbomii* (294.2 ± 107.4 pollen grains / bumblebee), was pollen of *L. rosea*.

Pollen germination

Germination was approximately 50% lower in pollen collected from flowers of forest fragments, than in pollen of flowers growing in the continuous forest (19.8% ± 13.7 in fragments and 33.4% ± 11.9 in continuous forest; average ± SE. Mann-Whitney Test, U = 278, $p < 0.001$). However, there was a higher variability at the fragments, since the germination capability ranged from 6.20 ± 3.75% to 34.92 ± 5.22%.

Seed set and fruit set

There were no significant differences between the proportion of fecundated flowers and fruit aborted or preyed among plants growing in fragments and in

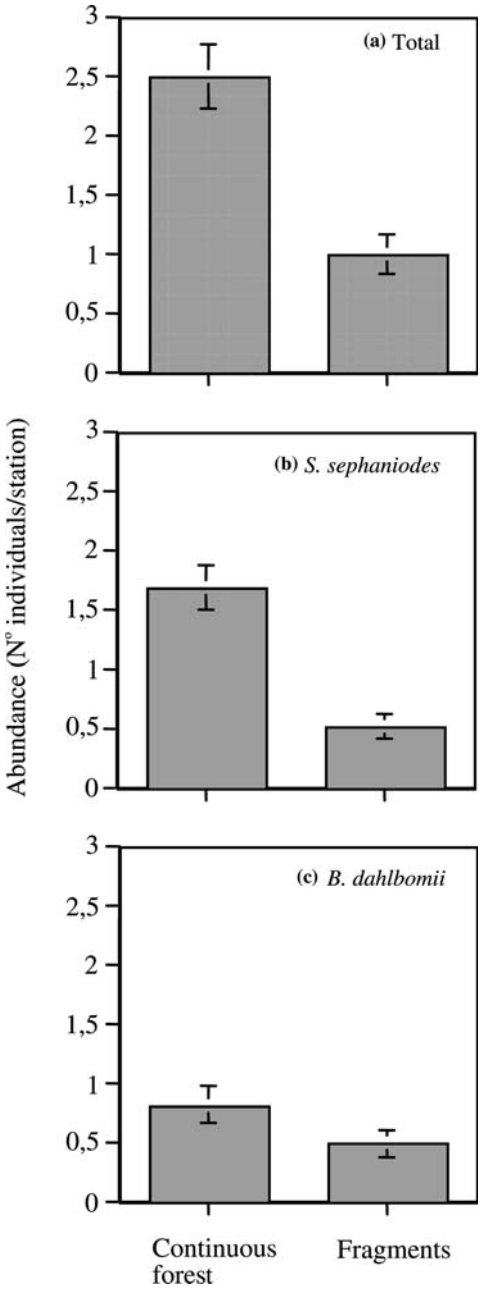

Figure 2. Pollinator abundance of *Lapageria rosea* in continuous and fragmented forest (average ± SE).

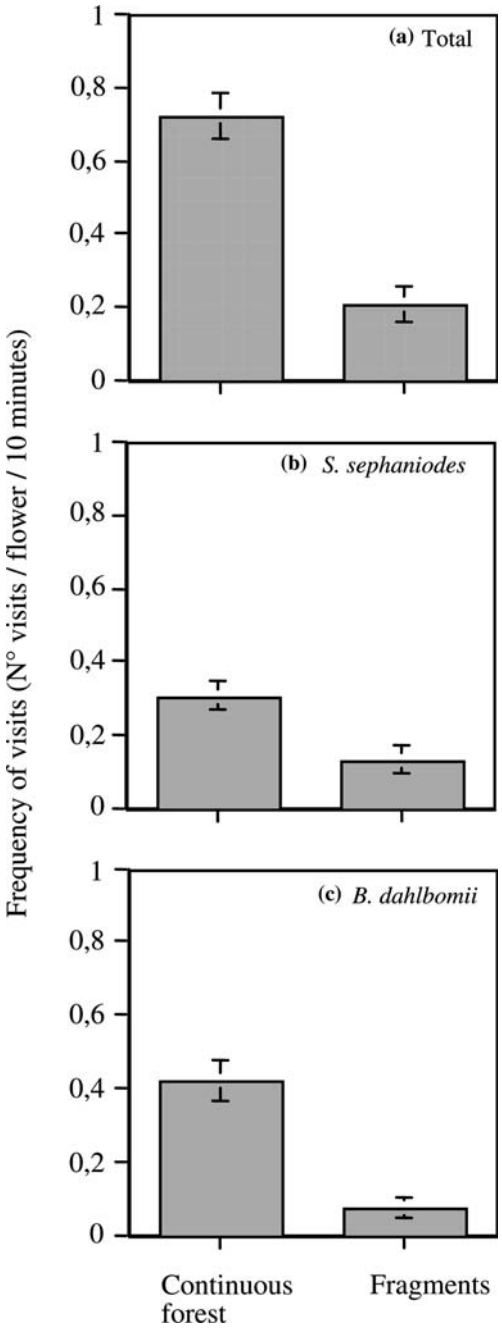

Figure 3. Frequency of visits of pollinators to *Lapageria rosea* in continuous forests and fragments (average ± SE).

Table 1. Fruiting of *Lapageria rosea* in continuous forest and fragments.

Site	No.	Flowers fecundated	Fruits aborted	Fruits preyed	Fruiting
Continuous forest	46	33 (71.8%)	1 (2.2%)	1 (2.2%)	31 (67.4%)
Forest fragments	44	32 (72.6%)	2 (4.6%)	4 (9.9%)	26 (59.1%)

No. = inicial number of flowers.

continuous forest. Hence, fruiting success did not differ between them ($\chi^2 = 2.98$, $p > 0.05$. Table 1). However, the number of seeds per fruit was around 12% lower in fragments than continuous forest (80.7 ± 3.4 seeds / fruit in continuous forest and 69.27 ± 4.5 seeds / fruit in forest fragments, $t = 2.018$; df = 128, $p = 0.05$). The number of seeds per fruit ranged from 51.2 ± 13.11 to 76.91 ± 6.66 seeds / fruit at the forest fragments.

Discussion

Lapageria rosea, despite being self-compatible, it requires pollinators for seed setting because it is autogamous (Humaña and Riveros 1994). Therefore, plants thriving in fragmented Maulino forests might be in a demographic vortex (sensu Soulé 1986). Reduced pollination leads to a depressed fitness compared to individuals living in continuous forests. The scenario faced by *L. rosea* might be representative of other species pollinated by hummingbirds and bumblebees in the menaced southern temperate rainforest of South America. Each individual of *L. rosea* is producing fewer seeds as a result of reduced pollination and diminished germination capability of pollen grains. Altogether, this reduction in reproductive success might in turn lead population size toward a demographic vortex rendering likely prone to extinction.

Neither nectar nor flower densities account for the depressed pollination rate of *L. rosea* in fragments. Despite lower air humidity in fragments, similar amounts of nectar of the same sugar concentration are produced by flowers regardless it thrives in forest remnants or the continuous forest. Therefore, flowers are equally attractive to pollinators as they offer the same reward for pollination services (Zimmerman 1988; Rathcke 1992). On the other hand, despite flower density tended to be lower in forest fragments, even in a fragment with a flower density similar to the continuous forest, visitation rate was depressed, suggesting that flower density alone cannot account for such a reduction. Coupled to a reduced flower density, the abundance of pollinators is depressed in forest fragments. In fact, the ratio of flowers / pollinators goes from 0.3 in the continuous forest, suggesting that each flower can be visited by more than one pollinator, to 2.5 in the fragments less visited, which implies that there is less than one pollinator for available flower.

Pollinators, besides providing fewer visits, carry also pollen of lower quality. Pollen from fragments germinate less frequently than pollen from continuous forests. Therefore, fewer ovules will be fecundated, explaining the reduced seed

set at forest fragments. *Lapageria rosea* at forest fragments have lower heterozygocity than those from continuous forest (Henríquez 2002), which could account for the reduced germination capability. Such a low heterozygocity implies higher levels of inbreeding among *L. rosea* from forest fragments. Pollen flow between the few individuals trapped within a fragment accounts for the inbreeding depression (Prober and Brown 1994), because higher rates of selfing (Reusch 2001), and more frequent mating between close relatives (Fenster 1991). In fact, pollen flow of *L. rosea* is restricted to a 15 m radius of the source flower into the floral neighbourhood (Valdivia, unpublished data), rendering the pollen flow between continuous forest and fragments unlikely.

Neither aborts nor fruits predation accounted for the depressed seed set in the forest fragments. Similar rates of fruit abortions indicate that there are not strong differences in resources availability among fragment and continuous forest (Stephenson 1981), suggesting that the lower reproductive success at fragments is consequence of the interaction between plant and pollinators.

Finally, regarding that *S. sephaniodes* and *B. dahlbomii* are the single hummingbirds and bumblebees resident to temperate rainforest of southern South America, and they visit a great deal of plants in this zone, a diminution in their abundance can lead to a reduction in pollination service in up to 20% of the woody species of the South American Temperate Rainforest, as for instance, *Escallonia sp.*, *Fuchsia magellania*, *Mitraria coccinea*, *Tristerix corymbosus*, which also growing at the Maulino forest (Aizen et al. 2002). Consequently, a great proportion of plants inhabiting of this forest may be facing a reduced reproductive success like *L. rosea*.

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