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Strengthened insectivory
in a temperate fragmented forest

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Ecología y Biología Evolutiva
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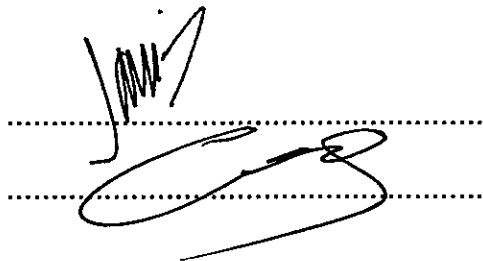
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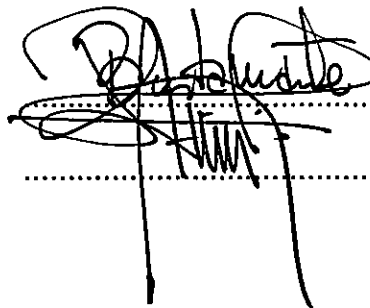
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RESUMEN

La fragmentación del hábitat modifica patrones y procesos ecológicos a través de cambios de la riqueza y abundancia de especies. En el Bosque Maulino costero tanto la riqueza como la abundancia de aves insectívoras aumenta en fragmentos de bosque respecto del bosque continuo. Las consecuencias de estos cambios sobre la intensidad de la insectivoría no han sido estudiadas. Mediante un experimento de campo examinamos, la depredación de larvas en un bosque fragmentado. La mayor riqueza y abundancia de aves forrajeando en fragmentos de bosque, se asoció a la proporción de larvas atacadas en fragmentos, la que fue 2.5 veces más alta en fragmentos que en bosque continuo. El aumento de la insectivoría en fragmentos de bosque coincide con menores niveles de herbivoría en fragmentos de bosque. Este patrón sugiere la intensificación de cadenas tróficas en fragmentos de Bosque Maulino.



ABSTRACT

Habitat fragmentation modifies ecological pattern and processes through changes in the species richness and abundance. In Coastal Maulino forest both species richness and abundance of insectivorous birds increase in forest fragments in relation to continuous forest. The consequences of these changes have not been studied. A field experiment was carried out in order to examine the larvae predation in a fragmented forest. Higher richness and abundance of birds foraging en forest fragments was related to the proportion of attacked larvae that was 2.5 times higher in forest fragments than in continuous forest. The increment of insectivory in forest fragments is in agreement with lower herbivory levels in forest fragments. This pattern strongly suggests the strengthening of food web in forest fragments of Coastal Maulino forest.



INTRODUCTION

Changes in land use and its associated habitat fragmentation, is one of the most pervasive effects of human activities (Davies et al. 2001). Habitat fragmentation changes the abundance of predators such as insectivores, which are especially sensitive to habitat fragmentation (Wilson et al. 1994, Sekercioglu et al. 2002). It is normally assumed that due to the decrease of insectivores in forest fragments, there should be an increase in the herbivore abundance (Terborgh et al. 2001). As a consequence cascading effects are usually expected (Schmitz et al. 2000). Insectivorous birds reduce the populations of herbivorous insects (Joern 1986, Fowler et al. 1991). Through such a reduction, birds might positively affect plants, decreasing the area of consumed leaves and increasing the fitness of the plants (Marquis 1984, Marquis and Whelan 1994, Van Bael et al. 2003).

Several studies had reported the relaxation of food webs as a result of decreased abundance of predators in forest fragments (Terborgh 1998). However, experimental approaches in order to evaluate mechanism for such patterns are lesser frequent (Debinski and Holt 2000). In this study we present evidence about the increase of native predators in a fragmented forest and a field test in order to evaluate the effects of these changes in predation intensity caused by the increase in predator abundance. If there is an increase in insectivorous birds, are the opposite than predator removal, is expected the strength of food webs in forest fragments, will be strenght.

In Chile, the coastal Maulino Forest has undergone an intensive replacement of native forest, to provide land for agriculture and more recently, to establish pine plantations (Lara et al. 1996). As a consequence, there are only some remnants areas of continuous forest (i.e., Los Queules National Reserve) and small forest fragments immersed in extensive pine plantations, acting as a matrix (Grez et al. 1997, Bustamante & Castor 1998, Estades and Temple 1999). Avian species richness and abundance, particularly insectivorous species, is significantly higher in forest fragments and pine

plantations than continuous forest (Vergara and Simonetti 2004, see also Estades and Temple 1999).

Here, although the richness and abundance of herbivorous insects are not significantly different between forests fragments and continuous forest (Jaña and Grez 2004), herbivory levels upon seedlings and adult trees of *Aristotelia chilensis* is higher in continuous forest than in forests fragments (Simonetti et al. 2004 *unpublished*, Vásquez 2004). Microclimatically- induced differences in palatability of leaves could account for differences in herbivory between forest fragments and continuous forest. However, palatability of leaves for lepidopteran larvae is not significantly different between habitats ruling it out as a potential cause of differences in herbivory (Appendix 1).

The higher density of avian predators and lower herbivory in forest fragments suggests that insectivory in Coastal Maulino forest could be higher in forest fragments. In this study, we examined experimentally the relationship between avian abundance and insectivory intensity upon herbivorous larvae in seedlings and adults trees of *A. chilensis*.

If in forest fragments there is a greater number of birds especially insectivorous ones, should be an increase of insectivory. However, it is not enough a higher number of birds. It is also necessary that these birds indeed consume herbivores insects in forest fragments.

Birds might be responsible for the herbivory reduction either through the consumption of herbivorous larvae or through nonlethal effects, which is increasing the predation risk for caterpillars reducing their time devoted to foraging (Lima 1998). If birds are diminishing the herbivory in forest fragments through increased insectivory; a) we expected that the avian foraging intensity, should be higher in forest fragments than in continuous forest, b) we expected that the insectivory levels (i.e., larvae predation intensity) in adult trees and seedlings of *A. chilensis* should be significantly higher in forest fragments and pine plantations than in continuous forest.

METHODS

The study was carried out at Los Queules National Reserve (a forest tract of 145 ha of native Coastal Maulino Forest; 35° 59' S, 72° 41' W), the surrounding pine (*Pinus radiata*) plantations and 10 forest fragments, ranging from 0.5 to 10 ha. Dominant tree species are *Nothofagus glauca* and *N. obliqua*, *Aristotelia chilensis*, *Gevuina avellana*, *Aextoxicon punctatum* and *Cryptocarya alba* (Bustamante et al. 2004). Pine plantations are, on average, 20 years old and had a variable understory cover (Vergara and Simonetti 2004).

Field work was conducted during the spring of 2003 (mid-September to December), the reproductive season of most birds in the area, and the period where larvae eclosion and higher foliar development also occur (Fuentes et al. 1977, Holmes et al. 1979, Holmes 1990, Torgensen et al. 1990). The synchrony in the phenology among three trophic levels could intensify insectivory in this period, because, even bird species that as adults do not consume insects (i.e., granivores, herbivores) prey upon insects to feed their nestlings (Morton 1973, Stutchbury and Morton 2001).

In order to assess the predation level, both avian richness and abundance were estimated using circular sampling plots of 50 m radius (Buckland et al. 1993). Fifty sample plots were randomly distributed among the studied vegetation types: continuous forest (N=20), forest fragments (N=15) and pine plantations (N=15). Each point was visited between 8:00 and 12:00 hrs at least three times. During each visit, two separate counts of 5 min were conducted (i.e., 6 counts per sample point). All observed or heard birds were recorded. Species richness was considered as the total number of species registered in each sample plot during the six counts and the abundance was assessed as the average number of individuals recorded in the six counts per plot (Vergara and Simonetti 2004).

Foraging intensity was assessed through direct observation of insectivorous birds using circular plots of 30m radius in 5 min periods. Each plot was sampled six times during morning, and three times during afternoon and

evening in continuous forest (N=240), pine plantations (N=180) and forest fragments (N=180). Of a total 3,000 min allocated to observe birds in different habitats, only 2.2% resulted in observations of birds foraging. The number of observation periods that rendered observations of foraging birds was not significantly different between habitats (ANOVA $F_{2,151}=0.3$ $P=0.74$).

Foraging intensity was measured using both population and individual level variables. At the individual level, foraging intensity was assessed tracking an individual insectivorous bird for up to 5 min and recording: i) the foraging rate, that is the numbers of preys captured per second and ii) foraging time, time spent searching for, capturing and consuming food in relation to others activities such as nest defense, parental care and resting. At the population level, foraging intensity was estimated as the number of birds foraging per plot in 5 min periods, considered the number of birds in the plot, spending time in search, capture and consume preys (Caraco 1979).

In order to assess the abundance of arthropods, particularly that of lepidopteran larvae, we sampled foliage invertebrates, using the shake-cloth method (Cooper and Whitmore 1990). Samples were taken separately from the canopy and understory, at each of 50 points randomly distributed among forest fragments (N=33), pine plantations (N=33) and continuous forest (N=43). At canopy and understory, in each plot, were randomly selected 10 plants (any specie) and 10 branches per plant. Each sample was considered as the summatory of individuals collected.

In order to estimate the intensity of predation by birds upon herbivorous larvae, we built plasticine model of caterpillars that provide a relative measures of predation across habitats (Loiselle and Farji-Brener 2002). Furthermore, artificial caterpillar method is able to detect differences in predation intensity produced by different densities of predators (See Appendix 2).

To assess the difference in the avian predation intensity among habitats and between seedlings and adults trees, we placed groups of artificial caterpillars in 40 randomly selected locations per habitat type (N=120). At each location, we set 30 artificial caterpillars, 15 of them placed on an adult tree and

15 on a seedling. This caterpillar aggregation simulated natural groups of lepidopteran larvae present in the study area (personal observation). After 24 hours, we recorded the proportion of artificial caterpillars marked by predators in each group respect to present larvae.

RESULTS

Bird Assemblage

A total of 26 species were recorded (Table 1). Species richness was significantly higher in forest fragments and pine plantations sites than in continuous forest (ANOVA $F_{2,47} = 21.26$ $P < 0.001$) (Figure 1). Forest fragments and pine plantations were not significantly different (Tukey $P = 0.72$), but both had almost twice the species richness of the continuous forest (Tukey $P < 0.001$). Out of the 26 species recorded, 65% of them were insectivorous. Insectivore richness was 1.5 times greater in forest fragments and pine plantations than in the continuous forest (ANOVA $F_{2,47} = 14.47$ $P < 0.001$) (Tukey $P < 0.01$). Forest fragments and pine plantations did not differ significantly in the richness of insectivorous birds (Tukey $P = 0.6$).

Table 1. Avian abundance in forest fragments, pine plantations and Los Queules National Reserve. Different letters indicate significant differences. Species recorded one in census were not compared, (p) species presence. C: carnivores, F: Frugivores, G: granivores, H: herbivores, I: Insectivores, N: Nectarivores. Secondary diet is in parenthesis (Estades 1997).

Scientific Name (Common Name)	Diet	Forest Fragments		Pine Matrix		Reserve		Test	
		Mean	± SE	Mean	± SE	Mean	± SE	F _{2,47}	P
<i>Anairetes parulus</i> (Tufted Tit-tyrant)	I (F)	0.60 ± 0.14	a	0.47 ± 0.14	a	0.18 ± 0.08	b	3.53	0.04
<i>Aphrastura spinicauda</i> (Thorn-tailed rayadito)	I (F)	1.33 ± 0.26		0.88 ± 0.20		1.17 ± 0.12		1.34	0.27
<i>Callipepla californica</i> (California quail)	G	0		p		0		0	
<i>Carduelis barbata</i> (Black-chinned siskin)	G (H)	0.33 ± 0.24		0.37 ± 0.11		0.03 ± 0.03		1.92	0.16
<i>Colaptes pitius</i> (Chilean flicker)	I	0.02 ± 0.06		0.04 ± 0.03		0.02 ± 0.01		0.32	0.73
<i>Corycaeus atratus</i> (Black vulture)	C	0		p		0		0	
<i>Curaeus curaeus</i> (Austral blackbird)	I (H)	0.64 ± 0.24	a	0.44 ± 0.14	a,b	0.02 ± 0.02	b	5.47	0.01
<i>Diuca diuca</i> (Common Diuca finch)	G	0.16 ± 0.05	b	0.34 ± 0.08	a	0.06 ± 0.02	b	9.32	0.001
<i>Elaenia albiceps</i> (White-crested Elaenia)	I (F)	2.07 ± 0.26	a	2.01 ± 0.23	a	0.65 ± 0.14	b	17.03	0.001
<i>Eugralla paradoxa</i> (Ochre-flanked Tapaculo)	I	0.50 ± 0.12	a	0.28 ± 0.07	a,b	0.06 ± 0.03	b	9.51	0.001
<i>Glaucidium nanum</i> (Austral pigmy owl)	C	0.00 ± 0.00		0.01 ± 0.01		0.02 ± 0.02		1.50	0.23
<i>Leptasthenura aegithaloides</i> (Plain-mantled Tit-spinetail)	I	0.01 ± 0.01		0.018 ± 0.02		0		0.76	0.47
<i>Milvago chimango</i> (Chimango caracara)	C (I)	0		0		p		0	
<i>Patagioenas araucana</i> (Chilean pigeon)	G	0.11 ± 0.03		0.07 ± 0.04		0.08 ± 0.04		0.28	0.76
<i>Phrygilus gayi</i> (Gray-hooded Sierra-finch)	G (H)	0.04 ± 0.03		0.07 ± 0.04		0.01 ± 0.01		1.47	0.24
<i>Picoides lignarius</i> (Striped woodpecker)	I	0.04 ± 0.03		0.01 ± 0.01		0.05 ± 0.03		0.50	0.61
<i>Pteroptochos castaneus</i> (Chestnut-breasted huet-huet)	I (G)	0.43 ± 0.09		0.47 ± 0.08		0.30 ± 0.07		1.32	0.28
<i>Pygarrhichas albogularis</i> (White throated tree-runner)	I	0.35 ± 0.11	a	0.13 ± 0.06	a, b	0.10 ± 0.04	b	3.48	0.04
<i>Scelorchilus rubecula</i> (Chucaco tapaculo)	I (G)	0.07 ± 0.05		0.01 ± 0.01		0.08 ± 0.04		0.88	0.42
<i>Scytalopus magellanicus</i> (Andean tapaculo)	I (G)	0.23 ± 0.12	a,b	0.38 ± 0.11	a	0.03 ± 0.02	b	4.24	0.02
<i>Sephanoides sephanioides</i> (Green-backed firecrown)	N (I)	0.34 ± 0.07		0.33 ± 0.09		0.18 ± 0.06		1.81	0.18
<i>Sylviorthorinchus desmursii</i> (Des Murs's wiretail)	I	0.49 ± 0.16	a	0.15 ± 0.06	b	0.10 ± 0.09	b	4.51	0.02
<i>Tachycineta meyeni</i> (Chilean swallow)	I	0.29 ± 0.12	a	0.14 ± 0.06		0.15 ± 0.06		1.02	0.37
<i>Troglodytes aedon</i> (House wren)	I	0.23 ± 0.09	a	0.08 ± 0.05	a,b	0.01 ± 0.01	b	4.68	0.01
<i>Turdus falcklandii</i> (Austral thrush)	I (F)	0.38 ± 0.10		0.26 ± 0.09		0.31 ± 0.07		0.53	0.59
<i>Xolmes pyrope</i> (Fire-eyed Diucon)	I (F)	0.16 ± 0.05	a	0.10 ± 0.04	a,b	0.03 ± 0.03	b	2.77	0.07

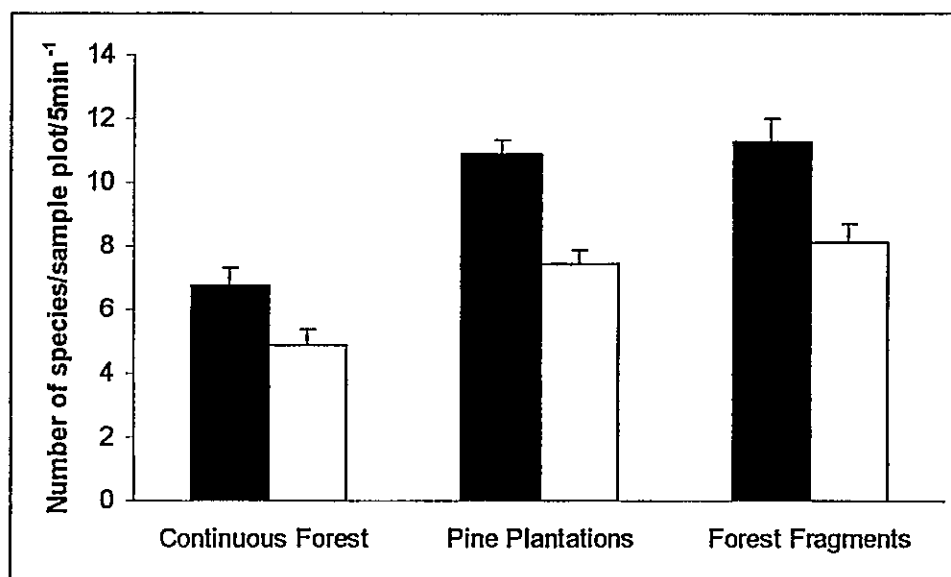


Figure 1. Total avian richness (black bars) and insectivore richness (white bars), recorded in continuous forest, forest fragments and pine plantations. Error bars indicate +1 SE.

Bird abundance was significantly higher in forest fragments and pine plantations (ANOVA $F_{2,47}=28.69$, $P<0.001$). Forest fragments had 1.3 times more birds than pine plantations, but that difference was only marginally significant (Tukey $P=0.07$). Avian abundance in forest fragments and pine plantations was 2.5 times greater than continuous forest (Tukey $P<0.001$, at each comparison). Twenty-three species were statistically evaluated in order to assess the avian abundance. Of them, 39% increased their abundance in forest fragments and pine plantations in relation to continuous forest. The 16 remaining did not show any difference.

The abundance of insectivorous birds in forest fragments was twice that of the continuous forest (ANOVA $F_{2,47}=20.13$ $P<0.001$; Tukey $P<0.001$) and it was marginally lower in pines than in forest fragments (Tukey $P=0.07$) but significantly higher than continuous forest (Tukey $P<0.001$) (Figure 2).

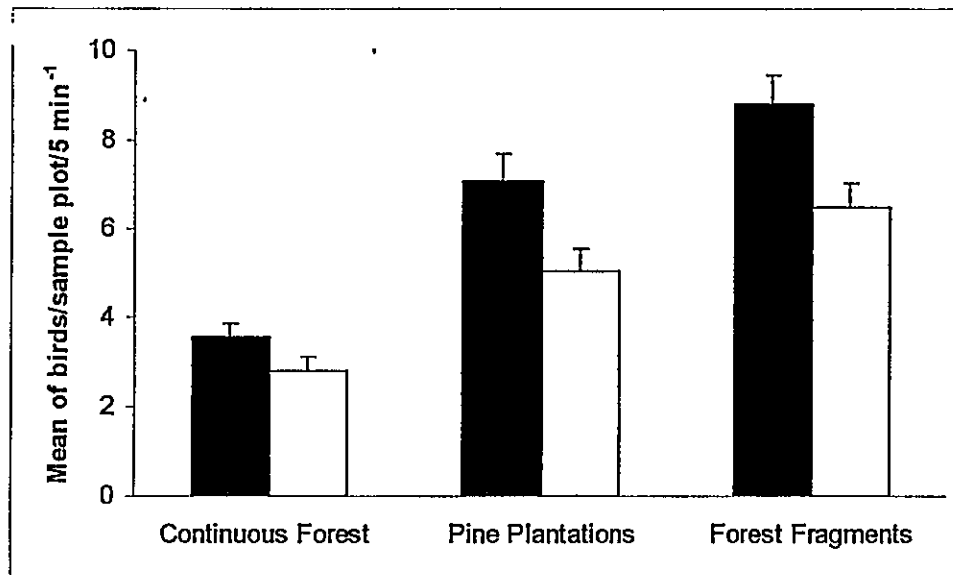


Figure 2. Total abundance of birds (black bars) and insectivore abundance (white bars) recorded in continuous forest, forest fragments and pine plantations. Error bars indicate +1 SE.

Avian Foraging Intensity

The number of birds foraging in forest fragments was 2.3 times higher than in continuous forest (ANOVA $F_{2,47}=10.33$, $P<0.001$; Tukey $P<0.001$) and 1.7 times higher than in pine plantations (Tukey $P<0.001$). The number of birds foraging per plot was not significantly different between the continuous forest and pine plantations (Tukey $P=0.75$) (Figure 3).

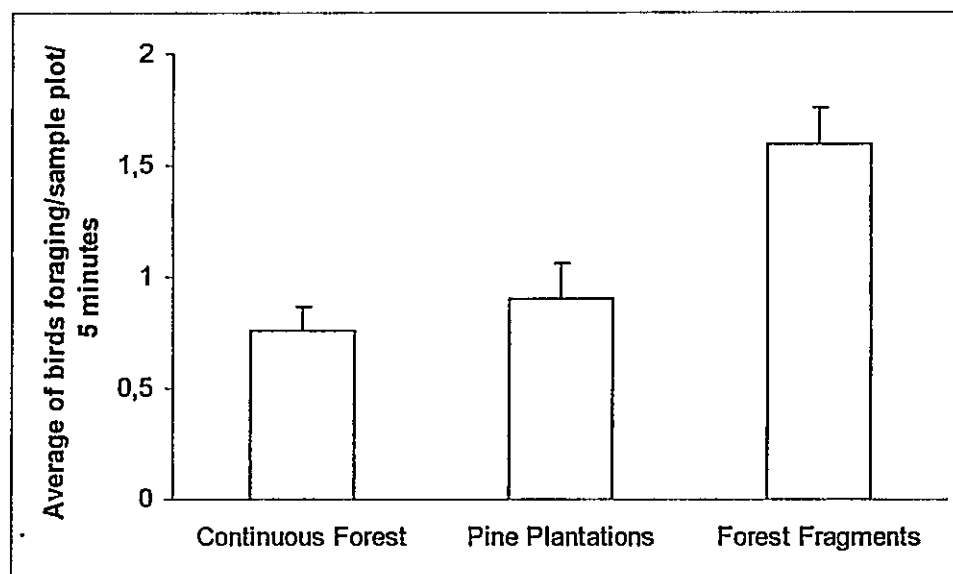


Figure 3. Number of bird foraging in continuous forest, pine plantations and forest fragments. Error bars indicate 1+ SE.

In 137.2 minutes of observations of bird behavior, a total of 153 insectivorous birds were observed in continuous forest (N=49, 40.2 min.), pine plantations (N=42, 40.1 min) and forest fragments (N=62, 57.2 min). Foraging time spent by individuals did not differ among forest fragments, pine plantations and continuous forest (Kruskal-Wallis test: $H_{2,153} = 5.01$ $P=0.08$) (Figure 4).

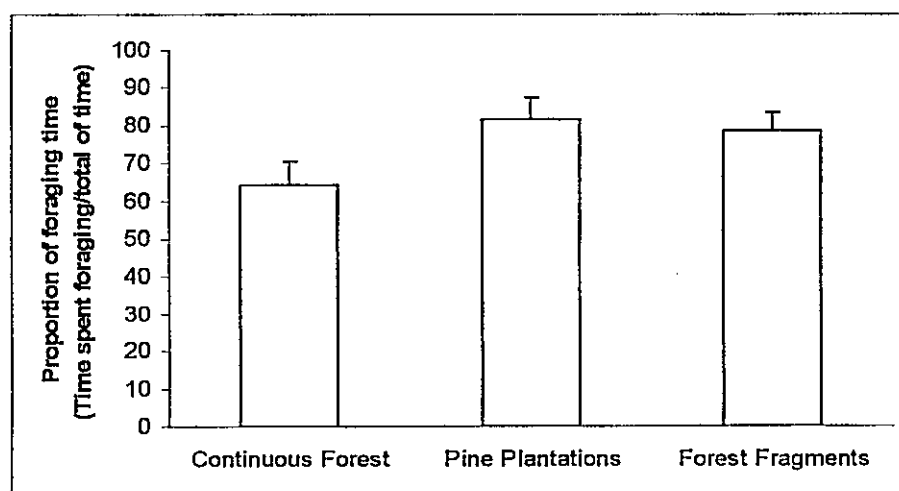


Figure 4. Foraging time in continuous forest, pine plantations and forest fragments. Error bars indicate +1 SE.

In 67.4 minutes of observations of foraging behavior, a total of 126 insectivorous birds were observed in continuous forest (N=39, 18.5 min.), pine plantations (N=34, 20.4 min) and forest fragments (N=53, 28.5 min.). Individual foraging rate was not significantly different among forest fragments, pine plantations and continuous forest (Kruskal-Wallis test, $H_{2,126}=1.58$ $P=0.45$) (Figure 5).

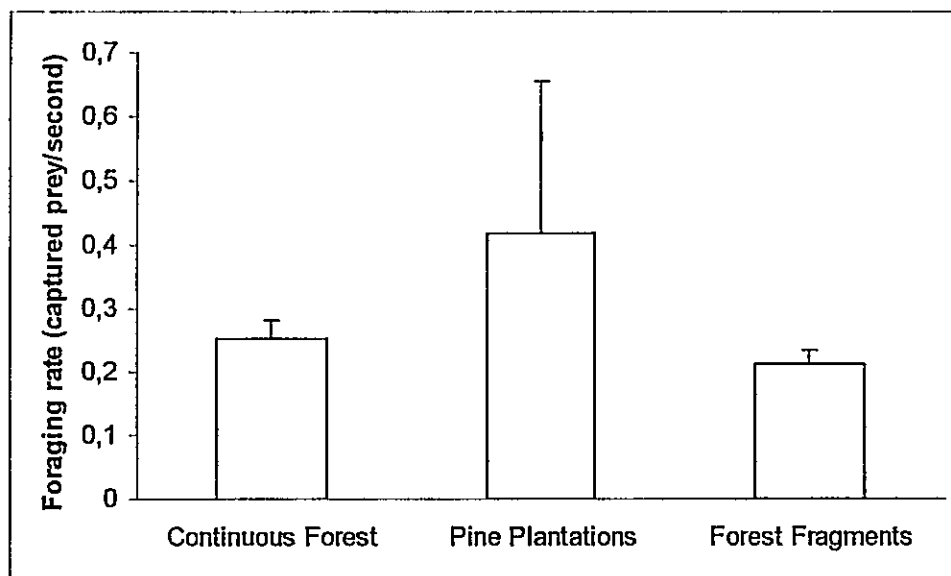


Figure 5. Foraging rate in continuous forest, pine plantations and forest fragments. Error bars indicate +1 SE.

Arthropod Assemblage

A total of 13 Orders of invertebrates were recorded (Table 2). The abundance of invertebrates was significantly different among habitats. At each habitat type,

Table 2. Invertebrate richness and abundance in forest fragments, pine plantations and Los Queules National Reserve. Means of individuals \pm SE.

	Forest fragments (N=18)		Pine Plantations (N=14)		Continuous Forest (N=25)	
	Canopy	Understory	Canopy	Understory	Canopy	Understory
Astigmata	0,00	0,13 \pm 0,13	0,93 \pm 0,39	0,00 \pm 0,00	0,00 \pm 0,00	0,00 \pm 0,00
Leptoptera	1,33 \pm 0,28	1,60 \pm 0,45	0,93 \pm 0,39	0,42 \pm 0,14	0,88 \pm 0,23	0,78 \pm 0,54
Larvae	0,56 \pm 0,24	0,73 \pm 0,39	0,93 \pm 0,39	0,37 \pm 0,14	0,28 \pm 0,17	0,06 \pm 0,05
Aranea	4,33 \pm 1,10	4,73 \pm 1,11	3,00 \pm 1,07	3,26 \pm 0,64	4,24 \pm 0,60	5,28 \pm 0,73
Blattidae	0,06 \pm 0,05	0,00	0,00	0,00	0,00	0,00
Coleoptera	5,22 \pm 1,13	5,27 \pm 1,28	3,29 \pm 1,02	5,53 \pm 1,89	4,96 \pm 0,59	4,06 \pm 0,52
Diptera	6,17 \pm 2,41	5,33 \pm 2,55	2,00 \pm 0,97	1,79 \pm 0,57	3,36 \pm 0,77	2,83 \pm 1,17
Hymenoptera	0,33 \pm 0,27	1,47 \pm 0,95	0,21 \pm 0,11	0,79 \pm 0,31	0,40 \pm 0,14	0,22 \pm 0,13
Formicidae	1,44 \pm 0,63	2,73 \pm 1,13	0,21 \pm 0,11	1,00 \pm 0,48	0,32 \pm 0,11	0,44 \pm 0,18
Homoptera	2,39 \pm 1,08	0,40 \pm 0,16	2,00 \pm 1,72	0,32 \pm 0,11	0,88 \pm 0,42	0,44 \pm 0,23
Orthoptera	0,17 \pm 0,12	0,33 \pm 0,18	0,71 \pm 0,33	0,11 \pm 0,07	0,44 \pm 0,15	0,33 \pm 0,16
Psocoptera	0,28 \pm 0,13	0,07 \pm 0,06	0,36 \pm 0,19	0,00 \pm 0,00	0,08 \pm 0,06	0,11 \pm 0,07
Trichoptera	0,28 \pm 0,10	0,07 \pm 0,06	0,00	0,00	0,08 \pm 0,06	0,61 \pm 0,54
TOTAL	22,11 \pm 3,92	22,47 \pm 5,03	13,71 \pm 4,47	13,21 \pm 2,54	15,84 \pm 1,39	15,06 \pm 1,88

the differences between canopy and understory were not statistically different (Table 3).

Table 3. Two-ways ANOVA for abundance of invertebrates.

Factor	SS	Df	MS	F	p
Habitat	1437,4	2	718,7	3,82	0,03
Canopy- Understory	4,29	1	4,29	0,02	0,08
Habitat * Canopy-Understory	9,25	2	4,63	0,03	0,98
Error	19376	103	188,1		

Arthropod abundance in forest fragments was 1.7 times larger than pine plantations (Tukey $P=0.03$). The difference in arthropod abundance between forest fragments and continuous forest was not statistically significant (Tukey $P=0.08$). Arthropod abundance in continuous forest and in pine plantations was not statistically different (Tukey $P=0.11$). The proportion of present lepidopteran larvae was not significantly different among habitats and canopy and understory ($\chi^2 = 0.12$ df= 2 $P=0.95$).

Predation Levels

Artificial caterpillars were preyed by birds and rodents. Birds were the main predator on caterpillars. The incidence of marks left by birds was 7.6 times larger than the number of larvae with marks left by rodents (t Student test $t=11.76$ $P<0.001$). Only one caterpillar was attacked by both, birds and rodents, so it was not considered in the analysis. As the larvae could be attacked as by birds as by rodents, we performed a two-way MANOVA (habitat effect and seedlings-adults of *A. chilensis* effect),

As a whole, predation of artificial caterpillars, was significantly different among habitats (Two-way MANOVA $W_{2,233}=6.91$ $P<0.01$) and between seedlings and trees of *A. chilensis* (Two-way MANOVA $W_{2,233}=4.46$ $P=0.01$) (Figure 6).

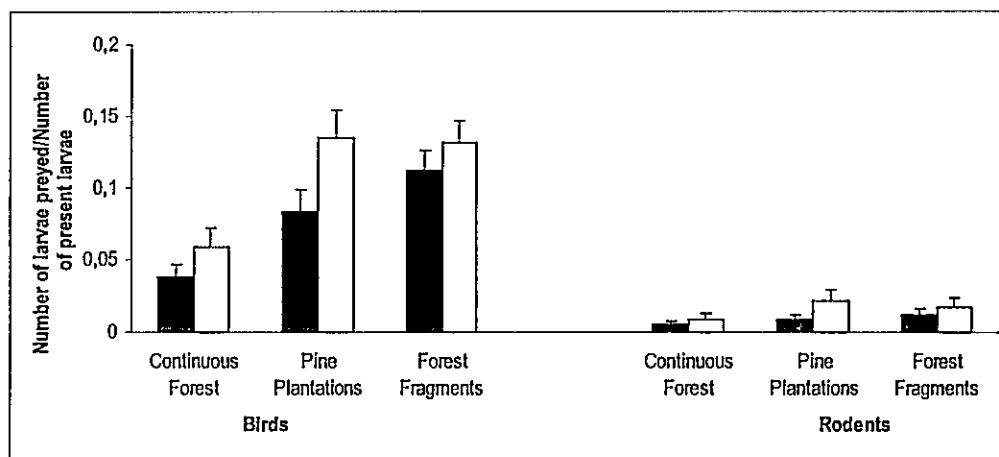


Figure 6. Predation level by birds and rodents in adults trees (black bars) and seedlings (white bars) of *A. chilensis* in continuous forest, forest fragments and pine plantations.

The proportion of caterpillars preyed upon by birds was 2.5 times larger in forest fragments than in continuous forest (Tukey $P < 0.001$). The predation level in pine plantations was two-fold larger than that of continuous forest (Tukey $P < 0.001$) and was not significantly different of predation levels in the forest fragments (Tukey $P = 0.70$) (Table 4).

Table 4. Two-way ANOVA for caterpillars preyed by birds.

Factor	SS	Df	MS	F	P
Habitat	0,239	2	0,12	13,1	0,001
Stage of plants (Seedlings/Adults)	0,056	1	0,056	6,06	0,01
Habitat * Stage of plants	0,013	2	0,006	0,7	0,50
Error	2,145	234	0,009		

Plasticine larvae located on seedlings of *A. chilensis* were preyed 1.4 times more frequent than adults trees (Tukey, $P = 0.013$). The predation level was not significant different in adult trees in forest fragments and pine plantations (Tukey, $P = 0.78$). However both variables were more than two times larger in relation to the predation level in the continuous forest (Tukey $P = 0.01$).

The proportion of caterpillars attacked by rodents was not significantly different among forest fragments, pine plantations and continuous forest (Two ways ANOVA $F_{2,234}=1.72$ $P=0.18$). The predation level by rodents in seedlings was marginally higher than predation level in adults trees (Two ways ANOVA $F_{1,234}= 3.41$ $P=0.06$).

DISCUSSION

Forest fragmentation modifies species interactions throughout the world, mainly through changes in the species richness and abundance. The increase in the abundance of native predators, such as avian insectivores, in forest fragments and plantations modifies the intensity of trophic interactions, intensifying insectivory and weakening herbivory in relation to continuous forest.

Forest fragmentation normally has been associated to the existence of forest patches where the richness and abundance of insectivores organisms decrease (Willson et al. 1994, Stouffer and Bjerregaard 1995, Stratford and Stouffer 1999, Serkerciouglu et al. 2002). In contrast, in this study both avian richness and abundance were higher in forest fragments and pine plantations than in continuous forest, and this trend was particularly important for insectivorous birds. The consistency of this pattern with studies conducted in Los Queules National Reserve (Vergara and Simonetti 2004) and others in Coastal Maulino forest (Estades and Temple 1999), show that the increase of birds, especially insectivorous ones, is a permanent effect of forest fragmentation. In contrast to studies that showed the decrease of insectivores, forest fragments are immersed in a coniferous forest matrix that is structurally similar to native forest, and that may have a very well developed understory. This fact is consistent with the hypothesis that indicates both, complexity of habitat and surrounding matrix characteristics, as principal variables to explain the abundance of insectivorous birds in forest fragments (Vergara 2001, Wethered and Lawes 2003).

Higher richness and abundance of birds, especially insectivorous, in forest fragments and pine plantations were translated in a higher number of avian foragers. Even though the numbers of avian foragers in forest fragments were significantly higher than the numbers in continuous forest, at the individual level birds did not change significantly their time budget or their foraging efficiency in relation to continuous forest, in contrast to studies that have shown that in fragmented landscapes, the foraging time is increased in relation to non fragmented landscapes because birds have to deal with a higher energetic cost of movement because gap-crossing in order to obtain preys (Hinsley 2000). It is assumed that forest fragments are immersed in an unsuitable matrix (i.e., gaps) that does not provide any food supply. In the study site, forest fragments are immersed in a coniferous forest matrix that offers an arthropod abundance similar to continuous forest. It suggests that the energetic cost derived of foraging trips among suitable patches, are prevented.

The arthropod abundance was significantly higher in forest fragments. However differences in the abundance of larvae across habitats were not statistically significant. The latter seems to disagree with the observations of Simonetti et al. (2004, *unpublished*) who found that the herbivory levels were higher in continuous forest than in forest fragments (whose plants are not different in palatability, appendix 1). This result might be a consequence of the direct and indirect effects of predators on preys. The direct effects should involve the predation intensity and its effects upon the population of preys through the season. The higher predation, exerted by a higher number of insectivorous birds in forest fragments decrease the larvae abundance in a higher magnitude than in continuous forest, such as at the end of the season, the abundance of larvae is lower in forest fragments than in continuous forest, explaining that the herbivory levels are lower in forest fragments. The indirect effects, in the other hand, should imply behavioral modification of preys as a response of predator presence (i.e., trait-mediated indirect interactions) (Abrams 1995). A higher density of insectivorous birds in forest fragments causes antipredator responses that include the reduction of the foraging effort

accordingly with the increment in the predators densities (Luttbeg and Schmitz 2000). Caterpillars, especially those preyed by birds have behaviors that tend to reduce the cues about this presence in order to avoid the predation (Heinrich and Collins 1983). Both, feeding and time spent remaining stationary are decreased in the presence of predators that imply the decrease of leaf damage (Rudgers et al. 2003). This kind of indirect effect might causes reduction in herbivore impact on plants (Schmitz et al. 2004).

The increase density of birds foraging in forest fragments agrees with the higher predation of artificial caterpillars observed in forest fragments and pine plantations in relation to continuous forest. This result is consistent with the lower herbivory levels observed in the same study site (Simonetti et al 2004 *unpublished*). After one growing season at the field, the magnitude of herbivory was significantly higher in continuous forest than in forest fragments for the three studied species: *Cryptocarya alba*, *Aristotelia chilensis* and *Persea lingue*. Furthermore, the relative growth rate in height of seedlings in continuous forest protected against insects was 30% more than not protected ones (Vega 2001, Simonetti et al. 2004, *unpublished*). This difference was significantly smaller in forest fragments. Likewise, in adult trees of *A. chilensis* the herbivory was significantly higher in continuous forest than in forest fragments, being up to three times higher in the first leaf cohort, but it had not effects over the growth rate (Vasquez 2004). Hence, the impact of the increase of insectivory in seedlings, had stronger consequences than in adults trees.

It has been frequently assumed that, the weakening of trophic interactions is a natural consequence of the habitat perturbations, because most of food webs have been disturbed by the removal of keystone predators (Micheli et al. 2001). However, the results of our study strongly support a strengthening of the insectivorous bird - caterpillar interactions triggered by the increment of predators as result of fragmentation process, a necessary condition to strongly suggest an intensification of food webs triggered by habitat fragmentation.

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Appendix 1. Have leaves of *Aristotelia chilensis* different palatability in different habitats?

Abiotic conditions might change leaf traits that determine plant palatability for herbivorous insects (Agrell et al. 2000). A decrease in soil humidity and an increment in air temperatures might change sclerophylly level (Montenegro et al. 1981), turning leaves less palatable (Larsson et al. 1986).

Habitat fragmentation generates changes in abiotic conditions between continuous forest and forest fragments (Davies et al. 2001). In coastal Maulino Forest, forest fragments have approximately 5% lower soil humidity than the continuous forest and tend to show higher daily maximum air temperatures (Henriquez 2002). Given that the continuous forest is wetter and colder than forest fragments, leaf quality (i.e., larger and thinner leaves) could be higher in continuous forest and consequently, it could account for the differences in herbivory between forest fragments and continuous forest

In order to rule out the effect of palatability as a cause of the differences of herbivory levels in Coastal Maulino forest, we conducted an experiment with *Aristotelia chilensis* leaves from continuous forest and forest fragments. If the quality of leaves is higher in continuous forest, the proportion of consumed leaves by caterpillars should be significantly higher in leaves from continuous forest than leaves from forest fragments.

Thirty tree caterpillars (*Ormiscodes* sp, Lepidoptera) were captured in pine plantations (*Pinus radiata*) in order to control the effect of familiarity with the leaves of either forest fragments or continuous forest. Caterpillars were maintained individually in Petri dishes and starved during one hour. Caterpillars were randomly allocated to one of two groups. The first group received 1 cm² of *A. chilensis* leaf from forest fragments. After 45 min, remnant leaves were collected and, after 15 min, the larvae were offered 1 cm² of *A. chilensis* leaves from continuous forest for another 45 min. Once the leaves were collected, the proportion consumed was measured. For the second group the protocol was the same, but it was inverted (i.e., first, leaves from continuous forest and then,

leaves from forest fragments). Only the caterpillars that ate in some treatment were considered.

Twenty nine caterpillars were considered in the analysis, 15 in the first group and 14 in the second group. The proportion of consumed leaf was not significantly different between forest fragments and continuous forest (Wilcoxon Test $Z=0.47$ $P=0.64$) (Figure 1).

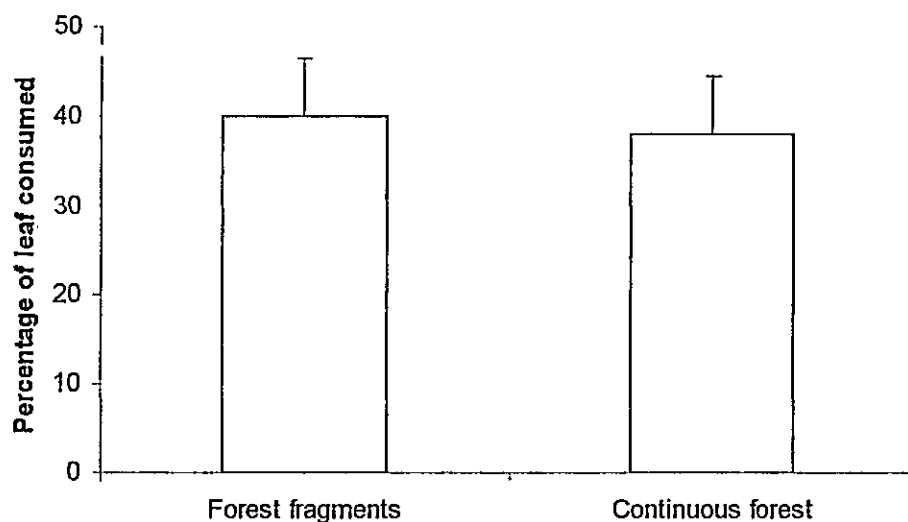


Figure 1. Leaf consumption (consumed proportion/1cm² leaf). Error bars indicate +1 SE.

Despite the existence of differences in abiotic conditions between forest fragments and continuous forest, the palatability of *A. chilensis* leaves did not differ between forest fragments and continuous forest.

Lower leaf quality, and therefore, lower palatability in forest fragments would explain the herbivory levels by limited resources, i.e., bottom-up effect (Price 2002). In Coastal Maulino forest however, the similarity in palatability strongly suggest that the differences in herbivory between forest fragments and continuous forest are not a consequence of bottom-up effects (Hairston et al. 1960).

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Appendix 2. Predation studies: Are artificial caterpillars a valid substitutes of natural caterpillar?

Several studies of predator-prey interactions have used artificial models of preys. Plasticine models have become popular in studies of predation because they not only allow the researcher to assess the relative rate of predation, but also they provide information on the identity of predators through the imprints left on the model surface (Ammon and Stacey 1997, Hannon and Cotterill 1998). Plasticine eggs have commonly used in nest predation studies. Lesser frequently, lepidopteran larvae have been used to study predation they sustain in different habitats and substrates (Roos & Pärt 2004, Thompson & Burhans 2004, Loiselle and Farji-Brener 2002). Studies of predation intensity have not tested whether artificial models receive the same predation levels than natural caterpillars and if these models are able to detect differences in predation intensity produced by different densities of predators.

In order to assess the similarity in predation levels between natural and artificial caterpillars and the difference in predation generated by two densities of predators, we conducted a laboratory experiment. If the natural and artificial caterpillars are perceived in the same way by birds, we expected that the number of caterpillars with beak marks should not be different between natural and artificial caterpillars. In the other hand, if two different densities of predators cause different predators, a higher bird density should be correlated with a higher number of attacked caterpillars.

In Coastal Maulino forest, insectivorous birds are two-fold in forest fragments than in continuous forest (Vergara & Simonetti 2004). Previously to develop a field experiment in order to assess the predation intensity between habitats, we performed a laboratory experiment carried out in the Santiago Metropolitan Zoo during March 2004, in a cage (3X3X2 m) with six species of Chilean birds (*Curaeus curaeus*, *Nothoprocta perdicaria*, *Sicalis luteiventris*, *Turdus falckandii*, *Sturnella loica*, *Diuca diuca*). All of species occur in Coastal Maulino zone (Estades & Temple 1999, Vergara & Simonetti 2004).

At 8:00 AM, we randomly placed (over shrubs and floor) 15 artificial caterpillars and 15 natural caterpillars (*Ormiscodes* sp. Lepidoptera) in the cage exposed to a high bird density (N=24). A larva was considered as preyed when it showed signs of having been attacked (beak marks). After 24 hours we recorded the number of larvae attacked.

Two days later, we carried out the same experiment with a low bird density (N=12 individuals). Each experiment (i.e., high and low density of birds) was replicated after 48 hrs.

Artificial caterpillars were equally preyed upon than natural caterpillars ($H_1 = 0.09$ $P=0.78$). High density of birds produced higher number of larvae attacked ($H_1=4.86$ $P=0.03$) (Figure 1).

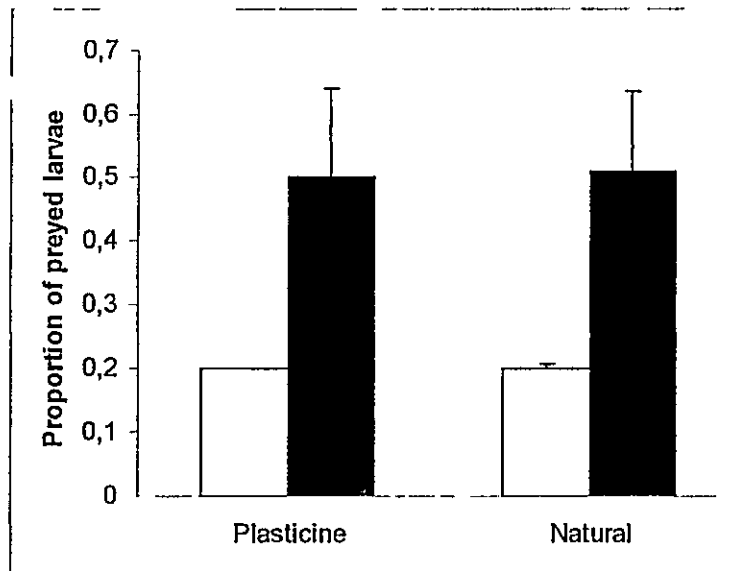


Figure 1. Proportion of natural and artificial caterpillars preyed by low bird density (white bars) and high bird density (black bars). Error bars indicate +1 SD.

This experiment shows that artificial caterpillars are a valid method to provide estimates of relative predation rates across habitats and predator densities. Plasticine eggs used for nest predation studies have demonstrated that the rate of predation is not reliable estimates of the predation pressure

(Zanette 2001, Burke et al. 2003). In contrast, we found that in captivity, plasticine larvae may be representative of predation upon lepidopteran larvae and may be a useful tool to detect differences in predation levels generated by different densities of predators.

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