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REGULAR PAPER

Negative effects of forest fragmentation and proximity to edges on pollination and herbivory of *Bomarea salsilla* (Alstroemeriaceae)

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Background – Habitat fragmentation may have detrimental effects on both plant-mutualistic (i.e. pollination) and plant-antagonistic interactions (i.e. foliar herbivory). Such double negative effects may lead to a change in fitness, because the negative effects of a loss of a mutualism may be counterbalanced by the positive effects of a loss of an antagonism. In spite of being of great importance, however, the assessment of such ecological relationships has traditionally been performed separately.
Approach – We evaluated fragmentation and edge effects on floral and foliar display, frequency of pollinator visits, foliar herbivory, and reproductive success, assessed as number of fruits per plant, number of seeds per fruit, and number of seeds per plant, on *Bomarea salsilla*, a xenogamous vine from southern Chile.
Results – Plants occurring at fragments and edges exhibited a smaller floral display and a larger foliar display, and were rarely visited and preyed upon by pollinators and herbivores, respectively. The number of fruits per plant, the number of seeds per fruit, and number of seeds per plant were lower in fragments and at edges than at the core of continuous forest. Although forest fragmentation had a detrimental effect on herbivory, herbivores did not play a modulating role on the lowered pollinator-mediated reproductive success of *B. salsilla* probably due to the scarcity of foliar attack.
Conclusion – Decreased reproductive success of *Bomarea salsilla* plants due to forest fragmentation and the creation of edge habitats was not counterbalanced by foliar herbivory as expected. The ecological scenario faced by *B. salsilla* may be a representative phenomenon of numerous other species of the fragmented forests of South America.

Key words – fitness counterbalance, forest fragmentation, herbivory, pollination.

INTRODUCTION

Disruptions in plant-animal interactions due to habitat fragmentation are among the key issues in conservation biology. As far as mutualistic interactions are concerned, since the pioneer publication on pollination by Jennersten (1988) increasing evidence has been gathered about the relevance of habitat fragmentation as a detrimental factor affecting plant reproduction (Aguilar et al. 2006, Aizen & Vázquez 2006). Nevertheless, negative relationships, such as foliar herbivory, have received much less attention than pollination in spite of being very important in determining plant reproductive success (e.g. Groom 2001, Kery et al. 2001, Colling & Matthies 2004).

In short, the reduction in habitat size and increase in isolation of fragments can reduce the diversity and abundance of both plant mutualists and plant antagonists (Kery et al. 2001, Steffan-Dewenter et al. 2006, but see Simonetti et al., 2006, del-Val 2007). Thus, a reduction in the abundance of pollinators may lead to a reduction in the frequency of pollinator visits and, consequently, a reduction in the reproductive success of plants (Aguilar et al. 2006, Aizen & Vázquez 2006). Inbreeding depression, triggered by the increased number of mates between close relatives in small-sized fragments, may also contribute to such a reduction (Cruzan 2001, Severns 2003). Nevertheless, a reduction in abundance in herbivores may allow plants to escape from the negative consequences of foliar removal, therefore increasing the reproductive success (Hendrix 1988, Strauss & Zangerl 2002).

The increase of edge habitats due to habitat fragmentation might also impinge upon plant reproduction. Plants occurring at edge habitats might face a change (i.e. positive, negative or neutral) in the strength of the interactions coupled to changes in the abundance of their plant mutualists and

plant antagonists, therefore positively or negatively affecting plant reproductive success (Murcia 1995). In this regard, it is worthwhile highlighting that the effects of inhabiting edges versus cores, or fragments versus continuous habitats, are interdependent processes resulting of the habitat loss and its subsequent subdivision (Fahrig 2003).

Furthermore, habitat fragmentation might significantly modify plant traits related to floral and foliar display due to changes in abiotic or biotic conditions (Aizen & Vázquez 2006). Reductions in floral and foliar displays may significantly reduce plant attractiveness to pollinators and herbivores repectively, thus negatively or positively affecting plant reproductive success (Hendrix 1988, Pellmyr 2002, Strauss & Zangerl 2002).

The net effect on plant reproductive success of a decrease in a mutualistic and an antagonistic interaction should depend on the strength of such interactions and the extent to which they are modified by habitat fragmentation and creation of edge habitats. Modifications in plant traits might also be contributing to modulate plant reproductive success. Thus, plants facing asymmetrical relationships, in terms of mutualisms and antagonisms, can experience a decrease or increase in reproductive success caused by habitat fragmentation. On the contrary, if plants face symmetrical relationships in mutualistic and antagonistic interactions, and these are equally modified by habitat fragmentation, plants occurring in fragmented habitats and at edges might have equal fitness because a loss of a mutualism (i.e. pollination) may be compensated by a loss of an antagonism (i.e. herbivory) (e.g. Kery et al. 2001, Colling & Matthies 2004).

Although habitat fragmentation and increase of edge habitats may simultaneously affect plant-pollinator and plant-herbivore interactions, the assessments of such ecological relationships have traditionally been performed independently (but see Groom 2001, Steffan-Dewenter et al. 2006, Johnson et al. 2004, Kolb 2008). This approach, albeit convenient, may lead to a misunderstanding of the isolated and combined effects on plant performance, thereby hindering our understanding of such ecological scenarios. The aim of this work is to evaluate the effect of forest fragmentation, including the effect of occurring in edge habitats, on the pollinator-mediated reproductive success of *Bomarea salsilla*, a native vine-type monocot from the temperate rainforests from southern Chile, while simultaneously considering the effect of its herbivores on plant performance. If forest fragmentation has a negative effect on pollinator visitation, a lowered reproductive success is expected in fragments compared to continuous forests. Plants inhabiting the edges might also be facing negative effects compared to the core of such habitats. Nevertheless, if forest fragmentation also negatively affects plant-herbivore interactions, some sort of compensation is expected in fragments and at edges.

MATERIALS AND METHODS

Study area and species

We conducted fieldwork in Maulino forest in the northernmost zone of the temperate rainforest from Chile (35º59'S 72º41'W; Bustamante et al. 2005). Specifically, we performed the study in Los Queules National Reserve and two neighbouring forest fragments. Los Queules is a protected area of 145 ha embedded in a large tract of 600 ha of continuous forest. Forest fragments, ranging from 1 to 6 ha, are patches surrounded by commercial plantations of *Pinus radiate* D.Don. Here, we defined four sites taking into account the spatial arrangement of plant populations: one core and one edge of continuous forest, both sites placed in Los Queules National Reserve, and one core and one edge of forest fragment, both sites placed in two different fragments nearby Los Queules National Reserve. While we defined cores as sites placed ≥ 50 m inwards the border of each site, edges were defined as sites placed ≤ 10 m inwards the forest margin. Distance between sites ranged from 0.5 up to 2.5 km. In the present study, we only included one site per category because no other site was found harbouring *B. salsilla* populations. Despite this statistical caveat we performed all the following analyses by assessing the effects of forest fragmentation and its proximity to edge habitats.

Bomarea salsilla Vell. (Alstroemeriaceae) is a protandrous, small-sized climbing perennial vine with red flowers that is found in the sclerophyllous and temperate forests of Chile from 33°S to 40°S (fig. 1) (Muñoz & Moreira 2003). In the study site, it flowers from c. November to January. Its breeding system is unknown; however, two pilot pollinator-exclusion experiments in the study site, devised to test for autogamy and agamospermy, demonstrated that *B. sal-*

Figure 1 – *Bomarea salsilla* (Alstroemeriaceae) occurring at the fragmented Maulino forest from southern Chile.

silla is a totally pollinator-dependent plant for seed set (i.e. a fully xenogamous plant). In the study site, floral visitors were hummingbirds, *Sephanoides sephaniodes* (Trochilidae); bumblebees and bees, *Bombus dahlbomii*, *Bombus terrestris*, and *Manuelia gayatina* (Apidae); butterflies, *Mathania leucothea* (Pieridae); and flies, *Acrophthalmyda paulseni* (Bombyliidae) (pers. obs.). Its herbivores are unknown; however, several leaf-eating herbivores, mostly insect larvae, have been observed preying upon *B. salsilla* (Valdivia, pers. obs.).

Plant density

To assess the overall plant density and density of reproductive individuals, we randomly set up twenty 4-m^2 plots at each site. We established these plots at the peak of the reproductive season and recorded the number of total plants as well as their reproductive state (vegetative or flowering).

Floral and foliar display size

To determine floral display size, assessed as the number of flowers per plant and perigone length, we randomly chose 50 plants at each site and counted the total number of flowers produced by each plant at the end of the reproductive season, in January 2006. In these plants, we determined tepal length in two randomly chosen flowers per plant, which were then averaged to estimate mean tepal length per plant.

Foliar display size, in terms of the total number of leaves per plant and mean leaf length, was assessed on the same set of plants of the assessment of floral display. We counted the number of total leaves per plant at the end of the reproductive season, and measured the length of two randomly chosen leaves per plant, which were then averaged to estimate mean leaf length per plant.

Frequency of pollinator visits and herbivory

To evaluate the frequency of pollinator visits, we determined the number of pollinator visits to fifty randomly chosen plants at each site at the peak of the flowering season. Observations were carried out during 10-min periods, from 8:30 to 17:30 h. Observation periods were repeated every half hour for each plant, thus yielding a total number of nineteen 10-min periods per plant. Observations were performed at each site simultaneously by different observers, in order to avoid any weather-mediated bias. Total number of observations was 3,800 periods (950 periods at each site). We averaged the total number of periods per plant to obtain a single estimate for each plant and to avoid non-normally distributed data sets. We considered a visit as such when the floral visitor touched at least one reproductive structure (i.e. pistil or anthers).

To evaluate foliar herbivory on adult plants, we randomly selected fifty individuals at each site at the end of the reproductive season in January 2006. In these plants, we recorded the cumulative herbivory by chewing herbivores using a Herbivory Index, *HI* (Dirzo & Domínguez 1995). We checked 25 randomly chosen leaves per plant, assessing the degree of foliar surface lost due to herbivores. Each leaf was assigned to one of the following six categories: 0, 1, 2, 3, 4, or 5, depending on whether 0%, 1–6%, 7–12%, 13–25%, 26–50%, or 51–100% of foliar surface was absent. Thereafter, we determined *HI* as follows:

$$HI = \sum_{i=0}^{5} x_i n / N$$

where n is the frequency of observations, x_i is the damage category, and N is the total number of observations. A single per-plant estimate of *HI* was thus obtained.

Reproductive success

At the end of the reproductive season, we determined the number of fruits per plant (w_1), the number of seeds per fruit (w_2), and then multiplied w_1 and w_2 in order to estimate the overall reproductive success for each plant. Plants were the same as those of foliar herbivory assessment. To assess w_1, we tagged and followed all flowers borne by single plants until the end of the reproductive season to determine fruit set. Thereafter, to estimate w_2, just prior to seed dispersal, we severed one to two ripe fruits per plant and then counted the number of total seeds per fruit; we finally averaged these values for attaining a single estimation for each plant.

Statistical analyses

We examined effects of forest fragmentation (continuous forest versus forest fragment) and proximity to edge (edge versus core of forest) on plant density as well as on floral and foliar display size using two-way analysis of variance (ANOVA). Similar models were used to test for effects on pollination and herbivory, except that we included floral and foliar display size as covariates (if significant in the previous models) to account for a size effect in the frequency of pollinator visits and foliar herbivory. Thereafter, we assessed the effects of fragmentation and proximity to edge on the number of fruits per plant (w_1), number of seeds per fruit (w_2), and number of total seeds per plant ($w_1 \times w_2$) by using two-way ANCOVAs considering foliar herbivory per plant as a covariate to evaluate a possible modulating role of herbivores on plant reproductive success. Because number of flowers per plant may also affect fruit and seed set, we also included it as a second covariate. All ANOVAs and ANCOVAs were performed by using type-III-sums of squares to assess interactions (i.e. complex dependent processes) between fragmentation and proximity to edges because these landscape modifications are not independent (Fahrig 2003). All statistical analyses were performed using the software package Statistica v. 7.0.

RESULTS

Plant density

There was a significant fragmentation and edge effect, as well as an interaction effect between fragments and edges, on overall plant density (ANOVA, Fragmentation effect (FE): $P < 0.001$; Edge effect (EE): $P = 0.017$: FE × EE: $P = 0.008$). In fact, overall plant density was significantly higher at the edge of the continuous forest compared to all other sites (mean ± 1se: 11.9 ± 1.3 plants / plot at the core of continuous forest; 20.9 ± 2.5 at the edge of continuous forest; 9.6 ± 1.2 at the core of forest fragment; 9.1 ± 1.4 at the edge of forest fragment). Density of reproductive plants (mean ± 1se: 2.7 ± 0.7

Table 1 – Effects of forest fragmentation (FE) and proximity to edge (EE) on: (a) frequency of pollinator visits to *Bomarea salsilla* plants and (b) foliar herbivory in the fragmented Maulino forest.
Results are from two-way ANCOVAs with number of flowers per plant, perigone length, and leaf length entered as covariates.

Source	*df*	*MS*	*F*	*P*
(a) Frequency of pollinator visits				
Fragmentation effect (FE)	1	< 0.01	4.95	0.027
Edge effect (EE)	1	0.13	9.50	0.002
Number of flowers per plant	1	< 0.01	0.01	0.917
FE × EE	1	0.04	2.85	0.093
Leaf length	1	< 0.01	0.10	0.075
Error	194	0.01		
(b) Foliar herbivory				
Fragmentation effect (FE)	1	1.39	8.51	0.004
Edge effect (EE)	1	1.39	8.54	0.004
FE × EE	1	1.82	11.14	0.001
Leaf length	1	0.04	0.22	0.638
Error	195	0.16		

plants / plot at the core of continuous forest; 4.5 ± 0.7 at the edge of continuous forest; 2.9 ± 0.4 at the core of forest fragment; 3.3 ± 0.6 at the edge of forest fragment); however, did not differ among sites (ANOVA, FE: 0.412; EE: 0.081; FE × EE: 0.258).

Floral and foliar display

There was a significant fragmentation and edge effect, as well as an interaction effect, on floral display, assessed as the number of flowers per plant (ANOVA, FE: 0.001; EE: < 0.001; FE × EE: < 0.001). Plants in forest fragments (core and edge) and plants from the edge of continuous forest exhibited a significantly lower floral display than those from the core of continuous forest (mean ± 1se: 10.2 ± 1.0 number of flowers / plants at the core of continuous forest; 6.6 ± 0.5 at the edge of continuous forest; 6.7 ± 0.4 at the core of forest fragment; 6.5 ± 0.5 at the edge of forest fragment). In terms of perigone length, there was a significant edge effect, but not a fragmentation effect (ANOVA, FE: 0.681; EE: < 0.001; FE × EE: 0.248). Plants found at the edges of continuous forest and forest fragments, as well as those from the edge of forest fragments, had shorter perigones than those from the core of continuous forest (mean ± 1se: 1.9 ± 0.03 cm / flower at the core of continuous forest; 1.8 ± 0.02 at the edge of continuous forest; 1.8 ± 0.02 at the core of forest fragment; 1.7 ± 0.02 at the edge of forest fragment).

There were no significant edge or fragmentation effects on foliar display size, assessed as number of leaves per plant (ANOVA, FE: 0.681; EE: 0.143; FE × EE: 0.239). The mean (± 1se) number of leaves per plant was 61.2 ± 3.4 at the core of continuous forest, 52.8 ± 3.8 at the edge of continuous forest, 58.8 ± 3.1 at the core of forest fragment and 57.9 ± 1.8 at the edge of forest fragment. In terms of leaf length, there was no significant effect of forest fragmentation, but the proximity to edges and the interaction between forest fragmentation and edge effects were significant (ANOVA, FE: 0.744; EE: < 0.001; FE × EE: < 0.001). Mean (± 1se) leaf length per plant was 7.3 ± 0.2 cm at the core of continuous forest, 6.6 ± 0.2 at the edge of continuous forest, 5.9 ± 0.1 at the core of forest fragment and 8.1 ± 0.2 at the edge of forest fragment.

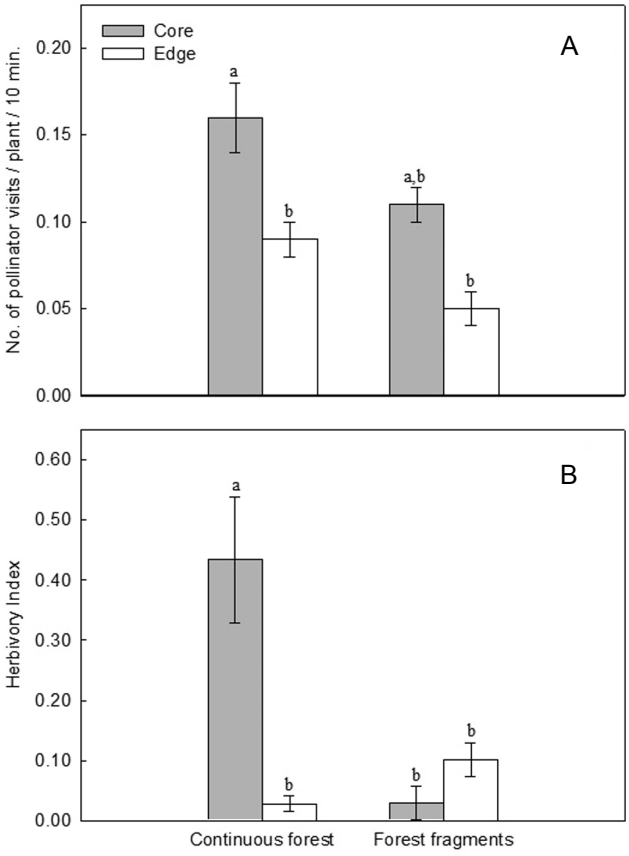

Figure 2 – Effects of forest fragmentation (continuous vs. fragment) and location (edge vs. core) on frequency of pollinator visits (A) and foliar herbivory (B) in *Bomarea salsilla* in the fragmented Maulino forest. Dissimilar letters depict significant differences ($P < 0.05$) following Tukey HSD tests. Results correspond to mean ± 1se.

Frequency of pollinator visits and herbivory

There were significant fragmentation and edge effects on the frequency of pollinator visits, but no interaction between both factors (table 1). Overall, plants of forest fragments were visited less often than plants growing in the continuous forest. In both the continuous forest and the forest fragments, pollinator visitation rates were lower at the edge than in the core of the forest (fig. 2A). Furthermore, floral display size had no effect on frequency of pollinator visits (table 1a).

Similarly, there were significant fragmentation and edge effects, as well as a complex interactive effect, on foliar herbivory which, however, was unrelated to foliar display size (table 1b). In fact, plants at the core and edge of forest frag-

Table 2 – Effects of forest fragmentation (FE) and proximity to edge (EE) on: (a) number of fruits per plant (w_1), (b) number of seeds per fruit (w_2), and (c) number of seeds per plant ($w_1 \times w_2$) in *Bomarea salsilla* in the fragmented Maulino forest.
Results are from two-way ANCOVAs with number of flowers per plant and foliar herbivory entered as covariates.

Source	*df*	*MS*	*F*	*P*
(a) Number of fruits per plant (w_1)				
Fragmentation effect (FE)	1	57.03	14.11	< 0.001
Edge effect (EE)	1	13.44	3.33	0.070
FE × EE	1	0.46	0.11	0.736
Number of flowers per plant	1	489.91	121.22	< 0.001
Foliar herbivory	1	0.05	0.01	0.914
Error	194	4.04		
(b) Number of seeds per fruit (w_2)				
Fragmentation effect (FE)	1	543.50	19.08	< 0.001
Edge effect (EE)	1	281.01	9.86	0.002
FE × EE	1	14.38	0.50	0.478
Number of flowers per plant	1	1662.95	58.38	< 0.001
Foliar herbivory	1	0.11	< 0.01	0.950
Error	194	28.5		
(c) Number of seeds per plant ($w_1 \times w_2$)				
Fragmentation effect (FE)	1	18362.80	24.39	< 0.001
Edge effect (EE)	1	7034.60	9.35	0.002
FE × EE	1	4978.20	6.61	0.011
Number of flowers per plant	1	179049.70	237.86	< 0.001
Foliar herbivory	1	1410.10	1.87	0.173
Error	194	752.80		

ments and those from the edge of continuous forest were significantly less preyed upon by herbivores than those from the core of continuous forest (fig. 2B). Foliar display size had no effect on herbivory (table 1b).

Reproductive success

There were both significant fragmentation and edge effects on the number of seeds per fruit and seeds per plant, albeit only a fragmentation effect on the number of fruits per plant (table 2). Plants at the core and edge of forest fragments and at the edge of continuous forest produced significantly less fruits per plant, seeds per fruit, and seeds per plant than those from the core of continuous forest (fig. 3). Furthermore, the number of flowers per plant had a significant effect on the reproductive success of *B. salsilla* (table 2). Herbivores, however, did not play a modulating role (table 2).

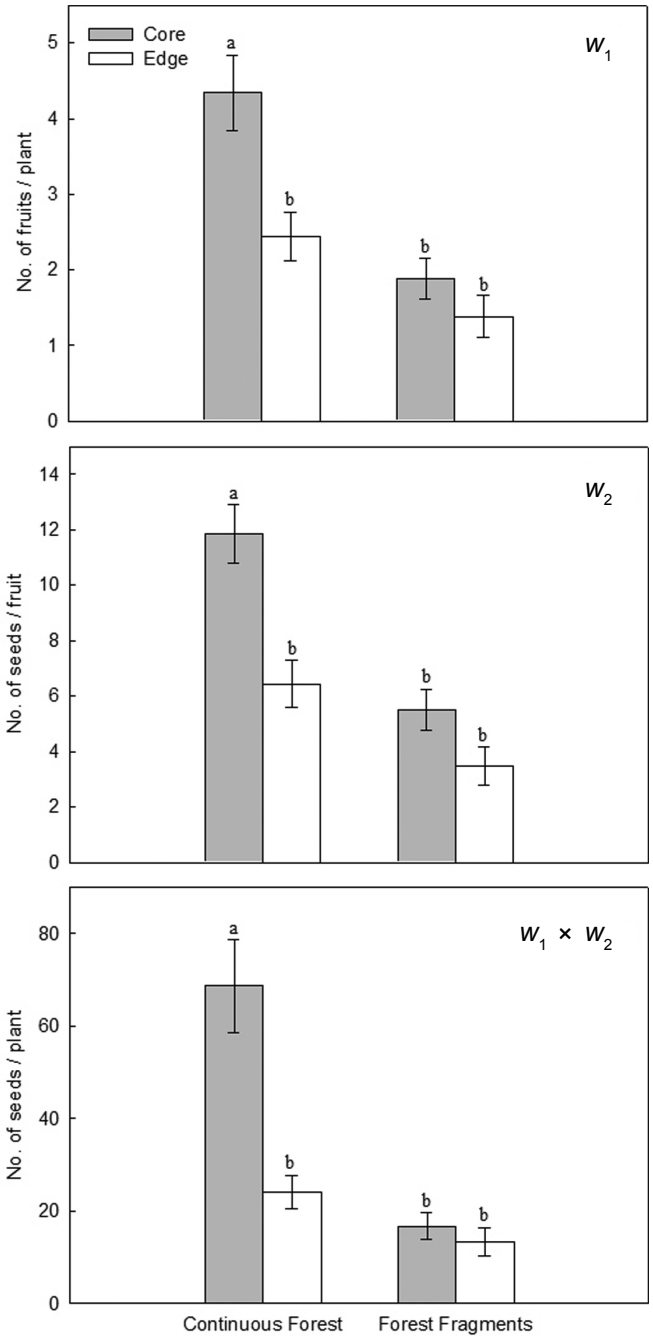

Figure 3 – Effects of forest fragmentation (continuous vs. fragment) and location (edge vs. core) on number of fruits per plant (w_1), number of seeds per fruit (w_2), and number of seeds per plant ($w_1 \times w_2$), in *Bomarea salsilla* in the fragmented Maulino forest. Dissimilar letters depict significant differences ($P < 0.05$) following Tukey HSD tests. Results correspond to mean ± 1se.

DISCUSSION

In comparison with the core of continuous forest, *Bomarea salsilla* plants occurring in forest fragments and edge habitats exhibited a smaller floral display size, were less visited and preyed upon by pollinators and herbivores respectively, and had a significantly lower fruit and seed set. Consequently, forest fragmentation and the increase in edge habitats sig-

nificantly affected plant reproductive success by modifying morphological features as well as plant-mutualistic and plant-antagonistic relationships.

Forest fragmentation, including its edge effect, significantly modified morphological aspects related to floral and foliar display size. Plants occurring in forest fragments exhibited a smaller floral display in terms of number of flowers per plant and perigone length. Decreased values of these traits related to floral display may significantly reduce the attractiveness of plants to pollinators and, thus, decrease the frequency of pollinator visits, thereby decreasing fruit and seed set (Pellmyr 2002). A similar pattern, however, was not observed with regard to foliar display size. In fact, plants at the edge of forest fragments had a larger foliar display, yet herbivory was lower compared to the core of continuous forest. Biotic and abiotic factors may explain such a pattern; however, the ultimate cause remains still to be clarified. Taken together, both floral and foliar display patterns suggest differences in the investment in vegetative and reproductive structures and, therefore, in energy budgets, as a result of forest fragmentation and the increase in edge habitats (Hendrix 1988). Changes in energy budgets and morphological trait patterns related to forest fragmentation and the proximity to edge habitats may have more consequences than those concerning reproductive success by affecting, for instance, the microevolutionary trends of plants. Certainly, this fact remains still to be clarified.Together with the lowered frequency of pollinator vists, which was unrelated to reproductive plant density, fruit and seed set were also lower in the core and edge of fragments and at the edge of continuous forest compared to the core of continuous forest as a result of the reduced pollination service, which was further modulated by the total amount of flowers per plant. This fact is of a more general occurrence because in the same fragmented forests, the hummingbird-pollinated vine *Lapageria rosea* exhibits a lowered reproductive success on account of a lowered pollination service triggered by forest fragmentation (Valdivia et al. 2006). Given that in these forests vines comprise 14.5% of all native plants with several hummingbird- and insect-pollinated endemic genera (e.g. *Boquila*, *Hydrangea*, *Lardizabala*, *Luzuriaga*; Aizen et al. 2002), an important number of plants facing reduced fitness due to forest fragmentation, including its edge effect, is indeed to be expected.

Herbivores, however, did not play a modulating role on plant fitness and did not counterbalance the pollinator-mediated decreased reproductive success of *B. salsilla*. This might be due to the scarcity of foliar attacks, which did not exceed five percent of leaf surface removal. In the fragmented Maulino forest, an increase in insectivorous animals in fragments compared to continuous forest may have triggered an increase in predation upon herbivorous larvae and, therefore, a reduction in herbivory through cascading effects (González-Gómez et al. 2006, Simonetti et al. 2006). Certainly, the weak effects of herbivores in our study system strongly contrast with other plants exhibiting a counterbalance in pollinator- and herbivore-mediated reproductive success in fragmented habitats (e.g. Kery et al. 2001, Colling & Matthies 2004). Nevertheless, because herbivores might play a modulating role in other phenological stages (e.g. seedling stage, Ledergerber et al. 2002) or even in the same phenological stage but in the next reproductive season, an assessment taking into account the overall life cycle would be desirable.

In *B. salsilla*, the net effect of fragmentation through mutualists and antagonists on reproductive success was negative despite the reduction in herbivory. Assessments taking into account both types of relationships on plant reproductive success are certainly required to fully understand the effects of human-mediated habitat disturbances on such types of interactions and their consequences on plant fitness in the highly diverse temperate rainforest from southern South America.

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