
Habitat Fragmentation Effects on Trophic Processes of Insect-Plant Food Webs

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Abstract: *Habitat fragmentation is the transformation of once-extensive landscapes into smaller, isolated remnants surrounded by new types of habitat. There is ample evidence of impoverished biodiversity as a consequence of habitat fragmentation, but its most profound effects may actually result from functional changes in ecological processes such as trophic interactions. We studied the trophic processes of herbivory and parasitism in insect-plant food webs composed of hundreds of species in a fragmented woodland landscape. We recorded all plant species, collected mined leaves, and reared leafminers and parasitoids from 19 woodland remnants. Herbivory and parasitism rates were then analyzed in relation to woodland size and edge or interior location. Herbivory by leaf-mining insects and their overall parasitism rates decreased as woodland remnants became smaller. For each remnant the intensity of both processes differed between edge and interior. Our results provide novel evidence of the magnitude of habitat fragmentation effects, showing they can be so pervasive as to affect trophic processes of highly complex food webs and suggesting a response associated with trophic specialization of the involved organisms as much as with their trophic level.*

Key Words: Chaco Serrano, edge effects, herbivory, leafminers, parasitism, specialization, trophic rank

Efectos de la Fragmentación del Hábitat Sobre Procesos Tróficos de Redes Alimenticias Insecto-Planta

Resumen: *La fragmentación del hábitat es la transformación de paisajes extensivos en remanentes pequeños y aislados rodeados por tipos de hábitat nuevos. Hay amplia evidencia del empobrecimiento de la biodiversidad como consecuencia de la fragmentación del hábitat, pero sus efectos más profundos pueden resultar de cambios funcionales en procesos ecológicos como las interacciones tróficas. Estudiamos los procesos tróficos de herbivoría y parasitismo en redes tróficas insecto-planta compuestas por cientos de especies en un paisaje boscoso fragmentado. Registramos a todas las especies de plantas, recolectamos hojas minadas y criamos minadores de hojas y parasitoides de 19 remanentes de bosque. Las tasas de herbivoría y parasitismo fueron posteriormente analizadas en relación con el tamaño del remanente y la localización del borde o interior. La herbivoría por insectos minadores de hojas y sus tasas de parasitismo declinaron a medida que los remanentes eran más pequeños. Por cada remanente, la intensidad de ambos procesos difirió entre el borde y el interior. Nuestros resultados proporcionan evidencia novedosa de la magnitud de los efectos de la fragmentación, y muestran que pueden ser tan penetrantes como para afectar a los procesos tróficos de redes alimenticias muy complejas y sugieren una respuesta asociada tanto con la especialización trófica de los organismos involucrados como con su nivel trófico.*

Palabras Clave: categoría trófica, Chaco Serrano, efectos de borde, especialización, herbivoría, minadores de hojas, parasitismo

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Introduction

Throughout the world, agricultural development and other human activities have led to native vegetation being reduced to isolated patches of varying sizes. Impoverished biodiversity resulting from habitat fragmentation may lead to functional changes in ecological interactions (Turner 1996; Laurance et al. 2001), which could alter the structure of communities (Fagan et al. 1999; Hunter 2002; Tscharrntke & Brandl 2004) and lead to truncation of food chains (van Nouhuys & Hanski 2002; Kondoh 2003). Trophic interactions involving negative feedbacks such as herbivory and parasitism should be particularly important because they strongly influence linkages among biodiversity, productivity, and stability of ecosystems (Worm & Duffy 2003). Recent studies have begun to unravel the interplay of relationships among habitat area, species diversity, and trophic interactions, with theoretical and empirically tested models predicting spatial effects on food web structure (Brose et al. 2004).

Despite their importance, functional effects have been drawn mostly from data on species richness and abundance, rarely measuring trophic processes directly (Didham et al. 1996; Tscharrntke & Brandl 2004). Furthermore, most researchers have focused on relatively simple systems (Didham et al. 1996; Kruess & Tscharrntke 2000a).

No study to date has addressed habitat fragmentation effects on trophic processes in insect-plant food webs of a full plant community. We analyzed herbivory and parasitism rates in relation to fragment size in food webs of plants, leafminers, and parasitoids in the Chaco Serrano of central Argentina. This system offers a “ready-made” experiment (Saunders et al. 1991): a fragmented landscape where patches of native vegetation appear isolated within an intensely managed matrix resulting from human activities that have, in the last 30 years, led to a 94% reduction in woodland cover (Zak et al. 2004).

Habitat fragmentation involves both loss of habitat and the breaking apart of the habitat, but the most dramatic and consistently negative effects on biodiversity can be attributed to habitat loss (Fahrig 2003). Here, we concentrated on habitat loss. We examined separately herbivory and parasitism trends in edge and core areas because edge-associated disturbances can negatively affect many species and ecological processes (Laurance et al. 2000; McGeoch & Gaston 2000; Weathers et al. 2001).

According to the trophic rank hypothesis, increased susceptibility to habitat fragmentation should be found at higher trophic levels (e.g., Kruess & Tscharrntke 1994; Holt et al. 1999; Kondoh 2003). Yet the specialization hypothesis predicts that specialized organisms are most sensitive to habitat fragmentation (Zabel & Tscharrntke 1998; Holt et al. 1999; Steffan-Dewenter & Tscharrntke 2000). In our system, parasitism is perpetrated mostly by generalist species occupying the upper trophic level, whereas leafminers tend to be highly specific (Valladares et al.

2001). Thus, conflicting predictions could apply: as remnant area decreases, parasitism rates decline faster than herbivory according to the trophic rank hypothesis, but the opposite could be expected from the specialization hypothesis.

Study Area and Methods

We studied an area in central Argentina (31°10'S to 31°30'S and 64°00'W to 64°30'W) with an elevation of about 700 m. The area was originally covered by Chaco Serrano, which is characterized by an open tree stratum up to 15 m high, 1- to 3-m-high shrubs covering 10–80% of the ground, a herbaceous layer (up to 95% cover), and many vines and epiphytes (Cabido et al. 1991). Agricultural and urban development is increasing in the area, and forest species are now restricted to remnants of various sizes (Zak et al. 2004). We included 19 of these remnants, ranging from 0.13 ha to more than 15,000 ha, in our study after analysis of digital satellite images (Landsat Thematic Mapper). The criterion for site selection was to cover a wide range of areas while keeping isolation and matrix characteristics as uniform as possible.

Woodland area was not correlated with latitude (Spearman rank correlation, $r_s = 0.20$, $p = 0.419$, $n = 19$), longitude ($r_s = 0.10$, $p = 0.673$, $n = 19$), or elevation ($r_s = 0.35$, $p = 0.145$, $n = 19$); therefore, environmental gradients unrelated to fragmentation are unlikely to have affected our results. Woodlands were embedded in an agricultural matrix largely dominated by wheat in winter and soy in summer, which on observation did not provide a suitable habitat for either leafminers or their parasitoids. Woodland remnants had been isolated for at least 7 years and were separated by 75–200 m (119.69 ± 12.39 m on average) from the next nearest woodland. Although the remnants were selected within a narrow isolation range, we checked for possible effects on the processes we studied. Isolation had no effect on either herbivory (regression analysis, $F = 2.001$, $p = 0.175$, $R^2 = 0.053$, $n = 19$) or parasitism rates ($F = 2.520$, $p = 0.131$, $R^2 = 0.078$, $n = 19$), so we excluded it from the analyses. In each woodland remnant, two transects were established along the edges (within 5 m from the border) and three in the interior (at least 10 m from the border). All transects were 100 m² (50 × 2 m).

Leafminer larvae feed and dwell inside a leaf, leaving internal tunnels (mines) easily detectable on the leaf surface. Mines offer an unmistakable record of herbivory, and rearing mining larvae to adults allowed us to estimate parasitism rates accurately. In each transect we collected leaves up to 2 m high on two occasions (November–December 2002 and February–March 2003). Collecting was conducted within the peak period of leafminer activity (Valladares et al. 2001). We took mined leaves

to the laboratory and reared adult leafminers and parasitoids (Valladares et al. 2001), which were identified and counted.

We estimated herbivory rates per remnant based on the mean number of mined leaves collected along the transects. Leaf density is independent of remnant area (L. Cagnolo, unpublished data). Parasitism rates were calculated as the sum of parasitoids divided by total adults (leafminers + parasitoids) reared from each remnant. To avoid overestimating the effect of gregarious parasitoid species, we calculated the average number of individuals emerging from one host, considering that this number of parasitoids represented one parasitoid killing one host, for overall parasitism calculations. We used a mixed-model analysis of covariance (ANCOVA) to test for relationships between herbivory and parasitism as response variables, with location (edge/interior) as the fixed factor and remnant area as the continuous independent variable. To examine the dependence between edge and interior data in each remnant, a compound-symmetry covariance structure was incorporated in the analysis instead of the conventional random-effect parameter (Littell et al. 1996). An exploratory model considering location and area plus the interaction between them was used previously to check for the lack of interaction between factor and covariate required for the ANCOVA (Steel & Torrie 1987). Data were transformed to the log (area, herbivory) or arc-sine square root (parasitism) to achieve normal distributions.

To compare area-related changes in herbivory (measured as number of mined leaves) and parasitism (percentage of hosts killed), new variables ("relative" herbivory and parasitism) were calculated using total (interior and edge) data from each remnant. We standardized these data as a proportion of the maximum value in each variable. Slopes of relative herbivory and parasitism rates/log area regressions were then compared using Student's *t* test.

Results

We collected 112,690 mined leaves from 129 woody and herb plant species for herbivory assessment (another 124 plant species were present but not mined). Laboratory

rearing of leafmining larvae yielded 9,944 adult leafminers (49 species of Diptera, 50 Lepidoptera, and 3 Coleoptera) and 7,515 parasitoids (more than 200 species of Hymenoptera so far identified) from which parasitism rates were calculated.

There were no significant interactions between edge or interior location and remnant area for either herbivory ($F = 2.88$, $df = 1,31$, $p = 0.099$) or parasitism rates ($F = 2.05$, $df = 1,31$, $p = 0.162$). Herbivory was significantly higher (Table 1; Fig. 1a) at the core of woodlands (704.51 ± 48.32) than at the edges (437.74 ± 51.92), whereas parasitism rates (Table 1; Fig. 1b) showed the opposite trend: higher at the edges ($49.79\% \pm 2.15$) than at the interior ($43.95\% \pm 1.8$). Parasitism rates did not reflect only parasitoid abundance trends because parasitoids were actually rarer at the borders than in the woodland interior (34.49 ± 5.15 and 43.40 ± 3.76 parasitoids/100 m², respectively; $t_{36} = 4.32$, $p < 0.001$).

Independent of interior or edge location, herbivory by leafminers significantly decreased as remnants became smaller (Table 1; Fig. 1a). In addition, leafminers suffered less mortality from parasitism (Table 1; Fig. 1b) in small than in large woodlands.

Relative herbivory and parasitism rates, calculated to allow their comparison despite use of different measurement units, had similar slopes ($t_{34} = 0.531$, $p > 0.05$) in regressions against woodland area (Fig. 2), suggesting that the decline of both processes with area reduction was equally pronounced.

Discussion

One of the most important consequences of forest fragmentation is a dramatic increase in the amount of edge habitat, which can influence critical ecological mechanisms by altering the nature of species interactions (Fagan et al. 1999; Laurance et al. 2000). Studies examining the effects of remnant edges show divergent results (Fagan et al. 1999; McGeoch & Gaston 2000; Laurance et al. 2001), as did our study here of trophic interactions. Both leafminer herbivory and parasitism in woodland remnants differed between edges and core areas, but their responses showed opposite trends.

Table 1. Results of mixed-model analysis of covariance examining the relationship between remnant area, edge/interior location, and rates of leafminer herbivory and parasitism in the Chaco Serrano.

	Source of variation	df	F	p	R ²	Slope	Intercept
Herbivory	location (edge/interior)	1,35	21.23	<0.001			
	remnant area	1,35	11.41	0.002	0.40	0.07	edge, 331.13 interior, 575.44
Parasitism	location (edge/interior)	1,35	7.48	0.009			
	remnant area	1,35	4.91	0.033	0.18	1.35	edge, 42.76 interior, 38.68

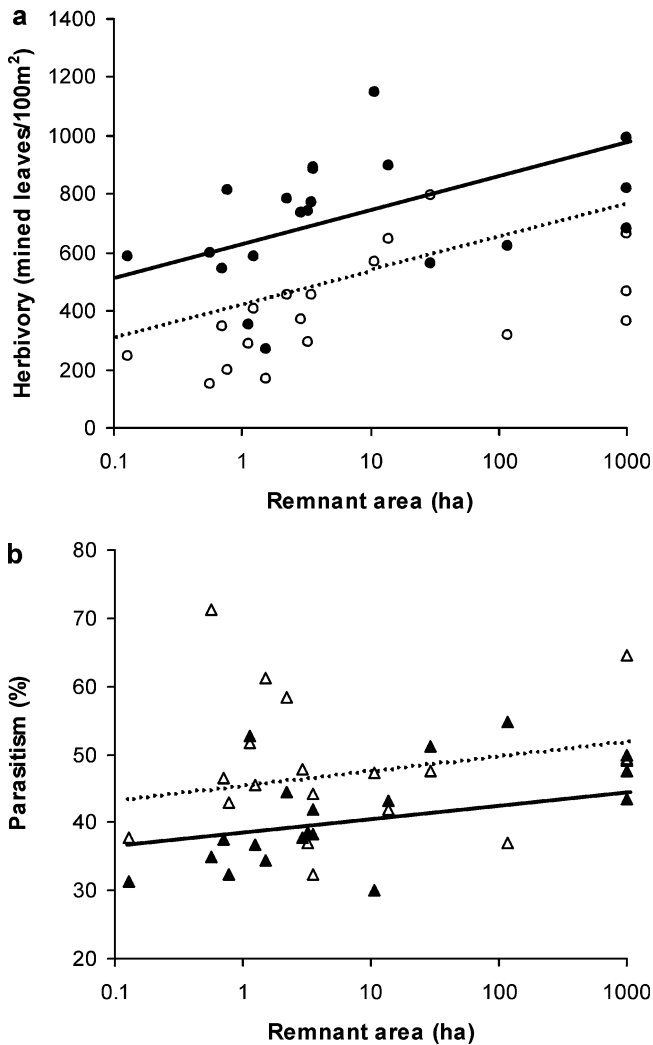


Figure 1. Relationships between trophic processes of insect-plant food webs and habitat fragmentation in the Chaco Serrano. (a) Herbivory by leaf-mining insects at remnant edges (\circ) and at their interior (\bullet) in relation to woodland area. (b) Parasitism on leafminers at the edge (Δ) and at the interior (\blacktriangle) of remnants as a function of area. Regression lines (solid, interior; dotted, edge) based on analysis of covariance. See also Table 1.

Increased herbivory at remnant interiors, where parasitism was lower, could be attributed to release from top-down control (Kondoh 2003), but the observed reduction in parasitism rates seems too small to be responsible for nearly doubling the rate of herbivory. More plausible explanations involve a negative response of leafminers to detrimental microclimatic changes near edges. Forest borders frequently have reduced humidity, increased light, and greater temperature variability (Saunders et al. 1991; Laurance et al. 2001; Hunter 2002), which may be particularly important in semiarid systems such as Chaco. Increased desiccation rates at the edges can induce pre-

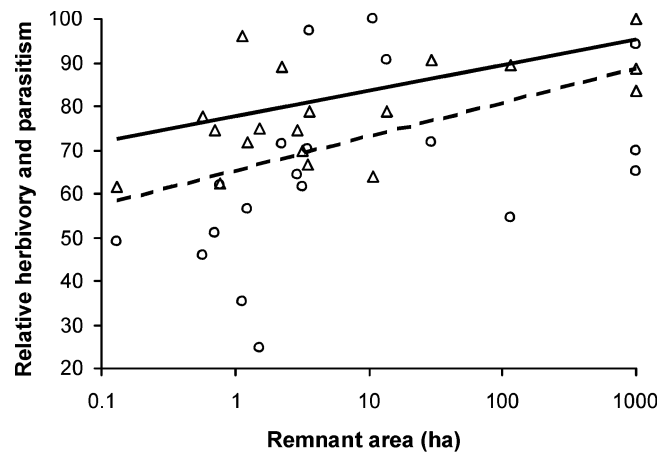


Figure 2. Relative rates (data as percentage of the maximum observed values) of herbivory (\circ) and parasitism (Δ) as a function of remnant area in the Chaco Serrano (relative herbivory [dashed line] = $58.47 + 7.69 \log \text{area}$, $F = 4.1$, $p = 0.059$, $R^2 = 0.19$, $n = 19$; relative parasitism [solid line] = $73.55 + 5.87 \log \text{area}$, $F = 9.4$, $p = 0.007$, $R^2 = 0.36$, $n = 19$).

mature leaf abscission, leading to reduced leafminer survival (Auerbach et al. 1995).

On the other hand, increased parasitism in remnant edges might be related to changes in parasitoid efficiency or behavior because parasitoids were actually less abundant at the borders than in the woodland interior. We propose two possible mechanisms for this result. Higher efficiency could result from improved visibility facilitating host location, which in leafminer parasitoids seems driven by visual clues (Salvo & Valladares 2004). Alternatively, parasitoids traveling parallel to edges due to a general reluctance to crossing them (Fagan et al. 1999) could also result in increased parasitism, although such effects have yet to be described for insects.

Independent of edge and interior location, leafminer herbivory and leafminer parasitism rates decreased with remnant area. Lower herbivore species richness and abundance are frequently associated with increasing habitat fragmentation (e.g., Kruess & Tscharntke 2000a; Hunter 2002), but despite the well-known impact of insect herbivores, effects of fragment size on herbivory rates have received scant attention (Didham et al. 1996; Groom 2001) and never at the scale of the present work. Fragmentation effects on herbivory thus seem strong enough to be perceived at scales varying from one or very few plant or herbivore species (e.g., Zabel & Tscharntke 1998; Arnold & Asquith 2002; Kruess 2003) to the high levels of complexity represented by the food webs studied here.

Although parasitism response to fragment area is better studied than herbivory, previous information on parasitism response is also scarce (Kruess & Tscharntke 2000b; Denys & Tscharntke 2002; Kruess 2003). Ours

is the first evidence of a pervasive impact of habitat fragmentation on this fundamental trophic process in a system involving hundreds of species.

Regression slopes have been used to compare species-area relationships (Steffan-Dewenter & Tscharrntke 2000), and we extended this use to trophic processes. Our results did not support a more prominent role for either the specialization or the trophic level hypotheses. The lack of significant differences between the slopes of herbivory and parasitism regressions on remnant area suggests that trophic specialization could be as important as trophic level in determining overall functional responses to habitat fragmentation in these food webs. This statement must be taken in the context of an intertrophic level comparison and not as a test of the specialization hypothesis per se, which would require a comparison within the same trophic group (e.g., Steffan-Dewenter & Tscharrntke 2000). Whether resources (bottom-up forces) or natural enemies (top-down forces) or both determine the abundance of insect herbivores and control plant biomass in terrestrial food webs remains an ongoing debate (Walker & Jones 2001). Habitat fragmentation is sometimes defined as a bottom-up force (Kondoh 2003), but its main effects could also result from top-down control release (Kruess & Tscharrntke 2000b; Kondoh 2003), leading to herbivore outbreaks in small habitats. Bottom-up and top-down control scenarios provide different responses to habitat fragmentation in theoretical models, highlighting a possible trade-off for herbivores between habitat reduction and elimination of predators (Bascompte & Solé 1998). We have shown that overall leafminer herbivory decreased in small habitats, despite the possible release provided by lower parasitism, which supports a bottom-up view of habitat fragmentation effects, at least for the scale of our study.

Habitat fragmentation affected trophic processes across highly complex food webs involving hundreds of species, as evidenced by reductions in overall herbivory and parasitism rates with decreasing habitat size and by differences in the intensity of both processes between edge and interior. Such effects become especially relevant when considering that insect-plant food webs account for about three-quarters of the Earth's total biodiversity. Complex trophic interactions within such food webs often influence ecosystem properties (Worm & Duffy 2003), and their negative feedbacks, such as herbivory and parasitism, could play a fundamental role in long-term ecosystem sustainability (Chapin et al. 1996). Thus, our findings could have profound implications for landscape ecology, conservation biology, and pest management.

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