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**TROPHIC CASCADES IN FRAGMENTED FORESTS:
INSECTIVOROUS BIRDS, HERBIVORY AND REPRODUCTIVE
SUCCESS OF *ARISTOTELIA CHILENSIS***

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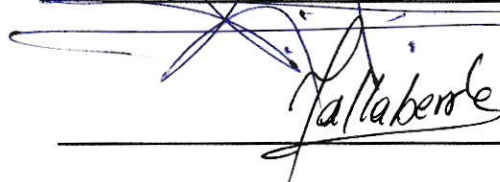
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There is a pleasure in the Woods...

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ABSTRACT

The effects of forest fragmentation on ecological interactions and particularly on food-webs have scarcely been analyzed. Herbivory is usually lower in forest fragments than in continuous forest. Here we hypothesize that the lower level of herbivory in forest fragments is the outcome of altered trophic cascades through changes in the abundance of predators with consequences on plant reproductive success. At the Maulino forest, in central Chile, we experimentally excluded birds from *Aristotelia chilensis* trees at both forest fragments and continuous forest, and analyzed during two consecutive growing seasons the herbivore insect abundance, herbivory, and plant reproductive success. We expected that insect abundance and herbivory should increase, and reproductive success should decrease in *A. chilensis* from which birds have been excluded, particularly in forest fragments where bird abundance and pressure on insects is higher. The abundance of herbivorous insect was lower in the forest fragments than in the continuous forest, only in the first season, and herbivory was lower in forest fragments than in the continuous forest throughout the study. Moreover, during the second growing season herbivory was higher in the excluded trees than in the control trees and, as we expected, a higher difference occurred in the fragments than in the continuous forest, but this was not statistically significant. Exclusion of birds did not affect the reproductive success of *A. chilensis*. Our results, after two years of study, demonstrate that birds determine the levels of herbivory upon *A. chilensis* in the Maulino forest, but do not support our hypothesis of altered trophic cascades in fragmented forest, since the

strength of the effect of excluding birds did not vary with fragmentation. Nevertheless, the stronger effects observed during the second season in the small fragments suggest that cascading effects may be detected over a longer time span.

Keywords: Top down control, temperate forest, fragmentation, bird exclusion, tri trophic interactions, indirect effects, herbivorous insect



RESUMEN

Los efectos de la fragmentación del hábitat sobre las interacciones ecológicas y particularmente sobre las redes tróficas han sido escasamente estudiados. Entre las interacciones ecológicas, la herbivoría es generalmente menor en los fragmentos de bosque que en el bosque continuo. Los niveles bajos de herbivoría en los fragmentos de bosque podrían ser el resultado de cascadas tróficas alteradas, debido a cambios en la abundancia de los depredadores, y ello podría tener consecuencias sobre el éxito reproductivo de las plantas. En el bosque Maulino, en Chile central, excluimos experimentalmente a las aves de los árboles de *Aristotelia chilensis*, tanto en los fragmentos de bosque como en el bosque continuo, y se analizaron durante dos temporadas consecutivas la abundancia de insectos herbívoros, herbivoría, y el número de flores y frutos producidos. Esperábamos un aumento en la abundancia de insectos y la herbivoría, una disminución en éxito reproductivo en *A. chilensis* cuando las aves fueran excluidas, en particular en los fragmentos de bosque donde la abundancia de aves y la presión sobre los insectos es mayor. La abundancia de los insectos herbívoros fue menor en los fragmentos de bosque que en el bosque continuo, sólo en la primera temporada y la herbivoría fue menor en los fragmentos de bosques que en el bosque continuo durante todo el estudio. Además, durante la segunda temporada la herbivoría fue mayor en los árboles excluidos que en los árboles controles, y como esperábamos una mayor diferencia a favor de las exclusiones ocurrió en los fragmentos que en el bosque continuo, aunque esto no fue estadísticamente significativo. La exclusión de aves no se

tradujo en cambios en el éxito reproductivo de *A. chilensis*. Nuestros resultados de dos años de estudio demuestran que las aves determinan los niveles de herbivoría sobre *A. chilensis* en el bosque Maulino, pero no soportan nuestra hipótesis de cascadas tróficas alteradas en el bosque fragmentado ya que la intensidad de los efectos de excluir las aves no varió con la fragmentación. Sin embargo, los efectos más fuertes observados durante la segunda temporada en los fragmentos pequeños sugieren que los efectos en cascada podrían detectarse en un plazo mayor.

Palabras claves: control descendente, bosque templado, fragmentación, exclusión de aves, interacción tri-trófica, efectos indirectos, insectos herbívoros.

INTRODUCTION

Deforestation and forest fragmentation are a worldwide menace to compositional, structural and functional biodiversity. The reduction and isolation of forest remnants disrupt ecological interactions and processes, with far reaching consequences upon biodiversity (Chapin et al. 2000). Changes in abiotic conditions as well as in the composition and abundance of species brought about by forest fragmentation can alter the magnitude of interactions, including plant-animal interactions, impinging upon the vegetation dynamics of forest remnants (Simonetti et al. 2006). Herbivory usually decreases in forest fragments (e.g., Benítez-Malvido et al. 1999; Arnold and Asquith 2002; Simonetti et al. 2007; Vásquez et al. 2007). Depressed herbivory can result from a template of bottom-up and top-down forces. Increases in leaf toughness as a response to a sunnier and dryer environment of the remnants as well as a reduction in the abundance of herbivores -either directly affected by the habitat reduction, or indirectly by changes in their relationships with their predators- could impinge upon herbivory either acting singly or in combination (Hunter and Price 1992). Although species interactions have been commonly addressed in fragmented environments, the potential impact of forest fragmentation upon trophic cascades has been scarcely analyzed (Fahrig 2003).

Trophic cascades most commonly unraveled in terrestrial systems are “species-level cascades” (Schmitz et al. 2000). That is, within a subset of the community, variations in the abundance of predators affects reproductive success of one or few of

the plant species (*sensu* Polis 1999), but when removed, carnivores had significant effects upon plant damage more often than on plant reproduction. Therefore, while herbivory might be altered by carnivores, this effect might not translate into further changes in plant abundance (Schmitz et al. 2000). Despite potential far-reaching consequences upon vegetation dynamics, if “species-level cascades” occur in fragmented forests is yet to be assessed (Terborgh et al. 2001). In this framework, we experimentally unravel if changes in herbivory in forest fragments emerge as a consequence of variations in carnivore abundance, and analyzed the consequences upon plant reproductive performance as well.

Chilean temperate forests, like others worldwide, have been extensively deforested and fragmented (Lara et al. 1996; Riitters et al. 2000). In central Chile, the Maulino forest is one of the most severely threatened forest types in Chile. This forest is unique as it contains a high number of endemic and endangered animal and plant species (San Martín and Donoso 1996). Currently, this forest remains as an archipelago of numerous forest fragments of small size and a few large ones, embedded in a matrix dominated by *Pinus radiata* plantations (Grez et al. 1998; Echeverría et al. 2006).

At this forest, insectivorous birds are 3.8 times more frequent in forest remnants than in the continuous forests (Vergara and Simonetti 2004). An increase in insectivorous birds might trigger cascading effects leading to reduced insect abundance, lower level of plant damage and, eventually, higher reproductive success (Simonetti et al. 2006). In fact, herbivory is reduced in Maulino forest fragments. Seedlings of several tree species, including *Aristotelia chilensis* (Elaeocarpaceae), *Cryptocarya alba*

and *Persea lingue* (Lauraceae), sustain 33% less foliar surface lost to herbivores in forest fragments compared to seedlings in the continuous forest (Simonetti et al. 2007). Herbivory upon the first leaf cohort in adult *A. chilensis* is also higher in the continuous forest (Vásquez et al. 2007). Coincidentally, at the beginning of the season (September), the abundance of *Sericoides obesa* (Scarabaeidae), probably one of the most important herbivorous on *A. chilensis*, is significantly higher in the continuous forest than in the forest fragments (De la Vega and Grez 2008).

The lower abundance of insects in forest remnants could be a consequence of the increased abundance of insectivorous birds that determine high predation rates on insects. In fact, insectivory is higher in forest fragments than in continuous forests, independently whether insect larvae are located upon seedling or adult *A. chilensis* trees as foraging grounds (González-Gómez et al. 2006). The higher abundance of birds, the higher probability of predation on insects and the reduced herbivory levels in forest fragments offer strong support to our claim that forest fragmentation alters trophic cascades in the Maulino forest. This has been observed to occur in eastern Pennsylvania (USA), where insectivorous birds and their attack upon simulated larvae are higher at the edges of forests, which is related to a lower level of leaf damage in *Lindero benzoin* Skoczylas et al. (2007). To our knowledge this study and the one from Terborgh et al. (2001) are the only evidences of altered top-down forces in fragmented systems.

Bottom-up factors can be rejected as an explanation of the low herbivory in the Maulino forest fragments. Herbivorous beetles and lepidoptera larvae do not discriminate leaves by their origin when feeding upon them (Silva and Simonetti 2009),

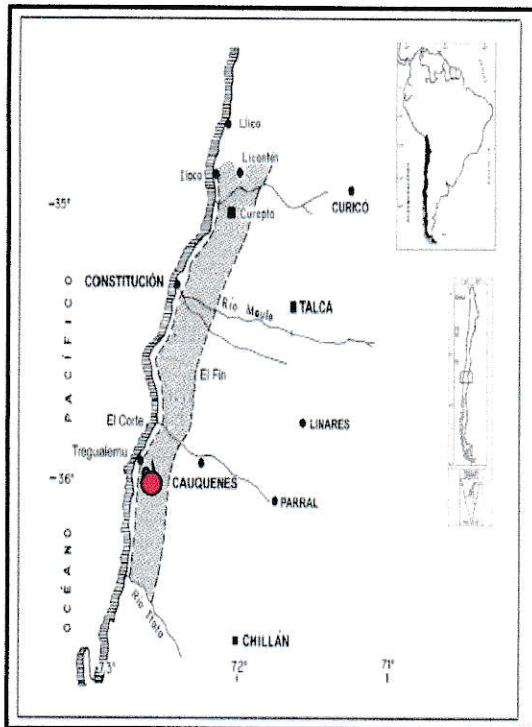
suggesting that if any leaf attribute (be it morphological or chemical) changes with fragmentation (Repetto et al. 2007), they are not relevant to herbivorous insects.

In this work we experimentally evaluated if changes in the abundance of insectivorous birds in the fragmented Maulino forest modify the herbivory upon *A. chilensis* due to changes in the abundances of herbivorous insects. That is, if birds are excluded from *A. chilensis* trees, insects ought to increase leading to higher levels of herbivory, particularly in forest fragments. At the continuous forest, where the abundance of birds is low, and insects are more abundant, experimental removal of birds should convey a minor effect in foliar damage compared to forest fragments.

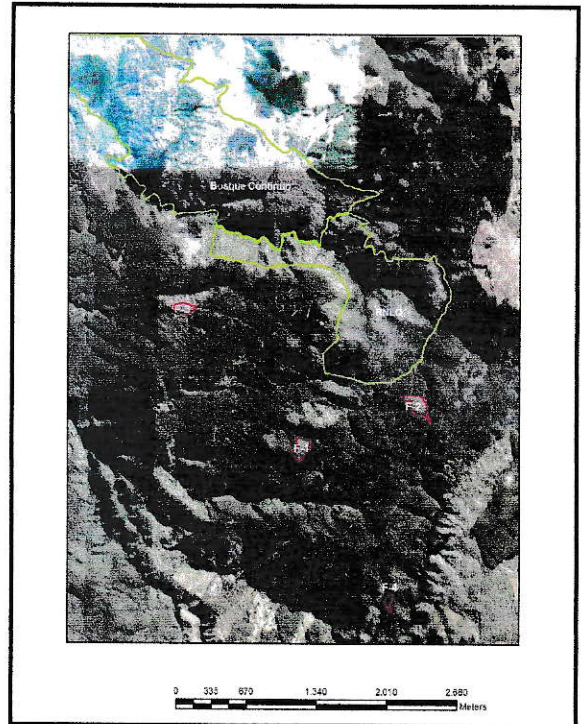
MATERIALS AND METHODS

Study site

The study was conducted during the 2006-2007 and 2007-2008 growing seasons (Austral spring and summer), at Los Queules National Reserve (LQNR (35°59'19''S, 72°41'15''W) and four neighbouring fragments of coastal Maulino forest embedded in a matrix composed by 20 year-old *Pinus radiata* plantations (Fig. 1). This landscape is dominated by pine plantations, covering 54% of the study area, whereas forest fragments and the continuous forest only spans 26% and 20%, respectively (Acosta-Jamett and Simonetti 2004). The Reserve (145 ha) is part of a large fragment of 600 ha, one of the largest extant tracts of continuous Maulino forest today, and therefore considered in this study as the “continuous forest”. The forest fragments ranged 1 to 3 ha, and were separated from each other and from the reserve by at least 2 km. Both continuous forest and forest fragments have similar species composition (Bustamante et al. 2005), dominated by *Nothofagus glauca* and *Nothofagus obliqua* (Nothofagaceae), which coexist with some endangered endemic species like *Gomortega keule* (Gomortegaceae), *Nothofagus alessandrii* and *Pitavia punctata* (Rutaceae) (Bustamante et al. 2005).



a)



b)

Figure 1. a) Geographical distribution of the coastal Maulino Forest (grey); the red circle indicates the location of Reserva Nacional Los Queules (figure from Bustamante et al. 2005); b) Study site showing the continuous forest (greenlines) and adjacent fragments (red lines) used in the experiments (figure from De la Vega 2007).

Study species

Aristotelia chilensis (Elaeocarpaceae) is an evergreen native tree up to 4 m tall, distributed in central Chile between 31°S and 40°S (Rodríguez et al. 1983). The production of new leaves and shoot growth occurs largely in spring. Their leaves are

preyed upon mainly by *Sericoides* sp. but also by some other coleopterans, lepidopteran and orthopteran insects (De la Vega and Grez 2008). It is a dioecious species; flowering occurs from August to September, and fruiting from October to December. Their flowers and fruits are arranged in inflorescences and infrutescences. *Aristotelia chilensis* is pollinated by insects, and visited by several insectivorous birds, like the White-crested Elaenia (*Elaenia albiceps*, Tyrannidae), the Fire-eyed diucon (*Xolmis pyrope*, Tyrannidae), and the Chucao tapaculo (*Scelorchilus rubecula*, Rhinocryptidae), among others (for a list of the insectivorous birds probably visiting *A. chilensis* see APPENDIX 1), which are usually more abundant in the small forest fragments than in the continuous forest (Vergara and Simonetti 2004, González-Gómez et al. 2006). In the Maulino forest, *A. chilensis* is a common species, being abundant at both continuous forest and forest fragments (Bustamante et al. 2005).

Study design

Forty adult trees were selected, 20 from forest fragments and from the continuous forest. Following Strong et al. (2000), criteria for tree selection was that an enclosure could be erected around the tree without disturbing adjacent vegetation, and that they will be separated by at least 20 m in average. Trees were selected from marked individuals known to have set fruits in the 2005-2006 season. In the forest fragments, trees were distributed in four fragments (Fragment 1 = 4 trees, Fragment 2 = 8 trees, Fragment 3 = 6 trees and Fragment 4 = 2 trees) depending on tree availability, but each fragment

contains both experimental and control trees.

Given *A. chilensis* is dioecious, we focused on female fitness. Selected trees were randomly assigned to one of the treatments: experimental (bird enclosure, see below) and control trees (allowing bird access).

Bird access was limited by caging trees. After Marquis and Whelan (1994), exclusion cages consisted on four side poles made of PVC plastic pipes (3.5 cm diameter) and similar plastic pipes connecting at the top, covered by one layer monofilament nylon gill netting, with 3.8 cm diameter holes (Fig. 2). This hole size prevents the entrance of birds but allow access to insects. Therefore, exclosures should not preclude herbivory, pollination and reproduction. The mesh nylon was translucent, reducing light < 5% and had no effect on air temperature (Mazía et al. 2004). Exclosures were set at the end of the 2005-2006 growing season (in March 2006), and effectively prevented bird access to trees. On average, the number of bird visits was higher in the control trees than in trees excluded from birds (0.6 ± 0.18 visit/tree/15 min in control trees vs. zero in excluded trees).

Response variables

In both the experimental and control trees we recorded: a) herbivore insect abundance, b) leaf herbivory, and c) plant reproductive success. These variables were measured monthly from September 2006 to March 2007 and September 2007 to March 2008.



Figure 2. The bird exclosure in the continuous forest.

Herbivore insect abundance

Herbivorous insects larger than 0.5 mm, belonging to Coleoptera, Lepidoptera and Orthoptera, the principal herbivorous insects associated with *A. chilensis* at the Maulino forest were sampled (De la Vega and Grez 2008). Sampling was performed during the night, because the principal herbivorous insects preying upon *A. chilensis* leaves (like *Sercoides* sp.) are nocturnal (De la Vega and Grez 2008). In each tree, two branches of similar size were randomly selected and carefully bagged; a small dose of an insecticide

(tetrametrina 0.4%, permetrina 0.1%) was sprayed into the bag, turning insects drowsy but not killed. After three minutes, all insects collected in each bag were placed on a white cloth for identification and counting; then, insects were returned to the tree. Additionally, a 6 m² white cloth was placed on the ground under the tree foliage in order to get all the insects that may have been falling down from the tree when bagging the branches.

Herbivory

Leaf predation was estimated *in situ*. After Vásquez et al. (2007), five branches developed during the season were randomly selected from each tree, and all newly emerging leaves were individually marked at a monthly interval. There, leaves all began with zero defoliation. A 1 x 1 cm transparent tag attached with a 0.3 mm fishing line to the petiole was used for marking each leaf, without altering leaf expansion or insect feeding. All leaves were monthly assigned to an herbivory category by visually inspection. Classes of leaf area lost were: 0 = 0% area removed, 1 = 1-5%, 2 = 6-12%, 3 = 13-25%, 4 = 26-50% and, 5 = + 50% (Benitez-Malvido et al. 1999) (Fig. 3). Herbivory level was estimated as: $H = \sum n_i(C_i) / N$, where i is the category of damage, n_i is the number of leaves in the i^{th} category of damage, C_i is the midpoint of each category (i.e., $C_1 = 3.5\%$, $C_2 = 9.0\%$, $C_3 = 18.5\%$, $C_4 = 37.5\%$ and $C_5 = 75.0\%$) and N is the total number of leaves sampled on the tree (Benitez-Malvido et al. 1999).

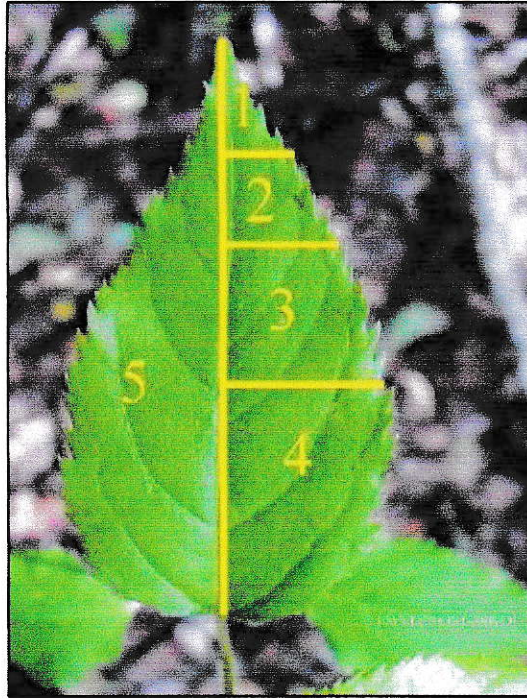


Figure 3. Diagram of herbivory classes: 0 = 0% area removed, 1 = 1-5%, 2 = 6-12%, 3 = 13-25%, 4 = 26-50% and, 5 = + 50%.

Plant reproductive success

In the same five twigs where herbivory was assessed, monthly from September to March, newly developed inflorescences and infructescences were marked with plastic tags. We counted the number of inflorescences/infructescences per branch and also the number of flower or fruits per branch.

Data analysis

Data were analyzed using generalized linear models in Statistica 6.0 (StatSoft 2001). Each tree was considered a replicate. Difference in herbivory between trees within the continuous forest and fragments were spatially independent; that is, herbivory values were unrelated to distance between trees (Mantel test, 10.000 iterations, 2006-2007 $r_s < 0.08$, $P > 0.27$, 2007-2008 $r_s > -0.07$, $P > 0.31$ in all cases).

The effects of habitat (continuous forest vs. small fragments), bird exclosures (trees with or without birds), and their interactions, on the accumulated herbivorous insect abundance per tree, the herbivory index per branch (average the five braches of each tree), the number of accumulated inflorescences/infrutescences and accumulated fruits per branch, were tested with repeated-measures two-way ANOVAs (rm-ANOVA, Type III), with time (months) as the repeated measure. These analyses were performed separately for each season, previous $\log(x+1)$ transformation and verification of the assumptions of the ANOVA. Only the accumulated abundance of herbivorous insects and the number of accumulated inflorescences/infrutescences and accumulated fruits for 2006-2007 season did not fulfill the assumptions of the ANOVA, thus previous to perform the rm-ANOVA we ranked the data (Conover and Iman 1981). Tukey HSD test was used for post-hoc comparisons. By the end of the experiment, the habitat * exclusion effects on the final herbivory per branch and accumulated number of fruits per branch, were tested with a two-way non-parametric analysis of variance (Scheirer-Ray-Hare test; Sokal and Rohlf 1995).

RESULTS

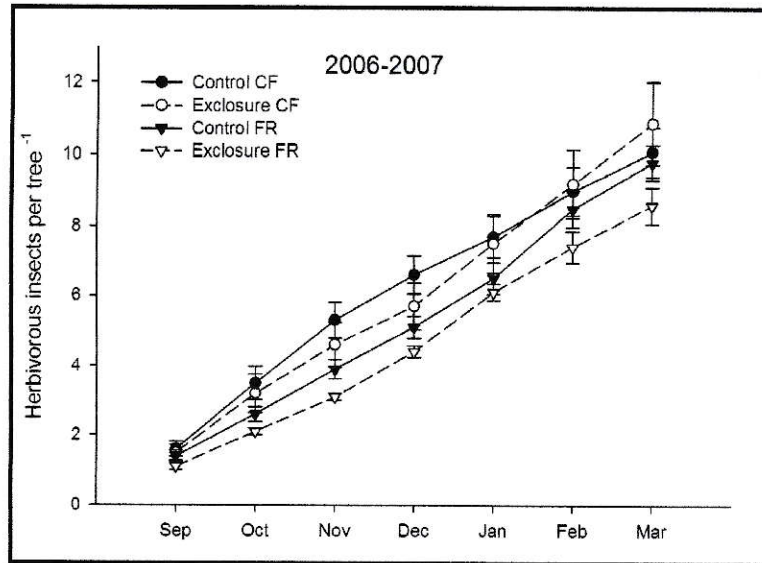
Herbivore insect abundance

During the 2006-2007 season, 430 herbivorous insects were captured. Orthoptera was the most abundant order (228 individuals), followed by Coleoptera (191 individuals). Lepidoptera larvae were scarce, with a total of 11 individuals collected through the whole season. The total abundance of herbivores was significantly higher in the continuous forest than in forest fragments (rm-ANOVA $F_{1,36} = 5.14$, $P = 0.03$; Fig. 4a). Particularly, the scarab beetles *Sercoides* sp. were significantly more abundant in the continuous forest than in forest fragments (rm ANDEVA, habitat*month, $F_{6,216} = 8.69$ $P \ll 0.001$; Tukey HSD $P < 0.01$), but this only occurred at the beginning of the growing season (September to December). Along the 2006-2007 season, the abundance of herbivorous insects did not differ between experimental and control trees (rm-ANOVA $F_{1,36} = 3.32$, $P = 0.08$; Fig. 4a), nor there was a significant habitat * enclosure interaction (rmANOVA $F_{1,36} = 0.004$, $P = 0.95$).

During the second season (2007-2008), 514 herbivores were counted. This time, Coleoptera was the most abundant order (248 individuals), followed by Orthoptera (186 individuals) and Lepidoptera (80 individuals). While the total abundance of insects did not differ between habitats (rm-ANOVA $F_{1,36} = 1.55$, $P = 0.22$) (Fig. 4b), similarly to

the 2006-2007 season, at the beginning of the season (October to December) *Sericoides* *sp.* was significantly more abundant in the continuous forest than in the forest (rmANDEVA, habitat*month, $F_{6,216} = 2.56$ $P = 0.02$; Tukey HSD $P < 0.004$, at each comparison). Again, there were no statistical difference in the herbivore abundance between excluded and control trees (rmANOVA, $F_{1,36} = 0.53$, $P = 0.47$), nor there was a significant habitat * exclosure interaction (rmANOVA $F_{1,36} = 0.85$, $P = 0.36$).

a)



b)

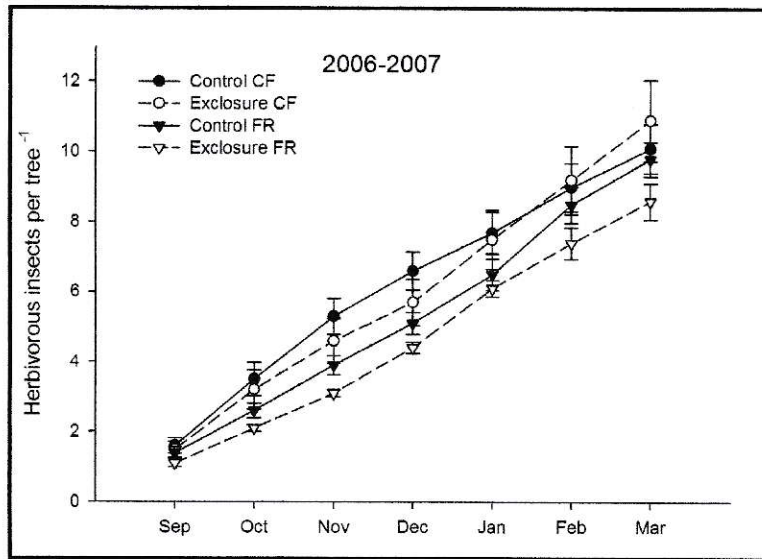


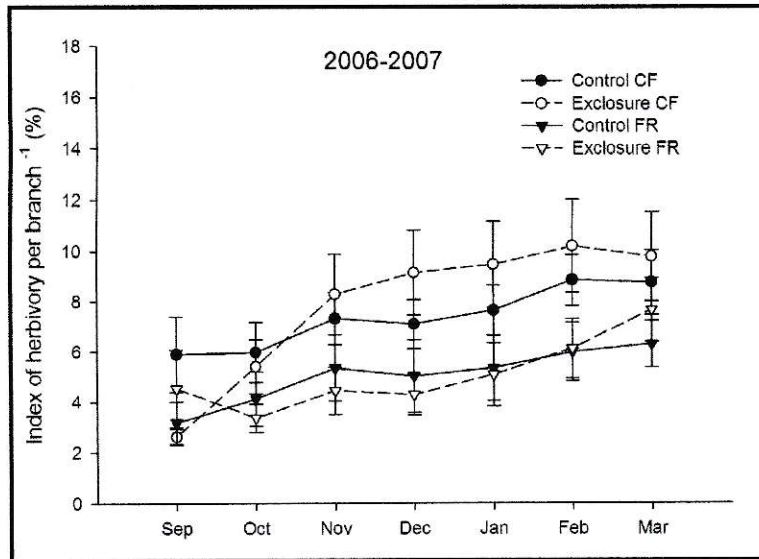
Figure 4. Accumulated herbivorous insect abundance in experimental (with exclosures) and control *A. chilensis* trees (mean/branch \pm 1 se) in the continuous forest and forest fragments. a) First season (September 2006 to March 2007, b) Second season (September 2007 to March 2008).

Herbivory

During the 2006-2007 season, herbivory was higher in the continuous forest than in forest fragments (rmANOVA $F_{1,36} = 6.75$, $P = 0.01$, Fig. 5a), but these differences disappeared at the end of the season (Tukey HSD $P \ll 0.001$). Although by the end of the season, area lost to herbivores was slightly higher in the experimental than in the control trees at both continuous forest (9.8 ± 1.78 versus $8.7\% \pm 1.29$) and forest fragments ($7.6\% \pm 1.26$ versus $6.3\% \pm 0.93$), herbivory did not differ significantly between experimental and control trees (rmANOVA $F_{1,36} = 0.001$, $P = 0.97$). There was no significant habitat * enclosure interaction in this variable (rmANOVA $F_{1,36} = 0.004$, $P = 0.95$).

During the 2007-2008 season, herbivory was also significantly higher in the continuous forest than in at forest fragments (rmANOVA $F_{1,36} = 4.82$, $P = 0.04$) (Fig. 5b). During this season, herbivory was significantly higher in the experimental than control trees (continuous forest, $13.0\% \pm 1.85$ versus $9.0\% \pm 2.61$; forest fragments, $11.0\% \pm 2.10$ versus $5.5\% \pm 1.07$, for experimental and control trees, respectively; (rmANOVA $F_{1,36} = 15.58$, $P < 0.001$; Fig. 5b). The herbivory ratios between experimental and control trees were 2.0 vs 1.4 in fragments and continuous forest, but these ratios were not statistically different ($H = 0.21$, $df = 1$, $P > 0.50$). There was no significant habitat * enclosure interaction in herbivory (rmANOVA $F_{1,36} = 0.61$, $P = 0.44$).

a)



b)

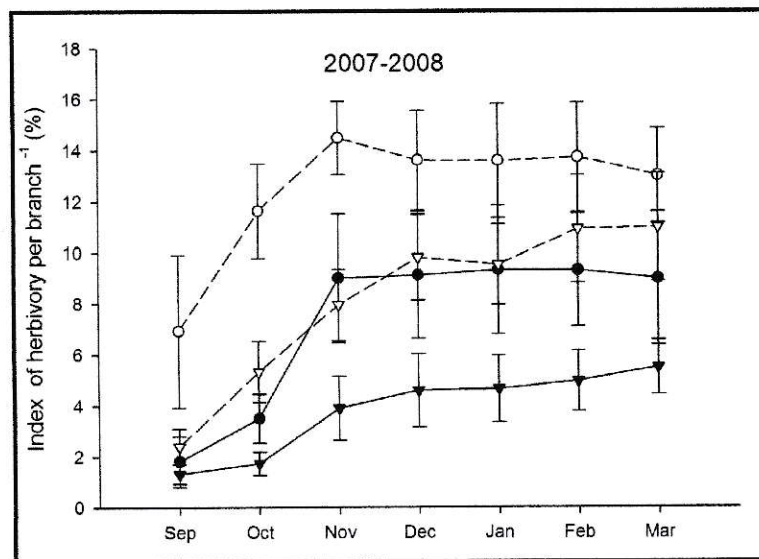


Figure 5. Herbivory index (mean index/branch \pm 1 se) in experimental (with exclosures) and control *A. chilensis* trees in the continuous forest and forest fragments, a) First season (September 2006 to March 2007, b) Second season (September 2007 to March 2008).

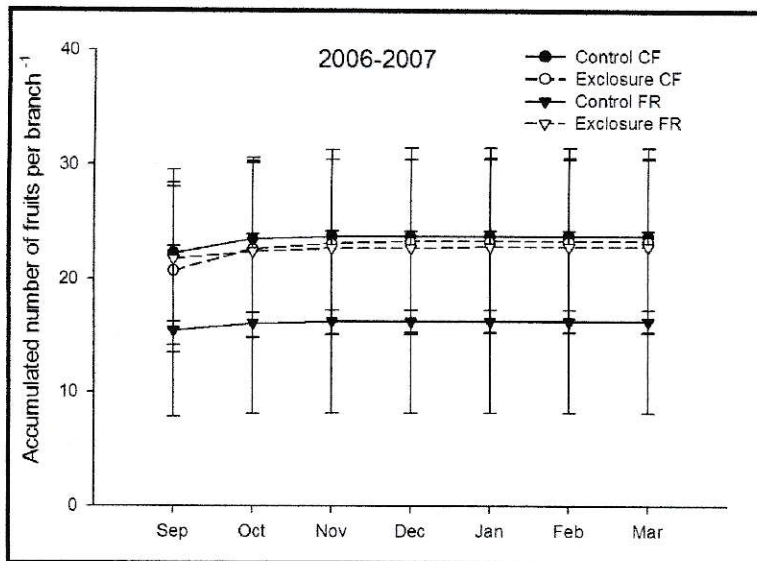
Plant reproductive success

During the 2006-2007 season, there was no significant difference in the number of inflorescences/infrutescences produced by trees in the continuous forest and forest fragments (rmANOVA $F_{1,36} = 0.03$, $P = 0.86$), nor there was a significant difference between experimental and control trees (rmANOVA $F_{1,36} = 0.01$, $P = 0.91$) or habitat * enclosure interaction (rmANOVA $F_{1,36} = 0.96$, $P = 0.33$). By the end of the season, in the continuous forest the average number of inflorescences/infrutescences produced per branch was 2.5 ± 0.83 in experimental trees and 2.8 ± 0.69 in the control trees, while in the forest fragments was 2.7 ± 0.72 and 2.2 ± 1.05 , for experimental and control trees, respectively. During this season, number of fruits produced per branch was similar in the continuous forest and in the forest fragments (rmANOVA $F_{1,36} = 0.07$, $P = 0.80$), and in the experimental and control trees (rmANOVA; $F_{1,36} = 0.004$, $P = 0.95$) (Fig. 6a). Nevertheless, from November on, more fruits/branch were produced in the experimental than in control trees (rmANOVA, enclosure*month $F_{6, 216} = 2.85$, $P < 0.001$) (Fig. 6a). There was no significant habitat * enclosure interaction (rmANOVA $F_{1,36} = 0.85$, $P = 0.36$). In total, in the continuous forest the number of fruits produced per branch was 23.34 ± 8.08 and 23.80 ± 6.61 , in the experimental and control trees, respectively, while in the forest fragments these numbers were 22.84 ± 7.87 in the experimental trees, and 16.20 ± 8.08 in the control.

During the 2007-2008 season, there was no significant difference in the number

of inflorescence/infrutescence produced per tree in the continuous forest and forest fragments (rmANOVA $F_{1,36} = 0.01, P = 0.99$), except in September when there was a higher production in the forest fragments (rmANOVA, Habitat*month $F_{6,216} = 7.36, P \ll 0.001$). Also, there was no significant difference in the number of inflorescence/infrutescence produced by experimental and control trees (rmANOVA $F_{1,36} = 0.03, P = 0.87$). Similarly, there was no significant habitat * enclosure interaction (rmANOVA $F_{1,36} = 0.003, P = 0.95$). The average number of inflorescences/infrutescences produced per branch in the continuous forest was 1.02 ± 0.43 in experimental trees and 1.04 ± 0.45 in the control trees, whereas in the forest fragments it was 0.88 ± 0.38 and 1.02 ± 0.54 in experimental and control trees, respectively. Throughout this season, the total number of fruits produced per branch did not differ between the continuous forest and forest fragments (rmANOVA, $F_1 F_{1,36} = 0.03, P = 0.86$), nor it differed between experimental and control trees (rmANOVA, $F_{1,36} = 0.28, P = 0.60$; Fig. 6b). By the end of the season, the total number of fruits produced in the continuous forest was 10.70 ± 5.61 in the experimental trees and 8.34 ± 2.86 in the control trees, while in the forest fragments it was 6.38 ± 2.76 and 11.74 ± 6.60 in the experimental and control trees, respectively, but they were not statistically different ($H = 0.002, df = 1, P > 0.90$). No significant habitat * enclosure interaction occurred in fruit production (rmANOVA $F_{1,36} = 0.005, P = 0.94$).

a)



b)

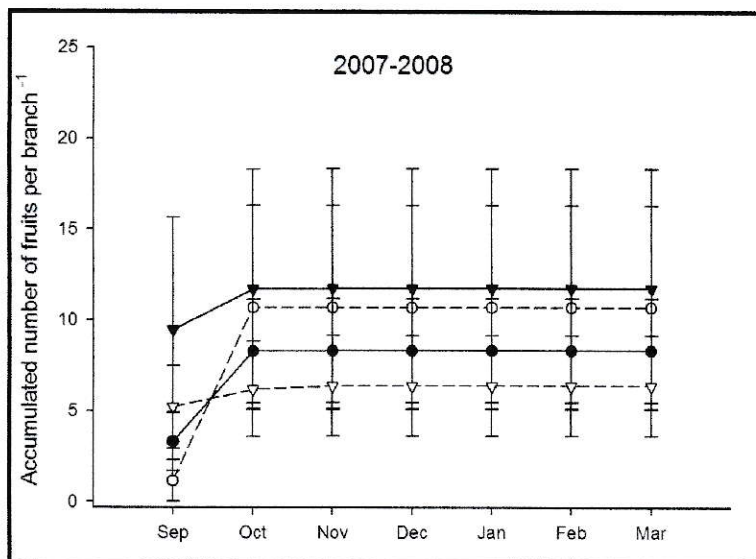


Figure 6. Accumulated number of fruits (mean/branch \pm 1 se) produced in experimental (with exclosures) and control *A. chilensis* trees in the continuous forest and forest fragments, a) First season (September 2006 to March 2007, b) Second season (September 2007 to March 2008).

DISCUSSION

Our results as well as all previous studies in the Maulino forest show that herbivory is consistently depressed by forest fragmentation. This not only has been observed in adult *A. chilensis* trees, like in this study and Vásquez et al. (2007), but also in seedlings of this species and other like *C. alba* and *P. lingue* (Vega 2001; Simonetti et al. 2007), and it seems to be a general phenomenon occurring also in other fragmented habitats (Benítez-Malvido et al. 1999; Arnold and Asquith 2002). This depressed herbivory in small forest fragments should be a consequence of a lower abundance of herbivore insects compared to the continuous forest, which is supported by our results. Total insects during the first season, or *Sericoides* sp. during the second season, reached lower abundances in small forest fragments where herbivory was also lower, related to the continuous forest.

The lower abundance of herbivorous insects and the lower herbivory in the small forest fragments should have been the result of a higher abundance of insectivorous birds. Therefore, trees excluded from birds should have had more leaf area lost to herbivores and more herbivorous insects than control trees. But this was only partially observed in our study. In spite that during the first season herbivory was similar in both excluded and control trees, during the second season herbivory was significantly higher in trees excluded from birds, supporting our hypothesis. This suggests that insectivorous birds trigger “species-level cascades” in the Maulino forest as it has been suggested to

occur in terrestrial systems (Schmitz et al. 2000). Nevertheless, neither the total abundance of herbivorous insect nor the abundance of *Sercoides* sp. varied between excluded and control trees. Therefore, the high level of herbivory in the excluded trees could have been the result of changes in the foraging behavior of herbivorous insects. Insects exposed to birds may engage in predator avoidance behavior, and be less efficient in foraging. But, when excluded from birds, they may spend more time feeding upon leaves (Schmitz 2005). This behavior have been observed to occur in the pollinator insects associated with *A. chilensis* in the Maulino forest, which spend more time in flowers of trees excluded from birds than in those visited by them (two-way ANOVA $F_{1,21} = 12.46$, $P = 0.002$; JL Allendes, unpublished data). Then, at the fragmented Maulino forest, the presence of birds seems to be mediating the interaction between herbivorous insects and *A.chilensis* through trait-mediated indirect interactions (*sensu* Wootton 1994).

If herbivory affect plant fitness, trees with higher herbivory should have a lower reproductive success, which in general we did not observed in our study. Fragmentation generally does not affect plant fitness (Aizen and Feisinger 1994; Cunningham 2000). Nevertheless, Troncoso (2007) observed that at the Maulino forest the number of infrutescences and fruits produced by *A. chilensis* were higher in the edge of the continuous forest than its interior and in small fragments. Therefore, to avoid possible confounding edge effects, we removed the data from trees located in the edges of the continuous forest from our analyses. The results remained consistent, that is to say, fragmentation did not affect *A. chilensis* fitness. The absence of fragmentation effects on

plant fitness is not an isolated result. Valdivia and Simonetti (2007) found that although fragmentation negatively affects frugivory this does not translate into an effect on the fitness of *A. chilensis*. This lack of effect on plant reproductive success is more probable when predation upon leaves is not intense. For example, the forced withdrawal of 20% of the foliage of *Colliguaya odorifera* (Euphorbiaceae), another Chilean shrub, did not reduce seed production; nevertheless a stronger or complete defoliation reduced plant fitness (Poiani and del Pozo, 1986). In several tree species of the Maulino forest, the percentage of defoliation usually ranges between 5.5% and 13% (Vega 2002; Vásquez et al. 2007; this study), and therefore it is likely that the area lost to herbivores, even in the continuous forest when herbivory was higher, was not enough to produce a decrease in plant fitness.

Growing evidence suggest that habitat fragmentation might modify the strength of trophic cascades (e.g., González-Gómez et al. 2006, Skoczylas et al 2007), and in the Maulino forest previous independent experiments and observations suggested that the fragmentation of this forest were altering trophic cascades through the increase in insectivorous birds, the decrease of herbivorous insects, the increase in herbivory and the decrease in the plant reproductive success in small forest fragments (Vergara and Simonetti 2004; González-Gómez et al. 2006; Vásquez et al. 2007, De la Vega and Grez 2008). If this were occurring at the Maulino forest, and because birds are more abundant in small forest fragments, excluding trees from birds in small fragments should trigger stronger effects than in the continuous forest. Our study did not provide strong support to this phenomenon. Although by the end of the second season, as predicted, in the

forest fragments herbivory was two times higher in the excluded than in control trees, and only 1.4 times higher in the continuous forest. Also by the end of the second season, as expected, in the small forest fragments the number of fruits decreased to half, from 11.74 in average in excluded trees to 6.38 in control trees, and in the continuous forest this difference was lower, which suggest a positive effect of birds on the reproductive success of *A. chilensis* in the small fragments. Therefore, after two years of study we were not able to statistically demonstrate that the fragmentation of the Maulino forest significantly alters trophic cascades. One explanation to the absence of significant habitat * exclusion interactions is the low number of replicates per treatment and therefore a low statistical power in our analyses, which is a usual limitation of field manipulative experiments (Holt and Debinski 2003). Other possible explanation is that the time span we have followed the effects of excluding birds is still insufficient for the effects to be evident. This explanation is supported by the stronger and, in some cases, significant effects of exclosures observed during the second season in comparison to the first year of the study when almost no effect occurred, thus a significant habitat * exclosure interaction may appear in the following seasons. For instance, as floral buds of *A.chilensis* appears at the beginning of the season, at the same time of foliar buds, it is very probable that its reproductive success do not respond to the herbivory upon newly emerged leaves but to that occurring in the previous season (Maron 1998).

In conclusion, our results, after two years of study, demonstrate that birds determine the levels of herbivory upon *A. chilensis* in the Maulino forest, but do not support our hypothesis of altered trophic cascades in fragmented forest, since the

strength of the effect of excluding birds did not vary with fragmentation. Nevertheless, the stronger effects observed during the second season in the small fragments suggest that cascading effects may be detected over a longer time span.

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**APPENDIX 1: Insectivorous birds probably predated upon herbivorous insects
associated with *A. chilensis* trees.**

Scientific name (Common name)	Diet	Specific diet	References
<i>Milvago chimango</i> (Chimango Caracara)	C (I)	no information available	González-Gómez et al. 2006
<i>Falco sparverius</i> (American Kestrel)	C (I)	Orthoptera/ Coleoptera	Jaksic et al. 1981, Mella J 2002, González-Gómez et al. 2006
<i>Bubo magellanicus</i> (Magellanic Horned Owl)	C (I)	Coleoptera	Mella J 2002, González-Gómez et al. 2006
<i>Athene cunicularia</i> (Burrowing Owl)	C (I)	Larvae of Coleoptera Tenebrionidae, Scarabaeidae, Elateridae, Curculionidae, Orthoptera, larvae of Lepidoptera	Jaksic FM 1981, Torres-Contreras et al. 1994
<i>Sephanoides sephaniodes</i> (Green-backed Firecrown)	N (I)	no information available	González-Gómez et al. 2006
<i>Colaptes pitius</i> (Chilean Flicker)	I	no information available	González-Gómez et al. 2006
<i>Picoides lignarius</i> (Striped Woodpecker)	I	no information available	González-Gómez et al. 2006
<i>Pygarrichas albogularis</i> (White throated Treerunner)	I	no information available	González-Gómez et al. 2006
<i>Aphrastura spinicauda</i> (Thorn-tailed Rayadito)	I (F)	unidentified Coleoptera	Rozzi et al 1996, González-Gómez et al. 2006
<i>Leptasthenura aegithaloides</i> (Plain-mantled Tit-Spinetail)	I	unidentified Coleoptera	Rozzi et al 1996, González-Gómez et al. 2006
<i>Pteroptochos castaneus</i> (Chestnut-breasted Huet-huet)	I (G)	no information available	González-Gómez et al. 2006
<i>Scelorchilus rubecula</i> (Chucazo Tapaculo)	I (G)	Scarabaeidae, Orthoptero, larvae of Coleoptera, larvae of Lepidoptera	Rozzi et al. 1996, González-Gómez et al. 2006
<i>Eugralla paradoxa</i> (Ochre-flanked Tapaculo)	I	no information available	González-Gómez et al. 2006
<i>Scytalopus magellanicus</i> (Magellanic Tapaculo)	I (G)	no information available	Rozzi et al. 1996, González-Gómez et al. 2006
<i>Xolmis pyrope</i> (Fire-eyed Diucon)	I (F)	no information available	González-Gómez et al. 2006
<i>Elaenia albiceps</i> (White-crested Elaenia)	I (F)	no information available	Fjeldsa J and N Krabbe 1990, González-Gómez et al. 2006

<i>Anairetes parulus</i> (Tufted Tit-Tyrant)	I (F)	unidentified Coleoptera/ Curculionidae	Rozzi et al 1996, González-Gómez et al. 2006
<i>Troglodytes musculus</i> (Southern House Wren)	I	no information available	Rozzi et al 1996, González-Gómez et al. 2006
<i>Turdus falckandii</i> (Austral Thrush)	I (F)	Scarabaeidae, larvae of Coleoptera	Rozzi et al 1996, González-Gómez et al. 2006
<i>Curaeus curaeus</i> (Austral Blackbird)	I (H)	no information available	Fjeldsa J and N Krabbe 1990, González-Gómez et al. 2006

symbols for diet are: C carnivores, F frugivores, G granivores, H herbivores, I insectivores, N nectarivores. Secondary diet is in parenthesis.

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