Effects of forest fragmentation on the granivory of differently sized seeds

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Abstract

The Maulino forest is a unique temperate ecosystem restricted to a small range of the coast of central Chile. This forest harbors many endemic species, and is threatened due to intensive deforestation and fragmentation. Currently the Maulino forest is composed of a suite of small fragments scattered in a landscape dominated by exotic plantations. The fragmentation of the Maulino forest has resulted in a higher abundance of granivores in small forest fragments compared with continuous forest. In order to determine if fragmentation-induced changes in granivore abundance affects the granivory of different size seeds, we experimentally assessed seed predation of a large-seeded species [*Nothofagus glauca* (Phil.) Krasser] and a small-seeded species [*Nothofagus obliqua* (Mirbel) Oersted] in the edges and interior of one continuous (large) forest and three small fragments (∼3 ha) surrounded by plantations of the exotic tree *Pinus radiata*. To determine what kind of granivores are preying upon seeds, seeds of both species were excluded from and exposed to large and small granivores. Granivory was higher in small fragments than in continuous forest, higher in the edges than in the forest interior, and higher upon large than on small seeds. Rodents, which were more abundant in forest fragments, were the main consumers. Thus, fragmentation indeed affects granivory increasing the consumption of seeds by predators inhabiting the Maulino forest remnants or coming from the matrix. This change may affect the future structure of the tree community in forest fragments.

Keywords: Forest fragmentation; Maulino forest; Granivory; *Nothofagus*; Conservation

1. Introduction

Habitat fragmentation may modify seed predation. The reduction and division of a continuous habitat into small fragments, including an increase of edges may modify the composition, abundance and distribution of granivores, and therefore, granivory (Sork, 1987; Terborgh, 1992; Terborgh and Wright, 1994; Asquith et al., 1997; Harrington et al., 1997). In tropical forests of Bolivia and Australia, granivory is lower in fragments than in continuous forest (Harrington et al., 1997; Rico, 2000), but in Mediterranean forests of Spain, seed predation is higher in forest fragments (Santos and Tellería, 1994, 1997) similar to small tropical islands as compared with mainland Panama (Sork, 1987; Asquith et al., 1997).

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Granivory rates also vary at forest edges. In tropical rainforests of Mexico and Belize and southern temperate forests of Chile, seed predation is lower near edges (Burkey, 1993; Díaz et al., 1999), whereas the opposite occurs in coniferous forests of western North American and Chilean shrublands (Bresciano et al., 1999; Jules and Rathcke, 1999).

Granivores such as mammals, birds, and insects are strongly affected by habitat fragmentation (e.g. Andrén, 1994; Turner, 1996; Didham et al., 1996; Gibbs and Stanton, 2001). For example, in temperate and tropical forests of Spain and Brazil, the abundance of rodents increases in small fragments and in forest edges compared with large fragments and the forest interior (Laurance, 1994; Malcolm, 1997; Santos and Tellería, 1994; 1997; García et al., 1998). Similarly, some bird species may be more abundant in small forest patches than in large ones (Andrén, 1994). Such an increase in abundance of consumers might account for the higher granivory rates in these forest fragments (e.g. Santos and Tellería, 1994). However, the abundance and diversity of rodents may also decrease with forest fragmentation (Turner, 1996; Harrington et al., 1997), which in turn could explain reduced granivory rates in some forest fragments. Birds might also decrease with fragmentation. In Australian rainforests, granivorous cassowaries occur in continuous forest or large fragments but are absent from small fragments (Harrington et al., 1997). Therefore, the effect upon seed predation is related to changes in the assemblage of granivores brought about by forest fragmentation.

The effect of forest fragmentation on granivory may also depend on seed size. Large seeds may be less preyed upon in forest fragments because their main consumers, large-bodied granivores, often are more readily depressed in forest fragments than are small-bodied granivores (Terborgh, 1992). Due to morphofunctional constraints (i.e. bill size), small granivorous birds, such as passerines, prey largely upon small seeds. Rodents might face fewer restrictions since they gnaw seeds, although their consumption could be limited by the hardness of the cover of large seeds (Brown and Ojeda, 1987; Baskin and Baskin, 1998; Terborgh, 1992; Alcántara et al., 2000). Therefore, forest fragmentation might result in different effects upon seed survival and recruitment of plant species depending on their seed size. However, such an effect has been rarely addressed (e.g. Díaz et al., 1999) despite the fact that size-biased consumption may have profound consequences on the community composition, structure, and dynamics of the remnant vegetation (Terborgh, 1992).

As in other regions of the world, temperate forests in Chile have been deforested and highly fragmented (Lara et al., 1995). Such habitat changes affect the diversity and abundance of native granivores, such as birds and small mammals (Muñoz and Murúa, 1989; Willson et al., 1994; Cornelius et al., 2000; Kelt, 2000; 2001). In the Maulino forest of central Chile, native granivores are more abundant in forest fragments than in the continuous forest (Fig. 1). Therefore, tree recruitment in these forest remnants might be altered depending upon the changes in seed mortality triggered by forest fragmentation via changes in the granivorous guild.

Forest fragments are of conservation concern, as they might serve as refuges for many tree species on the brink of extinction (Turner and Corlett, 1996). Their conservation value, however, might be hampered if changes in granivory alter the recruitment pattern of the remaining forests. Therefore, assessing the impact of forest fragmentation upon granivory rates is required to properly manage biodiversity in fragmented forests.

To test if forest fragmentation differentially affects the granivory of seeds of different sizes, and to assess what kind of granivores are preying upon those seeds in edge vs. interior of continuous and fragmented forests, we experimentally evaluated predation rates of seeds of two congeneric tree species from the Maulino forest in central Chile: *Nothofagus glauca*, a large-seeded species, and *Nothofagus obliqua*, a small-seeded species. Because the abundance of granivores is higher in Maulino forest fragments, we expected that: (1) granivory should be higher in fragments than in continuous forest; and (2) predation of large seeds should be higher in small fragments. Furthermore, we examined if granivory differed between edges and the interior of forests.

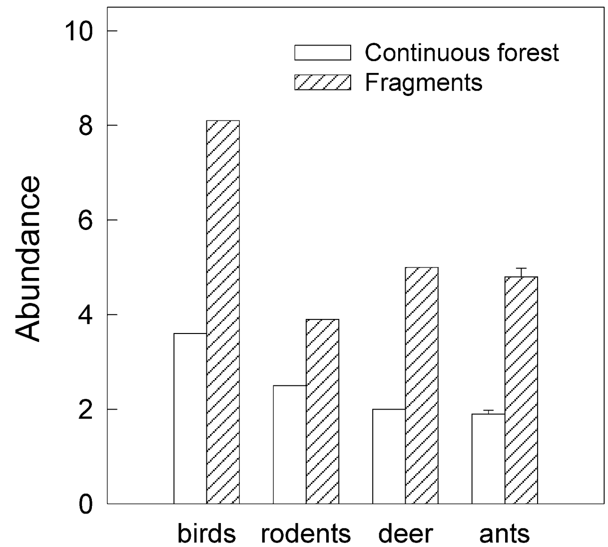

Fig. 1. Abundance of native granivores in the Maulino forests of central Chile. Figures are the number of birds/ha × 10 (Vergara, 2001), trapping success (individuals/trap-nights) for rodents (Saavedra and Simonetti, submitted for publication), number of records for deer (track/year), and abundance (individuals/pitfall trap × 10) for ants (unpublished) in forest fragments and continuous forest. All differences in abundance are statistically significant.

2. Methods

2.1. Study site

The Maulino forest is a temperate ecosystem distributed along the coast between 35°55′ S and 37°20′ S, ranging from 100 and 900 masl (Fig. 2A). This forest harbors a group of endemic tree species, including *Gomortega keule* (Mol.) Baillon, the single representative of the primitive family Gomortegaceae. The dominant species is *Nothofagus glauca* (Phil.) Krasser (Fagaceae), which coexists with many endangered endemic species such as *Nothofagus alessandrii* Esp. (Fagaceae), *Pitavia punctata* (R. et P.) Mol. (Rutaceae), and *G. keule*. Since the end of nineteenth century, the Maulino forest has been intensively deforested and fragmented, initially due to increased fuelwood production and cultivation, and more recently, due to its

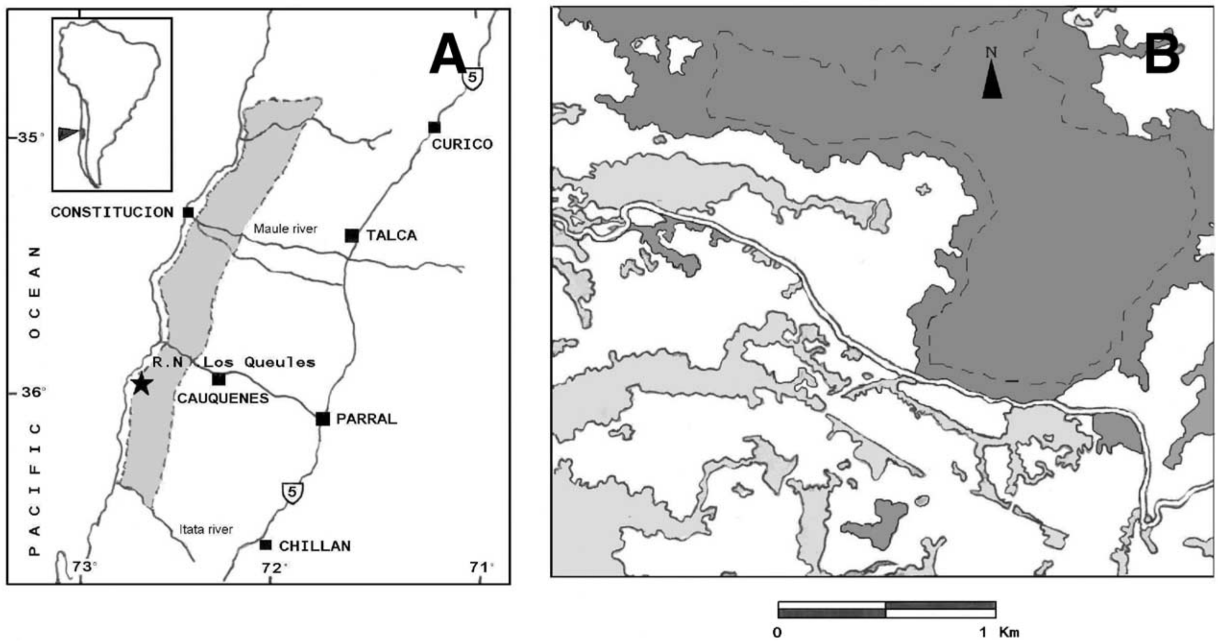

Fig. 2. (A) Geographical distribution of the Maulino Forest (grey) and location of Reserva Nacional Los Queules (modified from San Martín and Donoso, 1996). (B) Study site showing the continuous forest and adjacent fragments used in the experiments (dark gray areas). Other patches of native forest are shown in light gray, and matrix of pine plantations are in white. Dashed line indicates the limits of the Reserva.

replacement by *Pinus radiata* D. Don (Pinaceae) plantations, with the expansion of timber production and exports. Currently, a series of small fragments is scattered in the landscape surrounded by large areas with *P. radiata* (San Martín and Donoso, 1996; Grez et al., 1998; Bustamante and Castor, 1998).

2.2. Study species

Nothofagus glauca and *N. obliqua* are two caducifolious broad-leaved tree species of the Maulino forest. Their fruits contain three nuts and ripen between January and March. Each nut contains only one seed. *Nothofagus glauca* has seeds about 18 mm long weighing 526 mg, whereas *N. obliqua* seeds are 6 mm long and weigh 9.2 mg (Rodríguez et al., 1983; Donoso, 1994). Seeds of *N. glauca* and *N. obliqua* in our study site occur at a density of 4.7 ± 1.7 and 29.7 ± 8.5 per 1000 cm^3 of soil, respectively. They are preyed upon by rodents, which may prefer them over other tree seeds (e.g. Murúa et al., 1980; Rau et al., 1981; Donoso, 1992). As these two species are congeneric and their seeds share many structural similarities, we are able to identify more appropriately the effect of seed size on seed consumption than when comparing seeds from totally different families or life forms.

2.3. Experimental design

Granivory rates were assessed with a series of natural and field experiments. We utilized available fragments (a "natural" experiment) in which we set out seeds of *N. glauca* and *N. obliqua* to identify the effect of forest fragmentation, edges, and the kind of granivore on seed consumption in the Maulino forest. This was performed through the use of exclosures as described later.

To evaluate the effect of fragmentation on the granivory of *N. glauca* and *N. obliqua*, seeds were placed in continuous forest and in adjacent forest fragments. The continuous forest was located in the Reserva Nacional Los Queules (35°59′ S, 72°41′ W). This reserve is one of only two areas allocated to preserve the Maulino forest. It covers 147 ha but is part of a larger tract of continuous privately owned forests, making up a single area of at least 600 ha of Maulino forest, one of the largest extant tracts (Fig. 2B). Experiments also were performed in three small fragments adjacent to the continuous forest. Fragments were 3.4, 3.0, and 2.3 ha, separated from each other by at least 1 km. Both the continuous forest and fragments were surrounded by 20 year old *P. radiata* plantations (Fig. 2B).

To evaluate edge effects, seeds were placed in the border and interior of fragments and the continuous forest. Borders corresponded to the edge of the forest adjacent to a pine plantation. We considered edges to be 10 m wide, as defined by the presence of shrubby vegetation of native early successional species such as *Aristotelia chilensis* and exotic invasive species like *Teline monspessulana*. In fragments, the interior was considered the geometric center identified through GPS. Centers were located from 17 to 65 m of the closest edge, (mean: 38.6 m), whereas in the continuous forest, the interior was considered an area located at least 100 m from the closest edge (see Díaz et al., 1999). A wealth of published empirical evidence, as summarized by Murcia (1995) and Laurance et al. (2000) suggests that edge effects tend to disappear 50 or 100 m deep into the forest. In Southern Chile, nest predation by rodents and birds is lower in forest interior ($\geqslant$50 m) than on forest edges (15 m) (Wilson et al., 2001).

To evaluate if granivory was caused by large (>1 kg) or small (<500 g) granivores, seeds were placed exposed (i.e. control), and also in exclosures preventing access by vertebrates. Exclosures consisted of a 50 cm high cone of metallic mesh 30 cm in diameter (bottom) with 2.5-cm openings, closed at the top. These impermeable exclosures excluded both large and small vertebrates. To exclude large granivores only, some exclosures were semipermeable, the same size as impermeable ones but with two perforations 8 cm high and 10 cm wide at the base of the cones, allowing the entrance of small mammals and ground-dwelling birds. Insects had access to seeds in all conditions. Juvenile rodents might have entered into both types of exclosures.

In October 1998, 60 experimental stations were established in the continuous forest, 30 in the interior and 30 in the edge, each station separated by at least 10 m. Half of these stations included one impermeable exclosure and one control, and half were composed of one semipermeable exclosure and its control. At every fragment, we set 20 experimental stations, 10 in the interior and 10 in the edge, keeping the same distribution as in the continuous forest. Overall, 120 experimental stations were installed.

Ten marked seeds of each focal tree species were placed in every exclosure and control. We used each group of seeds as a sampling unit ($n=474$; we eliminated three exclusions—six groups of seeds—from the analysis as they were not firmly attached to the ground), assuming that the probability of seed predation was independent for each group. In fact, the number of large and small seeds predated was not correlated in any given treatment ($r_s<0.45$, $P>0.09$). Remaining seeds were counted after 4 days and periodically later on at 39, 79, 102, and 136 days after setting (March 1999). All seeds that disappeared from a radius of 30 cm of the station, and those with consumption signs (e.g. chewed; see Díaz et al., 1999) were considered to have been predated.

The effect of habitat fragmentation, location, exclosures, seed size and time on granivory were evaluated through a repeated measures ANOVA. For the exclosure effect, we separated both kind of controls (i.e. for semipermeable and impermeable exclosures). Prior to the analysis, data were transformed as to square-root $(x+0.5)$ to normalize distributions and stabilize variances. Because data did not meet the sphericity assumption, tested through Mauchly's test, we used the Greenhouse–Geisser adjusted probabilities. Post-hoc comparisons were performed by the Tukey HSD for Unequal Sample Sizes (Spjotvoll & Stoline test) (Zar, 1996, StatSoft, 2000).

3. Results

3.1. Fragmentation effects

Overall, after 102 days of experimentation, seed removal was significantly higher in fragments than in continuous forest, regardless of seed size. At the end of the experiment, seed predation was 34% greater in fragments than in continuous forest (47% of seed consumed vs. 35%, Table 1).

3.2. Edge effects

Seed predation was four times higher at forest edges than in the forest interiors (36% vs. 9%) after a month of experimentation. However, 79 days after starting the experiment, granivory in the interior of fragments became similar to the edges, and was twice that recorded in the interior of the continuous forest (42% vs. 21%, Fig. 3, Table 1).

3.3. Seed size effects

At all times, large seeds were consumed significantly more than small seeds. At the end of the experiment, 47% of large seeds were predated compared with 34% of the small ones (Table 1). While both large and small seeds were predated more extensively in fragments than in continuous forest (see earlier), large seeds also were

Table 1
Results of rm ANOVA for the effect of fragmentation, edge, exclosure, seed size and time on granivory of *Nothofagus* seeds

Source	df	MS	F	$P>F$	
Between-subjects					
Fragmentation	1	16.178	5.294	0.022	
Edge	1	90.627	29.654	<0.001	
Exclosure	3	13.448	4.400	0.005	
Seed size	1	18.348	6.004	0.015	
Error	442	3.056			
Within-subject					Adj $P>F$ G–G
Time	4	88.222	280.898	<0.001	<0.001
Time×Fragmentation	4	1.885	6.001	<0.001	0.002
Time×Edge	4	6.178	19.672	<0.001	<0.001
Time×Exclosure	12	1.141	3.634	<0.001	0.001
Time×Seed size	4	2.228	7.093	<0.001	0.001
Time×Fragmentation ×Seed size	4	0.762	2.427	0.046	0.084
Error	1768	0.314			

The P-value for inclusion in the table is 0.1. Greenhouse–Geisser $\varepsilon=0.546$.

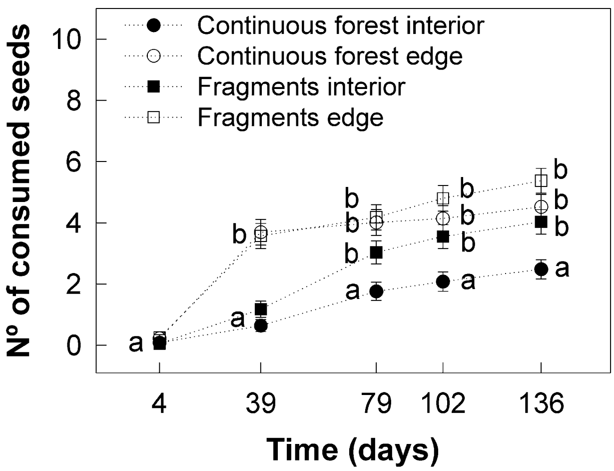

Fig. 3. Effects of fragmentation and edge on granivory. Different letters indicate significant differences ($P<0.05$) according to Tukey unequal N HSD test.

more heavily predated than small seeds both in fragments and in continuous forest. Overall, consumption of large seeds was 50% greater in fragments compared with that in continuous forest (57% of seed preyed vs. 38%, respectively). The consumption of small seeds increased only 16% in fragments and fewer seeds were predated compared with large ones (37% of seeds predated in fragments vs 32% in continuous forest).

Predation of large and small seeds was higher in the edges than in the interior of both fragments and continuous forest. However, consumption of large seeds increased in the interior of fragments by day 79, doubling the predation level reached in the interior of the continuous forest (55% vs. 25%). About 34% of small seeds were predated in all situations (Fig. 4, Table 1).

3.4. Exclosure effects

At all times, levels of granivory in the control and semipermeable exclosures were similar, and both were 83% higher than in the impermeable exclosures (44% vs. 24%, Fig. 5, Table 1). This was true both in the fragments and in continuous forest, regardless of seed size (Table 1).

4. Discussion

Fragmentation of the Maulino forest was differently related to granivory on small and large seeds. Granivory was higher in small fragments than in continuous forest, higher in edges than in forest interior, and higher upon large than on small seeds.

Similar to other temperate forests and small tropical islands (Sork, 1987; Santos and Tellería, 1994, 1997; Asquith et al., 1997; but see Harrington et al., 1997), the higher granivory in small fragments may be due to increased granivore abundance. In Spain, for example, there was a nine-fold increase in rodent abundance in small fragments, which is consistent with a higher seed predation rate there (Santos and Tellería, 1994). In the Maulino forest, granivores are more abundant in small

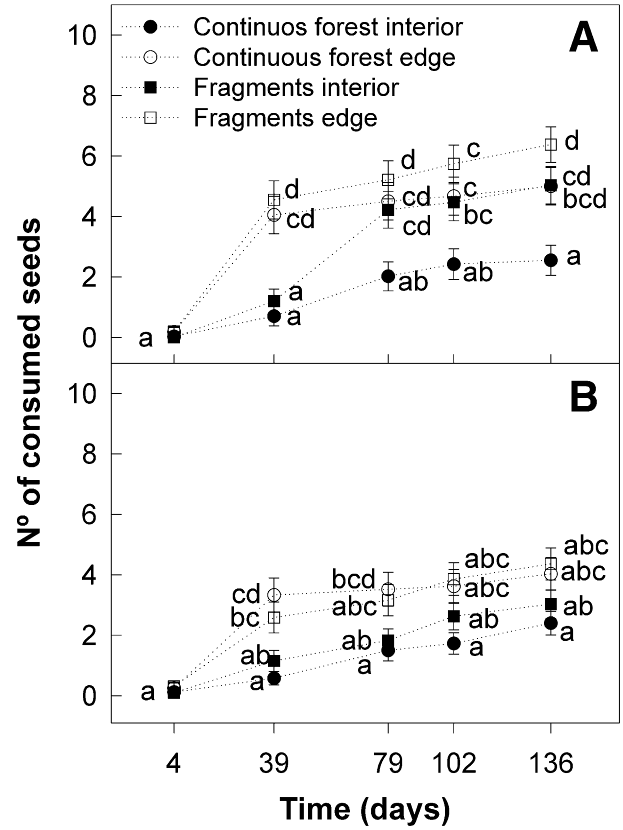

Fig. 4. Granivory on (A) large, and (B) small seeds in edges and interior of continuous forest and fragments. Different letters indicate significant differences ($P<0.05$) according to Tukey unequal N HSD test.

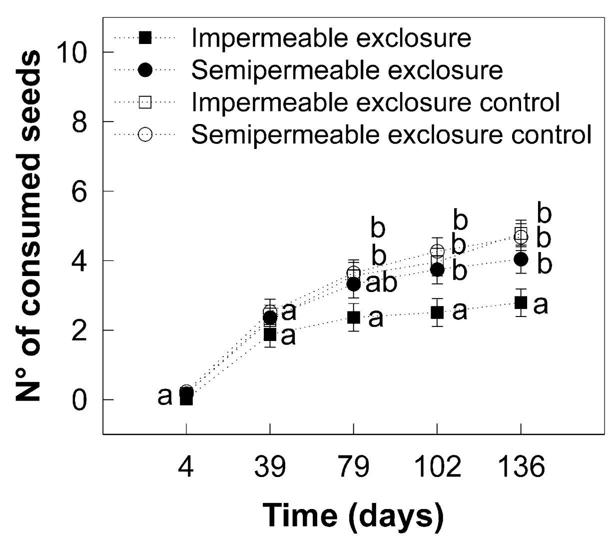

Fig. 5. Exclosure effects on granivory. Different letters indicate significant differences ($P<0.05$) according to Tukey unequal N HSD test.

fragments (see Fig. 1). Similar levels of granivory in semipermeable exclosures and controls (higher than in impermeable exclosures) suggests that small birds and rodents are the main consumers of seeds, as in other temperate ecosystems of Chile (Bustamante, 1996; Díaz et al., 1999).

Although the dwarf deer, *P. pudu,* which is probably the only large frugivore-granivore in the Maulino forest, is more abundant in fragments (Fig. 1), and is able to consume large seeds and fruits such as those of *Gevuina avellana* (e.g. Greer, 1965), the lack of effects on granivory after removing only large vertebrates (semipermeable exclosures) suggests that this uncommon consumer has a minor if any role preying upon the large fruits and seeds of *N. glauca*.

Although impermeable exclosures precluded the access of most vertebrate granivores, there was a low removal of seeds there, which can be attributed to insect consumption. Ants (unpublished) and ground-dwelling coleopterans (Moreno, 2001) are significantly more abundant in forest fragments than in continuous forest. Also, because the time span of the experiments included a reproductive season for rodents, it is likely that some juvenile rodents entered impermeable exclosures and preyed upon seeds there.

The higher consumption of seeds in semi-permeable exclosures compared with impermeable ones suggests that large rodents and birds should have been the main consumers, which had access to semi-permeable but not to impermeable exclosures. In the Maulino forest, small mammals such as *Oligoryzomys longicaudatus*, *Irenomys tarsalis*, *Abrothrix longipilis* and *Abrothrix olivaceus*, prey upon seeds (Meserve et al., 1988; see also Muñoz-Pedreros et al., 1990), are habitat generalists, thriving in native forest but also in the adjacent pine plantations (Saavedra and Simonetti, submitted for publication). Birds also thrive in fragments and pine plantations and are more abundant there than in continuous forest (Fig. 1, Vergara, 2001; see also Estades and Temple, 1999), which suggest that birds may also contribute to the higher granivory in forest fragments. As small fragments have a higher proportion of edge than do continuous forest, the high granivory in small fragments may result from rodents and birds coming from pine plantations and invading fragments (e.g. Vergara, 2001; Saavedra and Simonetti, submitted for publication). Coupled with these movements from the neighboring matrix, the increase in granivore abundance in fragments may also be a consequence of the more complex understory of the fragments, offering more suitable habitats for birds and rodents (e.g. Vergara, 2001), and resulting in higher granivory rates in fragments and edges. The higher granivory in edges has also been observed in other temperate and tropical forests associated with higher levels of consumer activity or abundance on edges (Tabarelli and Mantovanni, 1997; Bresciano et al., 1999; Jules and Rathcke, 1999; but see Burkey, 1993; Díaz et al., 1999).

The edge effect in fragments is short-term, disappearing after 39 days, with granivory in interior habitats converging on that observed in edges; in contrast, granivory in continuous forest remains lower in the forest interior. This phenomenon suggests that fragments as small as the remaining ones in the Maulino forest may lack true interior or "core" habitat for granivores; thus, these species disperse readily through whole fragments and consume seeds everywhere. This also points out the need for long-term studies to evaluate the edge effects on granivory, since their patterns may change through time (see Restrepo et al., 1999 for longer dynamics of plant–animal interactions at edges). In general, the effect of habitat fragmentation on granivory have been evaluated only for short periods of time such as a few days or weeks (e.g. Burkey, 1993; Díaz et al., 1999; Jules and Rathcke 1999), precluding the observation of late effects. Long lasting evaluations of granivory are particularly important for long-persisting seeds in the soil in seed banks, as cumulative granivory may be crucial for the final germination success and seedling recruitment of tree species who depend on their seed bank (Díaz et al., 1999).

The effect of forest fragmentation on granivory is seed-size dependent. In the Maulino forest, predation of large seeds was higher in small fragments than in continuous forest and in edges than in the interior of forests, but predation of small seeds was less affected by forest fragmentation or edges. This is the opposite of fragmentation effects in neotropical forests or in an Australian rainforest, where predation of large seeds is lower in fragments than in continuous forest (Harrington et al., 1997; Rico, 2000). This shows that there are variable effects of fragmentation upon biological interactions in different ecosystems. These differences relate to the differential composition of the granivore guilds and their susceptibility to habitat fragmentation. In summary, fragmentation of the Maulino forest leads to increased numbers of small granivores, mainly rodents which are habitat generalist, and in turn increased granivory especially on large seeds in small fragments and edges.

The absolute magnitude of granivory in the Maulino forest may be low compared with tropical ecosystems (e.g. Burkey, 1993; Harrington et al., 1997; Rico, 2000) but even this level of seed consumption is not insignificant for the future of the Maulino forest. Changes in granivory impact the dynamics of the fragmented forests. In fact, tree seedlings are 1.6 times more abundant in plots where granivores have been excluded for a 2-year period compared with controls. No such changes occur in the interior of continuous forest. Similarly, the recruitment of large-seed trees, including *N. glauca* and *Cryptocarya alba*, is higher in the continuous forest than in the forest fragments, in agreement with low predation rates there (Simonetti et al., unpublished). Consequently, the recruitment of large-seeded species and endangered species, such as *G. keule* and *P. punctata*, may be depressed, and small seeded plants, such as many invasive species, may be favored in forest fragments, resulting in dramatic changes of the original forest composition.

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