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Strengthened insectivory in a temperate fragmented forest

Abstract Habitat fragmentation modifies ecological patterns and processes through changes in species richness and abundance. In the coastal Maulino forest, central Chile, both species richness and abundance of insectivorous birds increases in forest fragments compared to continuous forest. Through a field experiment, we examined larvae predation in fragmented forests. Higher richness and abundance of birds foraging at forest fragments translated into more insect larvae preyed upon in forest fragments than in continuous forest. The assessed level of insectivory in forest fragments agrees with lower herbivory levels in forest fragments. This pattern strongly suggests the strengthening of food interactions web in forest fragments of coastal Maulino forest.

Keywords Avian foraging intensity · Food web · Habitat perturbation · Insectivorous birds · Larvae predation

Introduction

Habitat fragmentation changes the richness and abundance of predators such as insectivorous birds

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(Sekercioglu et al. 2004). Small fragments in tropical and temperate forests usually hold significantly lower richness and abundance of insectivorous birds than larger forest tracts (Willson et al. 1994; Sekercioglu et al. 2002). Such changes are expected to trigger trophic cascading effects (Schmitz et al. 2000). Given that insectivorous birds are capable of significantly reducing the populations of the herbivorous insects they prey upon, birds might indirectly increase plant fitness by decreasing herbivory (Marquis and Whelan 1994; Van Bael et al. 2003). Regarding forest fragmentation, a reduction of insectivores' abundance in forest remnants is assumed to release their herbivorous prey from predation pressure, increasing their number and unleashing herbivory (e.g., Terborgh et al. 2001).

Despite widespread evidence of changes in the abundance of insectivorous birds associated with forest fragmentation, no experimental studies have empirically evaluated the consequences of such changes on insectivory, a requirement for the occurrence of cascading effects (see Debinski and Holt 2000). Here, we report an experimental study that addresses the effects of changes in density of insectivorous predators triggered by forest fragmentation upon insect mortality.

In Chile, the coastal Maulino Forest has undergone intensive deforestation and fragmentation by agricultural fields and forestry plantations (Lara et al. 1996). Currently, a few patches of continuous forest remain in a suite of small fragments immersed in an extensive matrix of commercial pine (*Pinus radiata*) plantations (Grez et al. 1997). Here, avian species richness and abundance, particularly insectivorous species, is higher in forest fragments and pine plantations than in continuous forest (Vergara and Simonetti 2004; see also Estades and Temple 1999). Interestingly, in these forest remnants, herbivory upon seedlings and adult trees of *Aristotelia chilensis* like other plant species, is lower in forest fragments (Vásquez 2004; J.A. Simonetti et al., unpublished data), as would be expected if predators were impinging upon lower trophic levels (Schmitz et al. 2000). The higher abundance of avian

predators and lower herbivory in forest fragments suggests that insectivory should be higher in forest fragments. In this study, we experimentally examined the relationship between avian abundance and insectivory intensity on herbivorous larvae in seedlings and adult trees of *A. chilensis*, a common and widespread tree species in the coastal Maulino Forest and pine plantations. If higher avian abundance is correlated with a strengthened insectivory in forest fragments and pine plantations, insectivory should be higher than in continuous forest.

Materials and methods

The study was carried out at Los Queules National Reserve, a forest tract of 145 ha immersed in 600 ha of native forest of native Coastal Maulino Forest (35°59′S, 72°41′W), acting as a continuous forest, the surrounding pine (*Pinus radiata*) plantations and ten forest fragments, ranging from 0.5 to 5 ha. Dominant tree species are *Nothofagus glauca* and *N. obliqua*, *Gevuina avellana, Aextoxicon punctatum, Cryptocarya alba* and *A. chilensis* (Bustamante et al. 2004). Pine plantations hold a well developed understory composed of *A. chilensis, P. boldus*, among other native species.

Field work was conducted during the austral spring of 2003 (mid-September to December), the reproductive season of most birds in the area. At this time, insect larvae eclosion and higher foliar development also occur (Fuentes et al. 1977). The synchrony among these three trophic levels could intensify insectivory, because even bird species that are largely granivorous prey upon insects to feed their nestlings during the breeding season (Stutchbury and Morton 2001).

Avian richness and abundance were estimated using circular sampling plots of 50-m radius (Buckland et al. 1993). Fifty plots were distributed within the continuous forest ($n = 20$), forest fragments ($n = 15$, the largest five fragments with two plots and the remaining five with one plot) and pine plantations ($n = 15$). Sampling points were randomly distributed within each habitat, but if a plot partially or fully fell on a habitat edge, it was displaced until the census plot fell fully within the habitat to be sampled. Each point was visited between 0800 and 1200 hours at least 3 times during the season. During each visit, two separate counts of 5 min were conducted (i.e., six counts per sample point). All observed or heard birds were recorded. Species richness was assessed as the total number of species registered in each sample plot during all counts, and the abundance was assessed as the average number of individuals recorded in each count per plot (Vergara and Simonetti 2004). Differences among avian richness and abundance across habitats were assessed through one-way analysis of variance as data meet normality and homoscedasticity requirements. Tukey multiple comparisons (Honest Significant Differences) for unequal sample size were used as post hoc tests.

Avian foraging intensity was assessed through direct observation of insectivorous birds in circular plots of 30-m radius during 5-min periods. Each plot was sampled 6 times during the morning, and 3 times during the afternoon and evening in continuous forest ($n = 240$), pine plantations ($n = 180$) and forest fragments ($n = 180$). Only 2.2% out of 3,000 min allocated to observing birds yielded observations of foraging birds. The number of periods that produced observations of foraging birds were not significantly different between habitats (ANOVA $F_{2,151} = 0.3$, $P = 0.74$).

Avian foraging intensity was measured at both population and individual level. At the individual level, foraging intensity was assessed tracking an individual insectivorous bird for up to 5-min recording: (1) prey capture rate: the numbers of prey captured per time (seconds), and (2) foraging time: time spent searching for, capturing and consuming food relative to total sampling time. At the population level, foraging intensity was estimated as the number of birds per plot foraging on insects in 5-min periods, that is, birds that engaged at least once in foraging activities during the recording time. At the individual level, differences in prey capture rate and foraging time across habitats were assessed with a non-parametric test, Kruskal–Wallis, as data did not meet the requirement for a parametric test. However, at the population level, data did meet the normality and homoscedasticity assumptions, hence differences were analyzed using an ANOVA test.

The intensity of insectivory upon herbivorous larvae was experimentally assessed as the frequency of birds' attacks upon insect larvae. Larvae were plasticine models mimicking *Ormiscodes cinnamomea* (Feisthamel) larvae naturally occurring in the study area. Artificial larvae are valid subrogate of natural ones. Under indoor conditions, birds preyed upon artificial and real larvae at the same rate. These models do not provide an estimation of natural predation rates but they represent an estimate of relative measures of predation across treatments (Supplementary Material; see also Loiselle and Farji-Brener 2002).

To assess differences in the relative intensity of avian insectivory among habitats (i.e., forest fragments, pine plantations and continuous forest) and between seedling and adult trees of *A. chilensis*, we placed groups of artificial caterpillars in 40 randomly selected locations per habitat type ($n = 120$). At each location, we set two groups of 15 artificial caterpillars each, one group on an adult tree of *A. chilensis* (approximately 2 m above ground) and the other on a nearby conspecific seedling (approximately 0.3 m above ground). Larvae were attached to a branch using coiled wire. This aggregation of caterpillars simulated natural groups of *Ormiscodes* larvae clumped on the same branch as they naturally occur (Artigas 1994). The sampling unit was each group of larvae. After 24 h, we recorded the proportion of artificial caterpillars marked by a predator. Differences between the number of

larvae attacked by rodents and birds were assessed through Student t-test. Because larvae could be attacked by birds as well as by rodents, differences in the relative intensity of insectivory among habitats were analyzed through two-way MANOVA, with habitat and the age of the plant (i.e., seedling or adult) as effects. To locate the exact source of heterogeneity found by the MANOVA, univariate ANOVAS were performed. Data met requirements for a parametric test. Tukey multiple comparisons (Honest Significant Differences) for equal sample size was used as post-hoc tests. All statistical analysis were performed using STATISTICA 6.0.

Results

Bird assemblage

A total of 26 bird species was recorded (Table 1). Species richness was 1.6 times greater in forest fragments and pine plantations than in continuous forest (ANOVA $F_{2,47} = 21.26$, $P < 0.001$) (Fig. 1). Species richness in forest fragments and pine plantations were not significantly different (Tukey HSD $P = 0.72$), but both had almost twice the species richness of the continuous forest (Tukey HSD $P < 0.001$). Out of the 26

species, 17 of them (65%) were primarily insectivorous. Insectivore richness was 1.5 times larger in forest fragments and pine plantations than in the continuous forest (ANOVA $F_{2,47} = 14.47$, $P < 0.001$) (Tukey HSD $P < 0.01$). Forest fragments and pine plantations did not differ in the richness of insectivorous birds (Tukey HSD $P = 0.6$).

Total bird abundance was significantly higher in forest fragments and pine plantations than in the continuous forest (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 HSD $P = 0.07$). Avian abundance in forest fragments and pine plantations was 2.5 times higher than in continuous forest (Tukey HSD $P < 0.001$, at each comparison). Out of 23 species that were statistically assessed, 7 of them (39%) increased their abundance in forest fragments and pine plantations in relation to continuous forest. The 16 remaining species showed no significant differences between habitats.

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 HSD $P < 0.001$). It was marginally lower in pines than in forest fragments (Tukey HSD $P = 0.07$), but significantly higher than continuous forest (Tukey HSD $P < 0.001$) (Fig. 2).

Table 1 Avian abundance in forest fragments, pine plantations and Los Queules National Reserve (birds/plot/census)

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

Different letters indicate significant differences
Symbols for diet are: *C* carnivores, *F* frugivores, *G* granivores, *H* herbivores, *I* insectivores, *N* nectarivores
Secondary diet is in parenthesis (Estades 1997)
*Species recorded once in census and not statistically compared

Fig. 1 Total avian richness (*black bars*) and insectivore avian richness (*white bars*) in continuous forest (Los Queules National Reserve), pine plantations and forest fragments. *Error bars* indicate +1SE
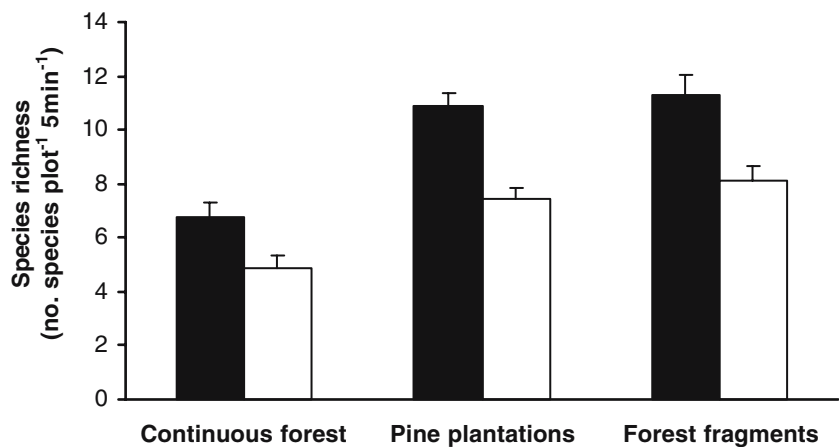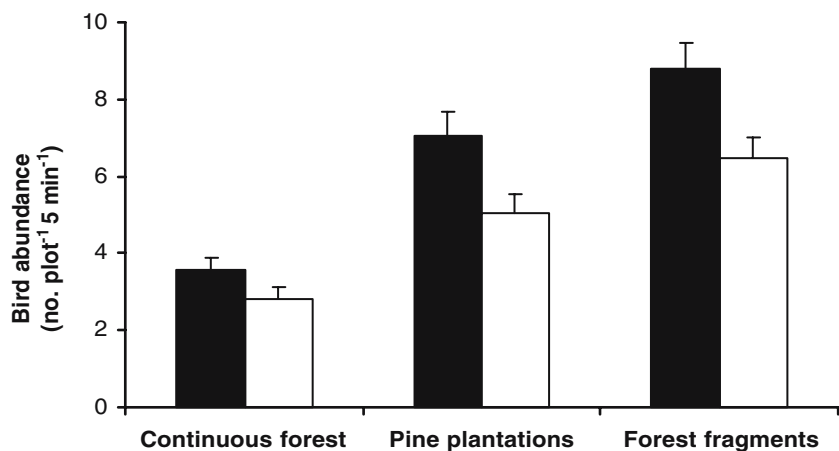

Fig. 2 Total abundance of birds (*black bars*) and insectivore bird abundance (*white bars*) in continuous forest (Los Queules National Reserve), pine plantations and forest fragments. *Error bars* indicate +1SE

Avian foraging intensity

The number of birds engaged in foraging activities (searching, handling and consuming prey) was 2.3 times higher in forest fragments than in continuous forest (ANOVA $F_{2,47} = 10.33$, $P < 0.001$; Tukey HSD $P < 0.001$) and 1.7 times higher than in pine plantations (Tukey HSD $P < 0.001$) (Table 2). This variable was not significantly different between the continuous forest and pine plantations (Tukey HSD $P = 0.75$). In 137.2 min of observations, 153 different insectivorous birds were observed, 49 individuals in the continuous forest (40.2 min.), 42 in pine plantations (40.1 min) and 62 in forest fragments (57.2 min). *Aphrastura spinicauda* and *Elaenia albiceps* accounted for over 73% of individuals observed at any site. Foraging time spent by individuals did not differ among forest fragments, pine plantations and continuous forest (Kruskal–Wallis $H_{2,153} = 5.01$, $P = 0.08$; Table 2). Regarding insectivorous birds, during 67.4 min of observations of foraging behavior, 126 different birds were observed, 39 in continuous forest 18.5 min), 34 in pine plantations (20.4 min) and 53 in forest fragments (28.5 min). Individual prey capture rate was not significantly different among forest fragments, pine plantations and continuous forest (Kruskal–Wallis $H_{2,126} = 1.58$, $P = 0.45$; Table 2).

Table 2 Avian foraging in forest fragments, pine plantations and Los Queules National Reserve

Variable	Continuous forest Mean ± SE	Pine matrix Mean ± SE	Forest fragments Mean ± SE
Number of bird foraging (average number of birds foraging/sample plot/5 min^{-1})	0.76 ± 0.10	0.90 ± 0.16	1.60 ± 0.16
Foraging time (time spent foraging/ total of time/bird)	64.39 ± 6.29	81.54 ± 5.80	78.42 ± 4.84
Prey capture rate insectivorous (captured prey/min/bird)	0.25 ± 0.03	0.42 ± 0.24	0.21 ± 0.02

Insectivory levels

Artificial caterpillars were preyed upon by birds and rodents. There was no evidence of larvae being attacked by arthropods or lizards. The frequency of marks left by birds was 7.6 times greater than the number of larvae marked by rodents (t-test, $t = 11.76$, $P < 0.001$). Only one caterpillar was attacked by both, birds and rodents.

Predation of artificial caterpillars was significantly different among habitats (Two-way MANOVA Wilks lambda $W_{2,233} = 6.91$, $P < 0.01$) and between seedlings and trees of *A. chilensis* (two-way MANOVA Wilks lambda $W_{2,233} = 4.46$, $P < 0.01$). The proportion of caterpillars preyed upon by birds was 2.5 times greater in forest fragments than in continuous forest (Fig. 3; two-way ANOVA $F_{2,234} = 13.1$, $P < 0.01$, Tukey HSD $P < 0.001$). The predation level in pine plantations was twice that in continuous forest (Tukey HSD $P < 0.001$) and was not significantly different from predation levels in the forest fragments (Tukey HSD $P = 0.70$) (Table 3). Plasticine larvae located on seedlings of *A. chilensis* were preyed on 1.4 times more frequently than those placed on adult trees (Two way ANOVA $F_{1,234} = 6.06$, $P < 0.05$, Tukey HSD $P < 0.05$). Predation level was not significant different in adult trees in forest fragments and pine plantations (Tukey HSD $P = 0.78$). However, both variables were more than twice those for predation in the continuous forest (Tukey HSD $P < 0.05$).

Discussion

Habitat fragmentation modifies species interactions through changes in the species richness and abundance. However, most habitat fragmentation studies have focused on patterns rather the analysis of the processes coupled to changes in predator abundance (Debinski and Holt 2000; Fahrig 2003). In particular, this is the first experimental research to address the effects of the increase in the abundance of native avian insectivores on the intensity of insectivory as a consequence of habitat perturbation.

Reductions in richness and abundance of insectivorous organisms have usually been associated with forest fragmentation (Stouffer and Bierregaard 1995; Sekercioglu et al. 2002). In contrast, in the Coastal Maulino forest, both avian richness and abundance are higher in forest fragments and pine plantations than in continuous forest, particularly among insectivorous birds. These increases are widespread at the Coastal Maulino forest through time. Sampling carried out during 2000 offer the same scenario, suggesting that the increase of birds, especially insectivorous ones, is a permanent effect of forest fragmentation (Estades and Temple 1999; Vergara and Simonetti 2004). Such an increase can be accounted for by the higher structural complexity of forest fragments, which hold a dense understory, aided by surrounding coniferous forest which might be a source of foraging resources (Vergara and Simonetti 2004; see also Grez et al. 2003).

Higher richness and abundance of birds in forest fragments and pine plantations, especially insectivorous ones, did translate into higher levels of insectivory in forest fragments and pine plantations relative to continuous forest. This increase is accounted for by the higher number of avian foragers and not by changes in the birds' behavior. At the individual level, birds allocated the same amount of time to foraging regardless of habitat. Furthermore, their prey capture efficiency is similar across habitat. Therefore, the increase in insectivory is due to a "mass effect" of the increased bird abundance. On the other hand, the higher predation

Fig. 3 Bird predation upon larvae in adults (*black bars*) and seedlings (*white bars*) of *A. chilensis* in continuous forest (Los Queules National Reserve), pine plantations and forest fragments
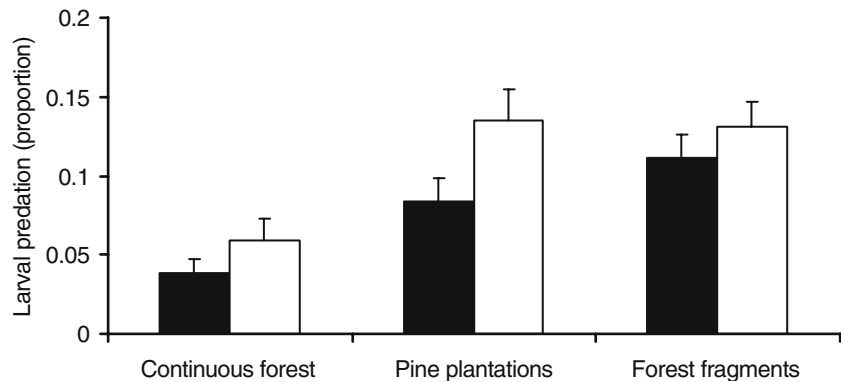
Table 3 Two-way ANOVA for caterpillars preyed by birds

Factor	SS	Df	MS	F	P
Habitat	0.239	2	0.12	13.1	0.001
Age	0.056	1	0.056	6.06	0.01
Interaction	0.013	2	0.006	0.7	0.50
Error	2.145	234	0.009		

rates on caterpillars in forest fragments agrees with the lower herbivory levels sustained by seedlings and adult trees in forest fragments compared to continuous forest (Vega 2001; Vasquez 2004; J.A. Simonetti et al., unpublished data). The increased insectivory of seedlings might be explained by the differences in abundance of ground foragers compared with canopy foragers among the different habitats. The abundance of ground foragers is 2.5 times higher in forest fragments and pine plantation than continuous forest, while the abundance of canopy foragers is 2.0 times higher in forest fragments and pine plantation than continuous forest. This difference might account for the differential increase among habitats and seedlings. Therefore, forest fragmentation seems to be triggering trophic cascading effects at the Maulino forest. Changing top consumers might benefit plants by altering the abundance or behavior of herbivores (cf. Schmitz et al. 2000).

The increase in insectivory in the Maulino forest fragments parallels increases in granivory and nest predation, changes accounted for by increased abundance of consumers like small mammals which, like birds, might be responding to the habitat heterogeneity in forest fragments (Donoso et al. 2003; Vergara and Simonetti 2003). The strengthening of the predator–prey interactions triggered by increased consumer abundance strongly suggests intensified food webs by habitat fragmentation. Frequently, though, it is assumed that habitat perturbations like forest fragmentation implies the weakening of trophic interactions (Micheli et al. 2001). However, our results emphasize the wide range of responses to habitat fragmentation and the need for experimental studies focused on species interactions and cascade effects through the community.

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