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La variación en la insectivoría en bosques fragmentados ¿Es un fenómeno permanente?

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ESCUELA DE PREGRADO – FACULTAD DE CIENCIAS – UNIVERSIDAD DE CHILE

"LA VARIACIÓN EN LA INSECTIVORÍA EN BOSQUES FRAGMENTADOS ¿ES UN FENÓMENO PERMANENTE?"

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Por

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Directores Seminario de Título: Dr. Javier A. Simonetti
M. Sc. Paulina L. González-Gómez

"Hay quien cruza el Bosque y
Sólo ve leña para el fuego"

-León Tolstói-

A Juan Francisco

Con la intuición de que,
en medio de esta existencia
-constantemente fragmentada-
lo nuestro sí es un fenómeno permanente.

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RESUMEN

La fragmentación del hábitat modifica las interacciones ecológicas a través de cambios en la riqueza y abundancia de especies. En el bosque Maulino costero, en Chile central, la abundancia de aves insectívoras aumenta en los fragmentos de bosque respecto al bosque continuo, lo cual se refleja en un aumento en la insectivoría y la consecuente disminución en la herbivoría en ambientes fragmentados. En el presente estudio, a través de una investigación de campo, analizamos la depredación de larvas herbívoras en un bosque fragmentado, comparando el nivel de insectivoría obtenido con el de un estudio similar realizado hace cuatro años.

La cantidad de larvas de insectos depredadas fue significativamente mayor en los fragmentos de bosque que en el bosque continuo, independientemente del año en el cual se evaluó la depredación de larvas. Este resultado sugiere que la variación en la insectivoría, producto de la fragmentación, sí es permanente. De este modo –dada la persistencia del fenómeno- las consiguientes modificaciones de las interacciones ecológicas efectivamente podrían repercutir en la adecuación biológica de los árboles, lo cual podría a su vez afectar la dinámica de regeneración del bosque Maulino costero.

ABSTRACT

Habitat fragmentation modifies ecological interactions through changes in species richness and abundance. At Maulino forest, on central Chile, the abundance of insectivorous birds increases on forest fragments as compared to continuous forest, which reflects on an increase in insectivory and the consequent decrease in herbivory on fragmented environments. In our study, through a field investigation we analyzed the predation of herbivores larvae in a fragmented forest, and compared the assessed level of insectivory with the level recorded on a similar study performed four years ago.

More insect larvae were preyed upon at forest fragments that in continuous forest, regardless of the year on which larvae predation was assessed. This result suggests that variation in insectivory level due to fragmentation is a permanent phenomenon. Hence, the subsequent modifications of ecological interactions could reflect on trees fitness, which in turn may affect the regeneration dynamic of the coastal Maulino forest.

Key words: avian insectivory, forest fragmentation, persistency of changes.

INTRODUCTION

Habitat fragmentation is the transformation of an extension of continuous habitat in a number of fragments of smaller total area, isolated from each other by a matrix of habitats different from the original (Wilcove et al. 1986). Fragmentation modifies ecological interactions through changes in species richness and abundance, including birds (Fahrig 2003). However, the effects of fragmentation on biodiversity are at least as likely to be positive (such as the increase in species richness and abundance, the increase in dispersal rate and the increase of overall immigration rate of a population) as negative (the increase of overall mortality rate, the reduction of overall population size, the reduction of overall reproductive rate of a population or the increase of predation on species at forest edges, among them), depending on the taxon (Fahrig 2003, Bustamante et al. 2005). Usually, habitat fragmentation modifies both species richness and abundance of insectivorous birds (Clout & Gaze 1984, Sekercioglu et al. 2002, Stouffer et al. 2006). In turn, changes in the abundance of birds could alter ecological interactions in which these form part of. For instance, a decrease in frugivore birds may affect negatively seed dispersal (Restrepo et al. 1999, Sekercioglu et al. 2004); a decrease in nectarivores has been associated with a decline in pollination (Sekercioglu et al. 2004); and an increase in insectivorous birds may be translated into higher insectivory (González-Gómez et al. 2006).

The coastal Maulino forest, in central Chile, has undergone an anthropogenic fragmentation process (Echeverría et al. 2006). Currently, the remaining forest consists of a series of small fragments immersed in an extensive matrix of pine (*Pinus radiata*)

plantations, which are periodically harvested (Echeverria et al. 2006). In the coastal Maulino forest, both the richness and abundance of birds increase in forest fragments as compared to continuous forest. However, fragmentation can affect birds differentially, according to their feeding ecology (e.g. causing a relative increase of insectivores species abundances, while the relative abundance of granivores decreases) (Clout & Gaze 1984, Estades 1994, Vergara & Simonetti 2004). In this forest, the abundance of insectivorous birds increases in forest fragments as compared to continuous forest (Estades 1994, Vergara & Simonetti 2004, González-Gómez et al. 2006).

Coupled to an increase of richness and abundance of insectivorous birds (twice as abundant in forest fragments that in the continuous forest), in the coastal Maulino forest, insectivory also increases (2.5 times) at forest fragments as compared to continuous forest (González-Gómez et al. 2006). However, since fragmentation – through the modification of landscape structure- increases the temporal variations in species richness and abundance of forest birds (Boulinier et al. 1998), the changes in avian abundance triggered by fragmentation might not be persistent. If they were persistent, the changes in biological interactions –insectivory among them- might affect the regeneration process of the coastal Maulino forest (Bustamante et al. 2005), through modifications on vegetation dynamics (Restrepo et al. 1999, Fahrig 2003, Simonetti et al. in press).

At Maulino forest, differences have been recorded in both the richness and abundance of birds, depending on their feeding biology (i.e. what they eat), between the continuous forest and forest fragments (Estades & Temple 1999, Vergara & Simonetti 2004, González-Gómez et al. 2006, Valdivia & Simonetti 2007). Similarly, it has been

recorded that at the coastal Maulino forest visit rates of insectivorous birds to a single tree is higher in forest fragments than in continuous forest, because there is a higher number of birds engaged in foraging activities in forest fragments than in the continuous forest (González-Gomez et al. 2006). In this study, we experimentally assessed the persistence of the changes in insectivory on fragmented environments, through comparing the current intensity of insectivory upon artificial insect larvae to the intensity of insectivory recorded on a previous study at the same site (González-Gomez et al. 2006). Consistent variation in insectivory in both periods would be indication of a persistent effect.

METHODS

Study site and species. We conducted our research in Los Queules National Reserve, a protected area of 145 ha embedded in a large tract of 600 ha of continuous forest located in the northernmost zone of the Southern temperate rainforest (35°59'19''S, 72°41'15''O), and in four forest fragments. Here, dominant tree species are *Nothofagus glauca, N. obliqua, Cryptocarya alba, Aristotelia chilensis, Gevuina avellana* and *Persea lingue* (Bustamante et al. 2005).

Artificial larvae were attached to *A. chilensis*. Among the insectivorous birds that could be feeding on these trees are Thorn-tailed rayadito (*Aphrastrura spinicauda)*, Des Mur's wiretail (*Sylviorthorhynchus desmursii*) and House wren (*Troglodytes aedon*). However, as most of the bird species on the study site belong to more than one trophic category, birds which are primarily frugivores -such as White-crested Elaenia (*Elaenia albiceps)* and Austral thrush (*Turdus falckandii*)- could also be feeding from insects as well (Vergara & Simonetti 2004).

Insectivory. The intensity of insectivory upon larvae was experimentally assessed as the frequency of birds attacks upon insect larvae, as previously described by González-Gomez et al. (2006) (see also Loiselle & Farji-Brener 2002). Briefly, larvae were plasticine models mimicking *Ormiscodes cinnamomea* (Feisthamel) larvae naturally occurring in the study area (fig.1).

Fig. 1 Cluster of *O. cinnamomea* larvae as it naturally occurs in *P. radiata* (left) and cluster of artificial larvae of *O. cinnamomea* placed on *A. chilensis* (right).

Such models have been effectively used to estimate relative predation rates in various taxa, especially avian predation, since birds are visually oriented (Bayne & Hobson 1997, Schneider et al. 1999, Rangen et al. 2000). Groups of artificial caterpillars were placed in 43 randomly selected locations per habitat type (n = 21 trees at continuous forest, n = 22 trees at forest fragments). We set a group of 15 artificial caterpillars on adult trees (approximately 2 m above ground), attaching them to a branch using coiled wire (fig.1, right). The sampling unit was a group of larvae. Artificial larvae were left for the action of insectivorous birds during 24 h, after which we recorded the proportion of artificial caterpillars marked by birds (fig. 2).

Fig. 2 Detail of two different artificial Caterpillar clusters showing marks left by avian attack.

Although these models do not provide a good estimation of natural predation levels, they serve as relative measures of predation across habitats (Martin 1987). Field work was conducted on October 2007, a period corresponding to an austral spring, which matches reproductive season of most birds of the area and a high abundance of herbivorous insects and foliar development (Jaña-Prado & Grez 2004).

The intensity of insectivory obtained was compared to the level of insectivory recorded on 2004, when the same methodology was used, but the groups of artificial caterpillars were placed in 80 randomly selected locations (n = 40 trees at continuous forest, n = 40 trees at forest fragments) (González-Gómez et al. 2006).

RESULTS

Predation of artificial caterpillars was significantly different among habitats. The proportion of caterpillars preyed upon by birds was 4.4 times greater in forest fragments than in continuous forest (Fig 3). In contrast, the predation level was not significantly affected by the year of sampling (Table 1). There is no interaction of year and habitat on larval predation (Table 1).

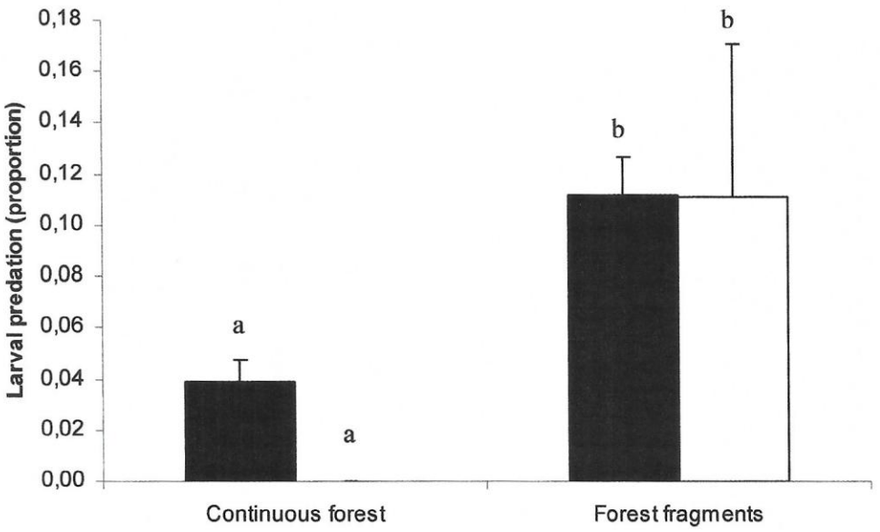

Fig. 3 Bird predation upon larvae in 2003 (black bars) and 2007 (white bars) on *A. chilensis* in the continuous forests and forest fragments (Mean + SE). Different letters represent significant differences.

Table 1 Two-way ANOVA for caterpillars preyed by birds.

Factor	SS	D*f*	MS	F	P
Habitat	0.238	1	0.238	13.757	0.0003
Year	0.01	1	0.01	0.571	0.451
Interaction	0.011	1	0.011	0.644	0.424
Error	2.061	119	0.017		

DISCUSSION

Fragmentation modifies species interactions through changes in the species richness and abundance. However, most habitat fragmentation studies have focused on patterns rather than on the functional consequences of the changes in species abundance (Debinski & Holt 2000). Moreover, only about 10% of the most recent publications regarding the ecology of fragmented environments address biological interactions (Fahrig 2003). Even fewer experimental data exist on the long-term consequences of habitat fragmentation (Debinsky & Holt 2000). This is the first experimental study that assesses the persistence of the insectivory increase as a consequence of habitat fragmentation.

Among other effects, habitat fragmentation might modify the relative abundance of different functional groups, which may in turn be translated into variations of the intensity of the biological interactions in which the species are involved (Simonetti et al. 2006). In this way, fragmentation might affect birds differentially, according to their feeding ecology (Clout & Gaze 1984, Estades 1994, Estades and Temple 1999, Sekercioglu et al. 2002, Vergara & Simonetti 2004). At Maulino forest, the abundance of insectivorous birds increases in forest fragments as compared to continuous forest (Estades 1994, Vergara & Simonetti 2004), causing an increase of insectivory at forest fragments (González-Gómez et al. 2006). Since fragmentation increases the temporal variation in species richness of forest birds, the persistence of the increase in insectivory previously reported (González-Gómez et al. 2006) was assessed in our study.

After a 4-year analysis we found that insectivory was 4.4 times greater in forest fragments than in continuous forest and was not significantly affected by the year of sampling. Apparently, the higher level of insectivory in forest fragments relative to continuous forest is a persistent phenomenon at Maulino forest, accounted for by a permanent increase of insectivorous birds (Estades and Temple 1999, Vergara and Simonetti 2004, González-Gómez et al. 2006). As other investigators suggested, the increase in the number of insectivorous birds in forest fragments is possibly due to an increase in the number of certain insects groups -such as epigeic beetles- (Grez et al. 2003) in the forest fragments, the higher structural complexity of forests fragments compared to continuous forest (Vergara and Simonetti 2004), and the effect of the neighboring coniferous forest which might act as a source of foraging resources (González-Gómez et al. 2006, see also Grez et al. 2003 and Vergara and Simonetti 2004).

Our results suggest that the difference on the intensity of insectivory among habitats persisted through time, being always significantly stronger in forest fragments than in continuous forest. There could also be a slight suggestion that the difference on the intensity of insectivory among habitats appears to increase through time, since during 2003 the insectivory reported was 2.5 higher on forest fragments than in the continuous forest, while during 2007 the insectivory assessed was 4.4 times higher on forest fragments compared to the continuous forest.

The differences on the insectivory reported on Maulino forest is mainly due to insectivores birds, since here birds are the most abundant insectivores, attacking experimental larvae almost 8 times more frequently than the other insectivores predator:

micro mammals (Simonetti et al 2006). The importance of top-down forces can vary across and also within habitats. The relative importance of birds at Maulino forest is very strong, since during 2003 the frequency of larvae being attacked by birds was 7.3 times greater than the number of larvae marked by rodents (González-Gomez et all 2006), while at the same study site artificial caterpillars were preyed upon only by birds during the present study (2007). The identity of predators here is very different from a similar experimental study in a tropical wet forest, were ants were the major predator on caterpillars (*ca 90%* of locations), a value 18 times greater than larvae predated by birds. Predation by birds represents only a 5% of the total larvae predation, while the rodents larvae attacks accounts by a 20% (Loiselle and Farji-Brenner 2001). The intensity of insectivory also differs greatly on the recently mentioned studies, since the percentage of caterpillars preyed upon was 8.8 times greater on a neotropical wet forest (Loiselle and Farji-Brenner 2001) than the percentage of caterpillars preyed upon on the present study. However, both studies concluded that an increase on the abundance of the third trophic level also serves to lower herbivory rates. Finally, both studies found differences on intensity of insectivory across the compared habitats: on the neotropical wet forest the predation levels were 1.5 times higher in the canopy than in forest understory (Loiselle and Farji-Brenner 2001), while on the present study the predation levels were 4.4 times higher in the forest fragments than in the continuous forests. It is interesting to consider than where the greater predation levels occurred (forest fragments and forest canopy) were similar habitats: both present more light for plant growth ((Loiselle and Farji-Brenner 2001) and generally it is a habitat dryer and with higher thermal oscillations than continuous forest and forest canopy (Simonetti et al. 2006).

The increase in insectivory at forest fragments could exert important effects on the vegetation on fragmented forests. At the individual level, insectivorous birds may increase the fitness of plants on which they forage through the consumption of leaf-damaging insects (Marquis & Whelan 1994, Van Bael et al. 2003). At the Maulino forest, this effect depends on the developmental stage of the plant: the removal of the plant's herbivore load increase seedling growth, while on adult trees it only affects foliage survival of the first cohort of leaves (Vásquez et al. 2007). These changes, added to the variations on frugivory, pollination and seed dispersal at Maulino forest, could lead to modifications on the composition and future dynamics of the vegetation on fragments compared to continuous forest (Bustamante et al. 2005, Simonetti et al. 2006). This information is essential for the design and implementation of effective management strategies that allow the biologic conservation of forest remnants.

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