UNIVERSIDAD DE CHILE

FACULTAD DE CIENCIAS

Éxito reproductivo de *Aristotelia chilensis* mediado por cambios en sus polinizadores y las aves insectívoras en un bosque fragmentado

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Santiago, junio 2011

Reproductive success of *Aristotelia chilensis* mediated by changes in its pollinators and pollinator-feeding predators in a fragmented forest

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Por

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Dedicado a:

“Natalia Lahsen, a mis padres Raúl Allendes y María Isabel Barros, a mi hermana María Isabel, a la familia Lahsen y a mis amigos”.

“La conservación es un estado de armonía entre el hombre y la tierra”,
A Sand County Almanac, Aldo Leopold 1949.

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RESUMEN

La fragmentación de hábitat modifica la riqueza y abundancia de especies y sus interacciones ecológicas. Cambios en la abundancia de insectívoros puede modificar el éxito reproductivo de las plantas. Cuando los insectívoros depredan sobre los polinizadores provocan una disminución directa en la abundancia y tasa de visitas a las flores y por ende, una disminución en la polinización y el éxito reproductivo de las plantas. Indirectamente los insectívoros también pueden disminuir el éxito reproductivo de las plantas a través de cambios conductuales en sus polinizadores. Evaluamos como la fragmentación del hábitat modifica la cadena trófica dada por las aves insectívoras, los insectos polinizadores y el árbol *Aristotelia chilensis*. Dado que en el bosque maulino la fragmentación afecta positivamente la insectivoría, entonces los polinizadores disminuyen por lo que esperamos una reducción en el éxito reproductivo de *A. chilensis* en los fragmentos, la cual, se incrementa cuando las aves insectívoras están presentes. La fragmentación de bosques incrementa la riqueza, abundancia de las aves insectívoras y la insectivoría. La riqueza y la abundancia de polinizadores no se ven afectadas por la fragmentación de hábitat. Los polinizadores realizan igual número de visitas en los fragmentos que en el bosque continuo, estas visitas son más largas cuando las aves insectívoras están excluidas. Consecuentemente las semillas provenientes de árboles excluidos germinan mas, el éxito reproductivo neto se incrementa en los fragmentos en árboles excluidos de las aves insectívoras. Los resultados expuestos aquí pueden ser representativos de un fenómeno de numerosas interacciones entre plantas y animales en los bosques fragmentados de Sur América y ciertamente fomenta la realización de posteriores estudios sobre este tema.

Palabras claves: Fragmentación del hábitat, insectivoría, polinización, germinación de semillas, bosque templado.

ABSTRACT

Habitat fragmentation modifies richness and abundance of species and their ecological interactions. Changes in abundance of insectivores can modify the reproductive success in plants. When insectivores prey on pollinators, they directly decrease their abundance and rate of flower visitations, hence declining pollination and reproductive success of plants. Indirectly, insectivores can also decrease the reproductive success of plants through changes in pollinator behaviour. Here we evaluate how habitat fragmentation modifies interactions between pollinator-feeding birds, pollinating insects, and the tree *Aristotelia chilensis* in the Maulino forest in Central Chile. Given that in the Maulino forest habitat fragmentation negatively affects pollination and positively affects insectivory, we expect a reduction in reproductive success of *A. chilensis* in fragments, which becomes stronger when pollinator-feeding birds are present. Forest fragmentation increases richness, abundance of pollinator-feeding birds and insectivory. Habitat fragmentation does not affect pollinator richness and abundance; pollinators perform similar number of visits in fragments and in the continuous forest but spend more time per visit when insectivores are absent, a fact that results in a better pollination service evaluated as higher germination of *A. chilensis* seeds. The net reproductive success in forest fragment increase in trees excluded of insectivory birds. The results herein reported may be a representative phenomenon of numerous other interactions between plants and animals in the fragmented temperate forest of South America.

Keywords: Habitat fragmentation, insectivory, pollination, seed germination, temperate forest.

INTRODUCTION

Habitat fragmentation modifies richness and abundance of species and ecological interactions in which they participate (Crooks and Soule 1999; Simonetti et al. 2006). In remaining habitats, insect-pollinator richness and abundance is usually reduced (Winfree et al. 2009), which negatively impacts pollination services and reproductive success of plants (Aizen and Vasquez 2006; Aguilar et al. 2006). Similarly, insectivorous species are negatively affected by habitat fragmentation (Sekercioglu et al. 2002) which might cause a reduction in the magnitude of insectivory .In fact, variations on species richness and abundance can trigger cascade effects by directly changing the rate of consumption upon their preys (Terborgh et al. 2001; Money et al. 2010), or by indirectly modifying their behavior (Durkas 2001; Simonetti et al. 2006). Nevertheless, this fact is still poorly understood in the context of fragmented habitats.

Regarding cascading effects, changes in the abundance of insectivorous species can indirectly modify the reproductive success in plants (Schmitz et al. 2000; Bridgeland et al. 2010; Mäntylä et al. 2010). When insectivores feed on pollinators, they directly cause a decrease in their abundance and their rate of flower visitations, therefore decreasing the quantity and quality of pollen received by flowers. This fact, in turn, might translate into a reduced pollination and reproductive success of plants (Dukas 2001; Suttle 2003; Knight et al. 2006). Indirectly, insectivores can also decrease the reproductive success of plants through changes in pollinator behavior (Lecomte et al. 2009), because the presence of insectivores may reduce the number and time of visits to flowers (e.g., Muñoz and Arroyo 2004). Both the direct and indirect effects of insectivores on pollinators might have negative effects on the quality of seeds, as well as on distal factors such as seed germination, among others (Dukas, 2001; Suttle 2003; Muñoz and Arroyo 2004).

Contrary to the general trend, in the Maulino forest in central Chile there is higher abundance of insectivorous birds in forest fragments rather than (González-Gómez et al. 2006), leading to higher levels of insectivory in forest fragments. (Lluch et al. 2009). On the other hand, like elsewbere, (Aguilar et al. 2006; Aizen and Vasquez 2006) habitat fragmentation of the Maulino forest negatively affects pollination and reproductive success both in terms of seed germination and number of seeds of plants such as *Lapageria rosea* and *Bomarea salsilla*, due to reductions in the abundance of insect pollinators and the rate of flower visits (Valdivia et al. 2006; Valdivia 2009). Forest fragmentation also affects negatively the qualitative reproductive success of *Aristotelia chilensis,* as seed germination is greater in the continuous forest than in forest fragments (Valdivia and Simonetti 2007). Nevertheless, even though in the Maulino forest fragmentation mighty contributes to reinforce the negative effects on pollination through increasing the magnitude of insectivory, no previous work has addressed this issue.

The objective of this work is to experimentally evaluate the effects of habitat fragmentation on the reproductive success of *A. chilensis*, a common tree of the Maulino forest, due to changes in pollinator diversity and behaviour, and due to changes on pollinator-feeding birds. Given that forest fragmentation reduces pollination and increases insectivory, we expect a reduction in the seed number and seed germination of *A. chilensis* in fragments, which is higher when pollinator-feeding birds are present.

Therefore, if birds are experimentally excluded from trees, reproductive success ought to be higher than in trees where birds have access, particularly in fragments (Fig. 1).

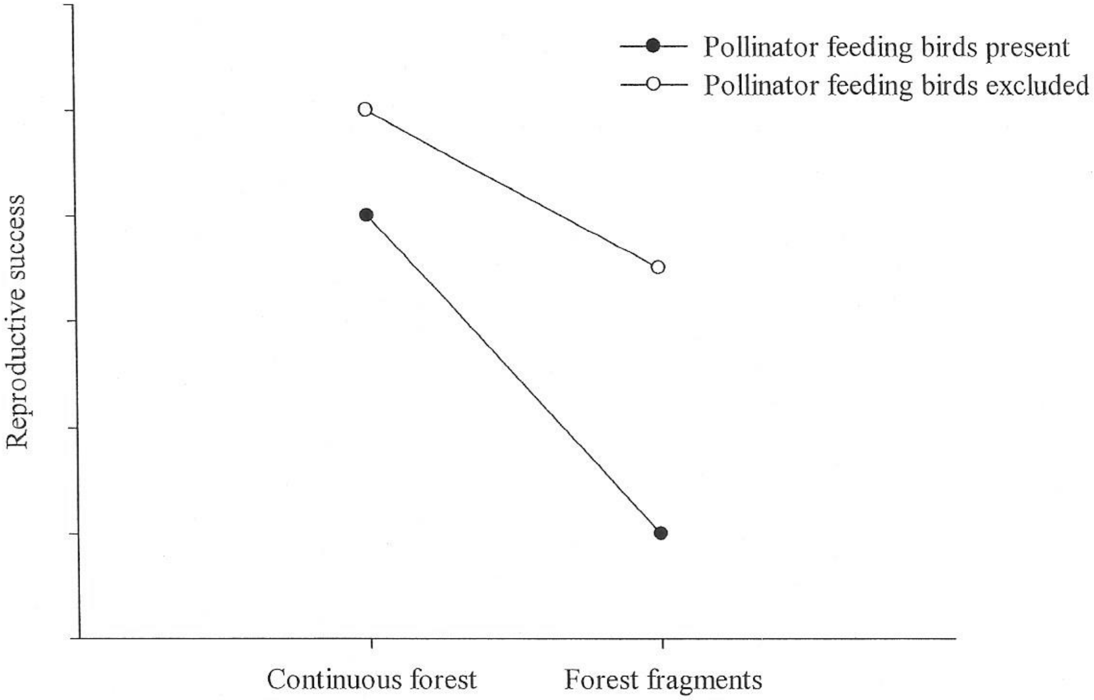

Figure 1 Hypothetical reproductive success of *Aristotelia chilensis* due to habitat fragmentation in presence and absence of pollinator-feeding birds.

METHODS

Natural history

We conducted fieldwork in the Maulino forest, which exhibits a high endemism and richness due to the confluence of the southern and northern biota (San Martín and Donoso 1996). This forest has been severely deforested and fragmented to 33% of its original area at a yearly rate of 4.5% (Echeverría et al. 2006). Therefore, it is currently included into the Chilean hot-spot for the conservation of biodiversity (Myers et al. 2000). Specifically, we carried out the study from September 2007 to January 2008 in Los Queules National Reserve (35°59'S, 72°41'W) and four neighbouring fragments (Bustamante et al. 2006). Los Queules National Reserve is a protected area of 145 ha embedded in a large tract of 600 ha of continuous forest, which will hereafter be considered as the continuous forest. Forest fragments range from 1 to 6 ha, all separated by at least 1 km. Both the continuous forest and fragments are surrounded by commercial plantations of *Pinus radiata.*

Aristotelia chilensis (Elaeocarpaceae) is an evergreen dioecious tree blooming from August to September, whose pollination depends entirely on insects (Mora 1999). Fructification occurs from December to January, the fruit being a purple berry which is dispersed by birds, (Troncoso 2007). Fruits contain 2 to 4 seeds (Verdi 2004). In the Maulino forest, *A. chilensis* is an abundant species inhabiting both forest fragments and continuous forest (Bustamante et al. 2006). Tree density is significantly greater in fragments than in the continuous forest (average ± SE: 43.9 ± 6.18 and 4.2 ± 0.99 trees / 400 m^2, respectively, Lagos 2007).

Experimental design

To assess the effects of forest fragmentation on pollination and the reproductive success of *A. chilensis* due to changes in the abundance of insectivorous birds, we performed a manipulative experiment. We randomly selected 20 adult females of *A. chilensis* in the continuous forest and 20 in forest fragments (total = 40). In each site, we excluded 10 trees from birds and left 10 without exclusion of birds as control trees. Trees were not equally distributed in the four fragments (2 to 8 trees per fragment depending on the availability of trees), but we always maintained the same number of excluded and control trees. This 2 x 2 factorial design allowed us to dissect the relative importance of habitat fragmentation and insectivorous birds on pollination and reproductive success of *A. chilensis.*

Bird exclusions consisted of cages about 3-m long, 4-m wide and 3-m high, assembled with four or more PVC tubes (3.5 cm in diameter) and similar tubes joined at the top, covered with monofilament nylon mesh with holes of 3.8 cm in diameter. This size of holes prevented the entry of birds, but allowed access to insects. This nylon is translucent, reducing light less than 5%, with no significant effect on air temperature (Mazía et al. 2004).

Richness and abundance of pollinator-feeding birds

To evaluate both richness and abundance of insectivorous birds, we set up circular plots of 30-m radius around each control tree (n = 20 at continuous forest, n = 20 at forest fragments). Each plot was visited twice between 08:00 and 12:00 h and twice between 16:00 and 20:00 h on different days. We recorded all insectivorous birds both, visually and acoustically, during 10-min periods. Additionally, we performed the same number of observations in the excluded trees in order to determine if any birds were present inside the exclusions. The total number of registered species in each plot during the four 10-min counts assessed richness; the abundance was assessed as the mean number of individuals recorded on each count by plots (González-Gómez et al. 2006).

Insectivory

In order to estimate the intensity of insectivory on insect pollinators, we made plasticine models of bees that provided a relative measure of number of attacks by birds to the insect pollinator (Skoczylas et al. 2007). We randomly placed five model bees in five blooming branches of *A. chilensis* located in the continuous forest and fragments (n = 25 for each tree) regardless of whether they were exposed or excluded to birds. The models were put together with flowers and after 24 hours we recorded the number of plasticine bees pecked by birds (González-Gómez et al. 2006).

Richness and abundance of pollinators

To estimate pollinator abundance we set up 40 plots, with a 1.5 m radius, centred on each experimental tree. In these plots we recorded pollinator presence in four periods of 10-min. duration between 9:00 and 18:00 h at the flowering-season peak. The richness was determined as the total number of registered species in the 10-min periods, while the abundance was assessed as the number of individuals registered during these periods.

Quantity and quality of pollinator visits to flowers of *A. chilensis*

We evaluated the quantity of pollinator visits, as the frequency of individual visits to flowers of *A. chilensis.* To evaluate the frequency of pollinator visits, in the same 10-min periods above-mentioned we recorded when pollinators touched and manipulated the pistil of flowers. Furthermore, we evaluated the quality of pollinator visits as the time spent during each visit, which was recorded with a hand-held chronometer. The frequency of visits of pollinators and the time spent on each visit to the flowers were estimated as the mean value of the four periods of observation in each tree.

Reproductive success

To estimate the reproductive success of *A. chilensis* we evaluated seed quantity, as the number of seeds per flower, and seed quality, as seed germination capacity. Thus, we randomly chose and tagged two branches in each experimental tree when the buds which gave rise to the flowers were visible in September 2008. In October 2008 the number of flowers that occurred from of the buds was determined and finally in January 2009 we registered the number of fruits and seeds produced by each flower. Thereafter, we determined the mean number of seeds per flower on a per-individual basis by averaging the values obtained in each branch.

To evaluate the quality of seeds, we performed a common-garden experiment of germination. Thus, we randomly selected 15 seeds (released from mature fruits) from each experimental tree, which were placed in 15 Petri plates inside a germination camera. The photoperiod was 12-h light and 12-h dark, while the temperature chosen was 20°C at light and 10°C at dark. When the germination curve reached an asymptotic shape, the experiment was finished. We considered a seed as germinated when the emerging root presented a 2-mm elongation (Valdivia and Simonetti 2007). Finally we evaluated the net reproductive success of *Aristotelia chilensis* by multiplying the quantity of seed per quality of seeds.

Statistical analysis

To evaluate statistical differences between the two habitat types (continuous and fragment forest) and the treatment of exclusion of birds (with and without birds) we performed the following tests:

a) Abundance and richness of insectivorous was tested though t test.

b) Insectivory was tested through Mann-Whitney U test and for frequency of visits of insects to *A. chilensis* flowers we performed a factorial ANOVA with modification Scheirer-Ray-Hare (Sokal & Rohlf 1995).

c) Time spent per insect visit to *A. chilensis* flowers as well as abundance and richness of insect pollinator, was evaluated through a factorial ANOVA test.

d) Quantity of seeds we also used a factorial ANOVA, but for quality of seeds of trees of *A. chilensis* we used a factorial ANOVA with error type III tests using binomial distributions.

e) Finally, the net reproductive success of *A.chilensis* was assessed with a factorial ANOVA with modification Scheirer-Ray-Hare and specific comparison with Mann-Whitney U test.

RESULTS

Richness and abundance of pollinator-feeding birds

We recorded a total of 10 species of insectivorous birds (Table 1). Richness of pollinator-feeding birds was 1.5 times higher in fragments than in the continuous forest (Table 1). Forest fragmentation and exclusion of pollinator-feeding birds had significant effects on richness of birds: the number of species of insectivore birds is higher in fragment and control trees (t test: Fragmentation effect (FE): t= 22.47, $P < 0.001$; Exclusion effect (EE): t = 357.98, $P < 0.001$). The abundance of pollinator-feeding birds was 1.7 times higher in fragments than in the continuous forest and control trees (Table

1; t test: FE: t= 30.45, $P < 0.001$; EE: t = 425.95, $P < 0.001$).

Table 1. Mean (±SE) abundance and richness of pollinator-feeding birds thriving at the fragmented Maulino forest in central Chile in *A. chilensis* trees exposed (control) and excluded (exclusion) to birds. Values depict numbers of individuals / plot / 10-min.Different letters depict significant differences ($P < 0.05$) after performing *t*-Student tests on log-transformed data.

Insectivorous	Continuous forest		Forest fragments	
	Control	Exclusion	Control	Exclusion
Anairetes parulus	0.15 ± 0.05^a	-	0.31 ± 0.10^a	-
Aphrastura spinicauda	1.49 ± 0.07^a	-	1.84 ± 0.13^b	-
Curaeus curaeus	0.02 ± 0.02^a	-	0.30 ± 0.09^b	-
Elaenia albiceps	1.22 ± 0.09^a	-	1.43 ± 0.07^a	-
Sylviothorhynchus desmursii	0.14 ± 0.04^a	-	0.14 ± 0.04^a	-
Tachycineta meyeni	0.18 ± 0.07^a	-	0.37 ± 0.10^a	-
Troglodytes aedon	0.02 ± 0.02^a	-	0.42 ± 0.07^b	-
Turdus falcklandii	0.10 ± 0.03^a	-	0.21 ± 0.05^a	-
Xolmys pyrope	-	-	0.20 ± 0.05	-
Zonotrichia capensis	0.07 ± 0.05^a	-	0.20 ± 0.05^a	-
Total abundance per plot	3.50 ± 0.38^a	-	6.10 ± 0.38^b	-
Total richness per plot	2.38 ± 0.13^a	-	3.77 ± 0.19^b	-

Richness and abundance of pollinators

We recorded a total of six species of pollinator insects (Table 2). There were no significant effects of forest fragmentation and pollinator-feeding birds on richness and abundance of pollinators (ANOVA, FE: F = 3.507, $P = 0.07$; EE: F = 1.855, $P = 0.18$); (ANOVA, FE: F = 3.778, $P = 0.060$; EE: F = 1.811, $P = 0.187$).

Table 2. Mean (± SE) abundance and richness of pollinating insects thriving at the fragmented Maulino forest in central Chile in *A. chilensis* trees exposed (control) and excluded (exclusion) to pollinator-feeding birds. Values depict number of individuals / plot / 10-min. were performing planned comparisons of ANOVA analyses. *Alien species

Pollinators	Continuous forest		Forest fragments	
	Control	Exclusion	Control	Exclusion
Bombus dahlbomii	0.03 ± 0.05	0.05 ± 0.07	0.03 ± 0.05	0.08 ± 0.07
**Bombus terrestris*	-	-	0.05 ± 0.05	0.05 ± 0.05
Colletes cianescens	0.03 ± 0.05	0.05 ± 0.05	0.08 ± 0.06	0.13 ± 0.11
Diphaglossa gayi	-	0.43 ± 0.12	0.18 ± 0.08	0.32 ± 0.20
Manuelia postica	0.40 ± 0.13	0.62 ± 0.16	1.15 ± 0.23	0.85 ± 0.08
Unidentified Syrphidae	0.03 ± 0.05	0.03 ± 0.05	-	0.05 ± 0.05
Total abundance per plot	0.75 ± 0.32	1.17 ± 0.39	1.33 ± 0.40	1.58 ± 0.40
Total richness per plot	0.58 ± 0.19	0.83 ± 0.27	0.90 ± 0.25	1.05 ± 0.24

Insectivory

The insectivory is higher in forest fragments than in continuous forest (Mann-Whitney U test FE: $Z = 3.023$, $P = 0.002$) (Fig. 2). There was no model larvae picked in exclusion trees, therefore, the exclusion of pollinator-feeding birds worked effectively (Mann-Whitney U test EE: Z: 3.44 P< 0.001).

Quantity and quality of pollinator visits

Forest fragmentation and pollinator-feeding birds did not had a significant effect on the quantity of pollinator visits, assessed as the frequency of pollinator visits (ANOVA, FE: H = 2.930, *P* = 0.087; EE: H = 0.063, *P* = 0.793) (Fig. 3A).

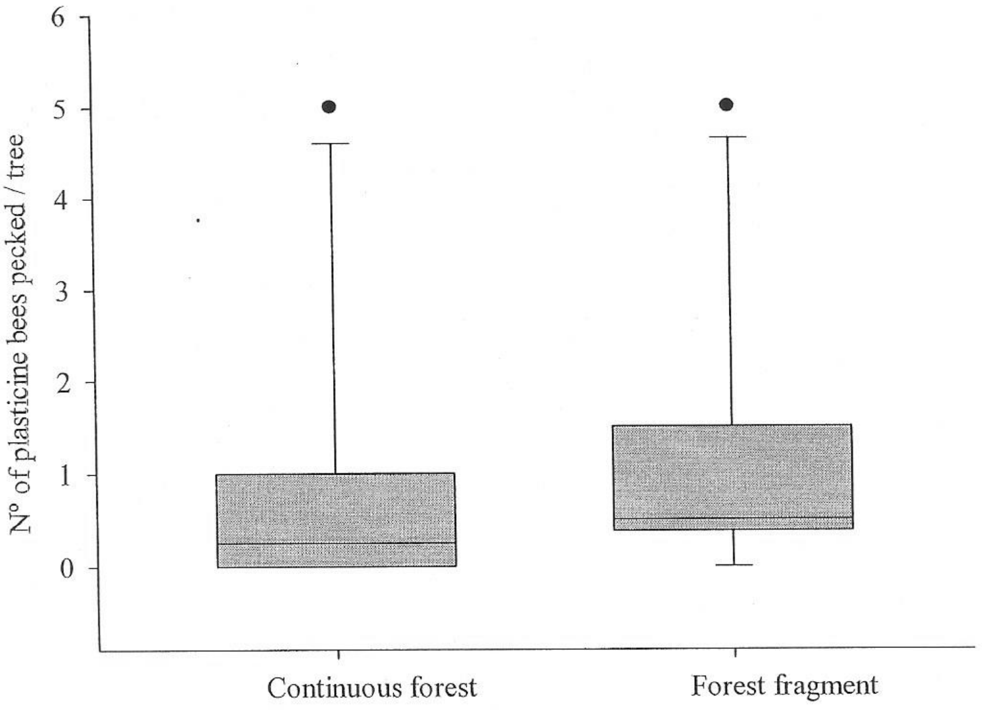

Figure 2. Insectivory on plasticine bees on trees of *Aristotelia chilensis* excluded and exposed to birds thriving at the continuous forest and forest fragments in central Chile.

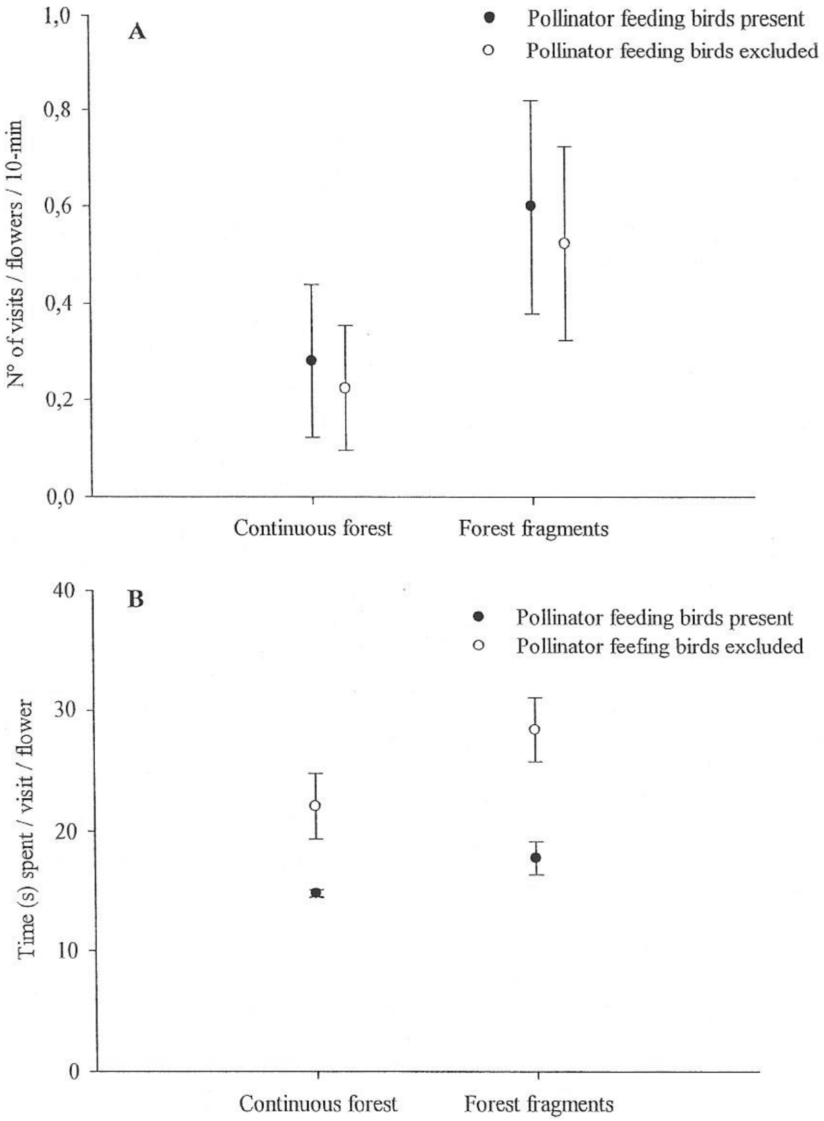

Figure 3. Quantity of pollinator visits (A), assessed as frequency of visits, and quality of pollinator visits (B), assessed as time spent per visit, to flowers of *Aristotelia chilensis* excluded and exposed to pollinator-feeding birds in continuous and fragmented forests in central Chile.

By contrast, pollinator-feeding birds had a significant effect on the time spent per each visit on each flower, insects expending more time in flowers of bird-excluded trees (ANOVA, FE: F = 3.334, *P* = 0.082; EE: F = 12,460, *P* = 0.002) (Fig. 3B).

Reproductive success

Fruit contained 1 to 7 viable seeds. There were no significant effects of forest fragmentation and pollinator-feeding bird exclusions on seed quantity, assessed as the number of seeds per experimental flower per tree (ANOVA, FE: F = 2.079, *P* = 0.160; EE: F = 1.622, *P* = 0.212) (Fig. 4A). However, seed quality, assessed as mean germination, was significantly affected by pollinator-feeding birds and habitat fragmentation (ANOVA, FE: W = 430.54, P < 0.001; IE: W = 464.29, P < 0.001 Fig. 4B). When the net reproductive success was compared, significant effects of forest fragmentation were found (ANOVA, FE: H = 0.04 P = 0.04; Fig.5). Specifically when only fragments were compared, we found significant effects of pollinator-feeding birds exclusions (Mann-Whitney U test: Z = -2.023, *P* = 0.04)

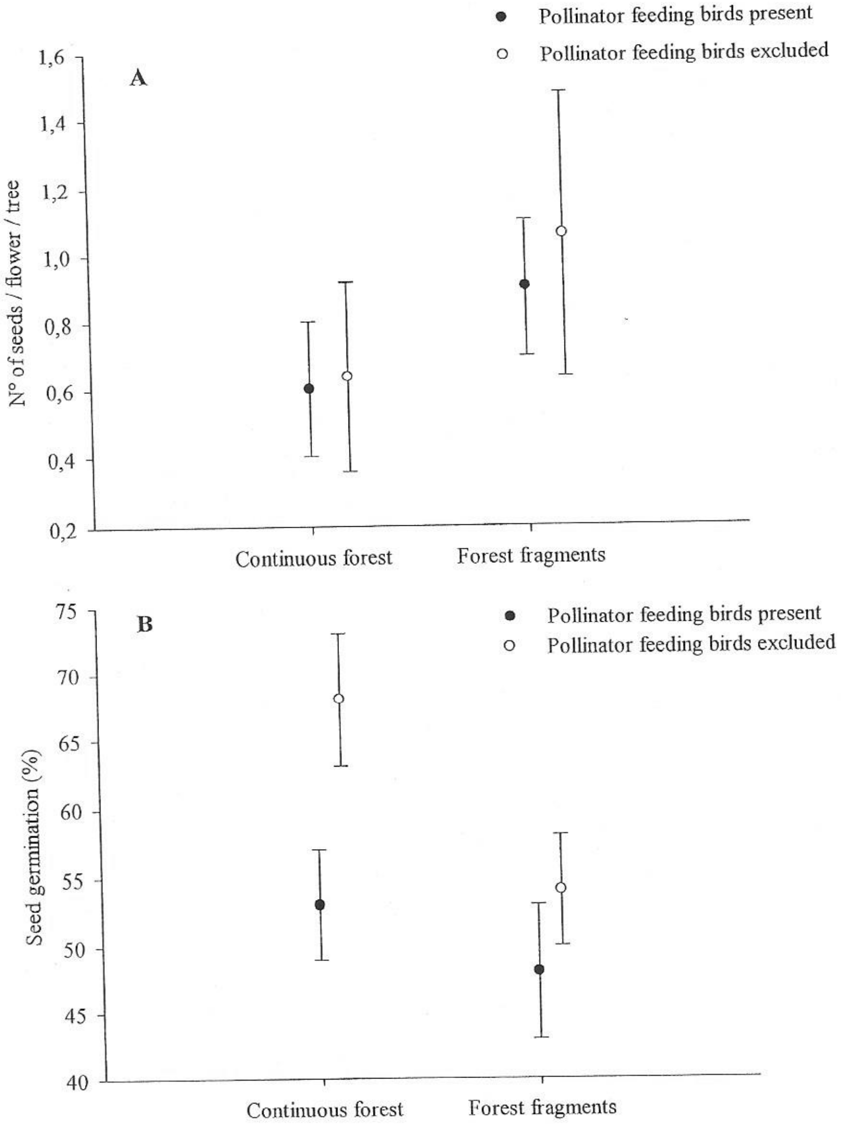

Figure 4. Quantity of seeds (A) and quality of seeds (B) of trees of *Aristotelia chilensis* excluded and exposed to pollinator-feeding birds in continuous and fragmented forests in central Chile.

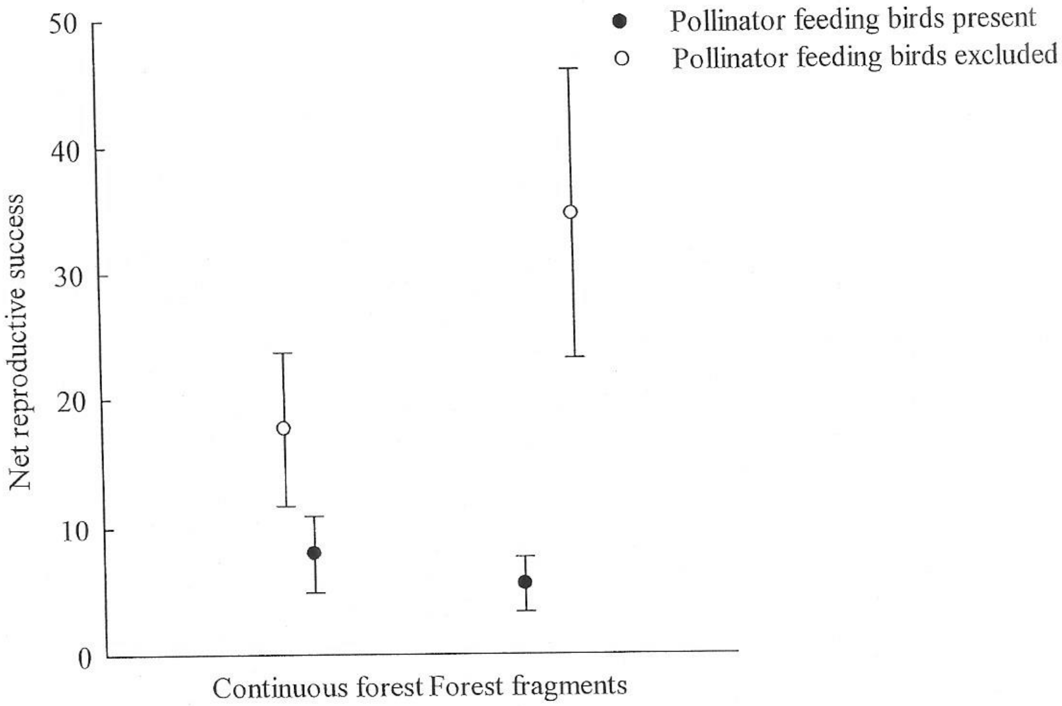

Figure 5. Net reproductive success of *Aristotelia chilensis* assessed as quantity of seeds per quality of seeds.

DISCUSSION

Forest fragmentation significantly affected the trophic cascade given by pollinator-feeding birds, pollinating insects, and plants, by modifying the behaviour of pollinators with consequence on the reproductive success of *A. chilensis*.

In the Coastal Maulino forest, both richness and abundance of insectivorous birds are higher in forest fragments than in the continuous forest, as has been detected over the last decade, which leads to infer that this phenomenon is permanent (Vergara and Simonetti 2004; Estades 2006; González-Gómez et al. 2006;). Such an increase can be accounted for by the higher structural complexity of forest fragments, which hold a dense understory, surrounded by coniferous forests which might be a source of foraging resources (Estades and Temple 1999). A higher insectivory in fragments agrees also with previous studies (González-Gómez et al. 2006; Lluch et al. 2009). Following this general tendency, our results support the contention of the constancy of the positive effects of forest fragmentation on insectivorous birds. In spite of this fact, pollinator richness and abundance were similar in forest fragments and continuous forest, indicating a complex numerical response of animals to forest fragmentation. In fact, our result is different with those reported by Valdivia et al. (2006), Valdivia (2009), and Valdovinos et al. (2009), who both recorded negative and positive effects, respectively, of forest fragmentation on pollinator richness in the same forest. Such a complexity may be observed because pollinating insects probably are able to move through the pine matrix, which might be taxon-dependent.

The absence of pollinator-feeding birds relaxes the evasive behaviour of pollinators, therefore increasing the time spent on each visit to flowers. Because of the strong insectivory in forest fragments, insect behaviour was significantly modified. In forest fragments, where pollinator-feeding birds thrive more than in the continuous forest, pollinators performed a similar number of visits than in the continuous forest. We don't see between habitats an improvement of food intake by pollinators. This is probably because a similar total amount of floral resources is offered by forest fragments and continuous forest.

The significant indirect effects on pollinator behaviour due to habitat fragmentation, results in changes in the reproductive success of *A. chilensis* because the seed germination is higher in the continuous forest than fragments, agreeing with Valdivia and Simonetti (2007). *Aristotelia chilensis* has a self-incompatible reproductive system so we expected a significant effect on seed set, which does not occur because pollinators pass from the fragmented forest to the continuous forest through the pine matrix (Valdovinos et al. 2009) so the probability of pollination of flowers is the same. The seed germination capability increases because the pollinator makes longer visits to the flowers. The above facts highlight the resilience capability of the chain of interactions given by pollinator-feeding birds, pollinating insects, and plants after suffering strong modifications in the habitat in which they occur. Here there is an indirect effect of insectivory bird on *A. chilensis*. The net reproductive success in trees where insectivores were excluded is higher in the forest fragments. This shows the effect of fragmentation in the fragment forest where the effect of pollinator-feeding birds is stronger and depressed the reproductive success of *A. chilensis*. Although the plasticity of *A. chilensis* (Reppeto et al. 2007) which allows having the same photosynthetic rate in fragments as those in the continuous forest. The results herein reported may be a representative phenomenon of numerous other interactions between plants and animals in the fragmented temperate forest of South America, suggesting a more complex scenario in the response of ecological interactions to forest fragmentation.

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