

# Habitat Fragmentation and Species Loss across Three Interacting Trophic Levels: Effects of Life-History and Food-Web Traits

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**Abstract:** *Not all species are likely to be equally affected by habitat fragmentation; thus, we evaluated the effects of size of forest remnants on trophically linked communities of plants, leaf-mining insects, and their parasitoids. We explored the possibility of differential vulnerability to habitat area reduction in relation to species-specific and food-web traits by comparing species-area regression slopes. Moreover, we searched for a synergistic effect of these traits and of trophic level. We collected mined leaves and recorded plant, leaf miner, and parasitoid species interactions in five 100-m<sup>2</sup> transects in 19 Chaco Serrano woodland remnants in central Argentina. Species were classified into extreme categories according to body size, natural abundance, trophic breadth, and trophic level. Species-area slopes differed between groups with extreme values of natural abundance or trophic specialization. Nevertheless, synergistic effects of life-history and food-web traits were only found for trophic level and trophic breadth: area-related species loss was highest for specialist parasitoids. It has been suggested that species position within interaction webs could determine their vulnerability to extinction. Our results provide evidence that food-web parameters, such as trophic level and trophic breadth, affect species sensitivity to habitat fragmentation.*

**Keywords:** body size, leaf miners, natural abundance, parasitoids, species-area relationship, species loss, trophic breadth, trophic level

Fragmentación de Hábitat y Pérdida de Especies en Tres Niveles Tróficos Interactuantes: Efectos de la Historia de Vida y los Atributos de la Red Trófica

**Resumen.** *La fragmentación del hábitat no afecta de la misma manera a todas las especies; por lo tanto, evaluamos los efectos del tamaño de los remanentes de bosque sobre comunidades relacionadas tróficamente: plantas, insectos minadoras de hojas y sus parasitoides. Exploramos la posible vulnerabilidad diferencial a la reducción en la superficie del hábitat en relación a atributos específicos de las especie y de la red trófica mediante la comparación de las pendientes de regresión de la relación especie-área. Más aun, evaluamos un efecto sinérgico de estos atributos y del nivel trófico. Recolectamos hojas minadas y registramos las especies e interacciones entre plantas, minadores de hojas y parasitoides en 5 transectos de 100 m<sup>2</sup> en 19 remanentes de bosque en el Chaco Serrano en Argentina central. Las especies fueron clasificadas en categorías extremas de acuerdo con su tamaño corporal, abundancia natural, amplitud trófica y nivel trófico. Las pendientes de las relaciones especies-área difirieron entre grupos con valores extremos de abundancia natural o especialización*

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*trófica. Sin embargo, los efectos sinérgicos de la historia de vida y los atributos de la red alimenticia solo fueron encontrados para el nivel trófico y la amplitud trófica: la pérdida de especies relacionada con el área fue mayor para los parasitoides especialistas. Se ha sugerido que la posición de las especies en las redes de interacción pudiera determinar su vulnerabilidad a la extinción. Nuestros resultados proporcionan evidencia de que los parámetros de la red trófica, como el nivel trófico y la amplitud trófica, afectan la sensibilidad de las especies a la fragmentación del hábitat.*

**Palabras Clave:** abundancia natural, amplitud trófica, minadores de hojas, nivel trófico, parasitoides, pérdida de especies, relación especies-área, tamaño corporal

## Introduction

Habitat loss, fragmentation, and degradation have led to forest retraction all over the world, which poses a major threat to biodiversity (Sala et al. 2000). As fragmentation proceeds, the amount of habitat decreases and spatial configuration of habitat changes, which increase the proportion of edge habitat and the distance between populations (Fahrig 2003). Although these features have the potential to alter community composition, the most dramatic effects on biodiversity are caused by reductions in the size of habitats (Watling & Donnelly 2006).

Larger habitats frequently support a more diverse biota, a pattern widely demonstrated by species-area relationships. Such relationships are among the most robust generalizations in ecology (Connor & McCoy 1979; Rosenzweig 1995; Drakare et al. 2006) and underlie consideration of habitat size as a major feature for species conservation (Saunders et al. 1991). Proposed factors in species-area relationships include area *per se* (i.e., mainly higher extinction and lower immigration rates in smaller habitats), habitat diversity (i.e., a wider range of environmental conditions in larger habitats allows more habitat-specialist species to develop), and sampling effects (i.e., sampling effort covaries with habitat area) (Connor & McCoy 1979; Hill et al. 1994). Results of recent studies show the importance of spatial scale on species-area relationships (Kruess 2003; Drakare et al. 2006), probably because the underlying processes also vary with scale.

Although a large amount of evidence points to the negative effects of habitat reduction on species diversity (Fahrig 2003; Watling & Donnelly 2006), not all species are equally sensitive. If differential susceptibility to habitat loss is not random and is related to specific traits, identification of these traits would contribute to ecological theory and to the setting of priorities in applied conservation biology (Henle et al. 2004). Life-history traits related to dispersal, establishment, or persistence could be particularly important in this regard (Davies et al. 2000; Steffan-Dewenter & Tscharnkte 2002).

Body size is usually linked to several life-history attributes that may affect its sensitivity to disturbance (Brown 2007). For example, larger species could be most affected by habitat loss, given their larger space requirements (Matter et al. 2002; Greenleaf et al. 2007) and

lower population densities (Cohen et al. 2003; White et al. 2007). Conversely, positive links between large body size and dispersal capability (Greenleaf et al. 2007), or life span in the case of plants (Matthies et al. 2004), could ameliorate or delay effects of habitat fragmentation. Thus, opposite predictions could be made in relation to effects of habitat fragmentation on species of different sizes. For plants and small insects, life span and dispersal capabilities, respectively, should be more important than space requirements and population densities, putting large-sized species in a better position to deal with a fragmented landscape.

Natural abundance of species is another important trait in this context. Small populations are highly vulnerable to stochasticity and therefore are prone to local extinction, whereas abundant species can rely on their resistance to stochasticity and their higher chance of being "rescued" from neighboring populations if local extinction occurs (Davies et al. 2000; Steffan-Dewenter & Tscharnkte 2002).

Results of recent studies suggest that species vulnerability to extinction may be related not only to demographic characteristics but also to the structure of the interaction network in which they are embedded (Allesina & Bodini 2004; Jonsson et al. 2006). In this context food webs provide two appealing traits to explore: trophic breadth and trophic level.

Trophic breadth in relation to habitat fragmentation has been addressed in Tscharnkte et al. (2002). Because they are strictly dependent on their resources, specialists are expected to be more vulnerable than generalists (Davies et al. 2000; Henle et al. 2004). Supporting this prediction, specialist insects are negatively affected by fragmentation (Steffan-Dewenter & Tscharnkte 2000; Krauss et al. 2003; Swihart et al. 2006), whereas generalists insects may benefit from it (Krauss et al. 2003; Sumerville 2004).

Species at higher trophic levels may be more susceptible to extinction after habitat loss because they are affected by direct (horizontal) effects on their populations and indirect (vertical) effects on their resource populations (e.g., Bascompte & Solé 1998; Hanski 1999; Solé & Montoya 2006). Moreover, species in higher trophic positions tend to need large areas of habitat (Kruess & Tscharnkte 1994) and have lower population densities

(Tscharntke et al. 2002; Davies et al. 2004). Parasitoids and predators are more extinction-prone than their prey in fragmented landscapes (e.g., Zabel & Tscharntke 1998; Komonen et al. 2000; Hoyle 2004), but not always (e.g., Mikkelsen 1993; Starzomski & Srivastava 2007).

In central Argentina human activities have led to a 94% reduction in woodland cover over the last 30 years (Zak et al. 2004), leaving a fragmented landscape of native Chaco Serrano woodland remnants within an intensively managed agricultural matrix. In this system fragmentation has affected plant communities (Cagnolo et al. 2006) and insect herbivory and parasitism rates (Valladares et al. 2006). We evaluated the effects of forest fragmentation, measured as changes in habitat area, on trophically linked communities of plants, leaf-mining insects, and their parasitoids. We also explored the possibility of differential vulnerability to habitat reduction relative to species-specific and food-web traits (body size, natural abundance, trophic position, and specialization). We expected fragmentation effects to be most pronounced for small, specialized, higher-trophic-level species that are not abundant. Moreover, we hypothesized that there is a synergistic effect of life-history traits and trophic level that places small, rare, and specialized parasitoids at maximum risk.

## Methods

### Study Area

We studied an area of Chaco Serrano in central Argentina (31°10'S to 31°30'S and 64°00'W to 64°30'W, elevation 700 m) that is part of the most extensive dry forest in South America (Moglia & Giménez 1998). The Chaco Serrano is characterized by an open tree stratum that is up to 15 m high and is dominated by *Fagara coco* and *Lithrea molleoides*. Shrubs, primarily *Celtis pallida* and *Acacia* spp., in the area are 1–3 m high and cover 10–80% of the ground, and a herbaceous layer covers up to 95% of the soil. There are also many species of vines and epiphytes (Cabido et al. 1991).

We selected 19 sites that covered a wide range of areas and kept isolation and matrix characteristics as uniform as possible. Three of these sites represented continuous forests (10,514, 4,200, and 1,587 ha), whereas the others spanned a size gradient from 117 ha to 0.13 ha (mean of 11.98 [SE 7.19]). All remnants had been isolated for at least 7 years, and the distance to the nearest larger remnant ranged between 75 and 200 m. The woodlands were mainly used for cattle grazing and were embedded in an agricultural matrix largely dominated by wheat in winter and soy or maize in summer.

### Sampling

At each of the 19 sites we established five 50-m-long and 2-m-wide transects. Leaf miner larvae feed and dwell

inside a leaf, leaving internal tunnels (mines) easily detectable on the leaf surface (Hespenheide 1991; Connor & Taverner 1997). Along each transect we collected all reachable mined leaves in November–December 2002 and in February–March 2003 at the time of peak leaf miner activity (Valladares et al. 2001). We took mined leaves to the laboratory and reared the insects from larval to adult stage. We counted and identified these adults, and because mine shape is species specific (Hespenheide 1991), we were able to accurately identify tritrophic interactions (plant–herbivore–parasitoid).

We collected vegetation data in April–May 2003. At each site we recorded the complete floristic composition in two 500-m<sup>2</sup> plots, assigning each plant species to one of the following cover-abundance categories: <1%, 1–5%, 6–25%, 26–50%, 51–75%, and >75% (Braun-Blanquet 1950). Our sampling effort did not encompass the complete floristic composition of sites, as we only sampled vegetation according to the minimum sample size proposed in previous phytosociological studies in the area (Cabido et al. 1991; Zak & Cabido 2002). Because sampling effort and the number of species recorded are usually related (Magurran 2004), the total area and the area sampled were kept constant in all sites to avoid sampling artifacts that could influence the effects of habitat area on species richness (Hill et al. 1994).

### Species Traits

Species were classified according to body size, natural abundance, and trophic breadth. Plant height data were derived from the literature and herbarium measurements. We measured insect body length on at least five specimens per species. Within each trophic level we listed species from the largest to the smallest. Species in the upper third of the list were classified as large species (plants 2.25–15.5 m tall; leaf miners 3.6–10 mm long; parasitoids: 2.25–8 mm long), and those in the lower third were classified as small species (plants 0.02–0.9 m tall; leaf miners 1.075–1.625 mm long; parasitoids, 0.4–1.6 mm long).

We constructed species rank-abundance plots and classified species in the upper third as common and species in lower third as rare. For plants the average of the midpoint cover category from the two 500-m<sup>2</sup> plots in each site was used, so rare species were those with  $\leq 0.06\%$  average site cover, and common species were those with  $\geq 0.16\%$  cover. On the basis of average density of mines (leaf miners) and adult insects (parasitoids) per site, species were classified as rare ( $\leq 0.008$  mines/m<sup>2</sup> and  $\leq 0.0012$  individuals/m<sup>2</sup>) or common ( $\geq 0.08$  mines/m<sup>2</sup> and  $\geq 0.04$  individuals/m<sup>2</sup>). This categorization was based on data from sites in which the target species was recorded at least once. Species abundance values we obtained were validated with those from independent sources. For plants we found a correlation of 73% ( $p < 0.001$ ,  $n = 74$ ) and 72% ( $p < 0.001$ ,  $n = 42$ ) with the data presented in

Cabido et al. (1991) and Zak and Cabido (2002), respectively. For insects we used a previous survey of ours in the same area and found a correlation of 70% for leaf miners ( $p < 0.001$ ,  $n = 91$ ) and 56% for parasitoids ( $p < 0.001$ ,  $n = 97$ ).

To assess trophic breadth we ranked species by decreasing number of larval host use. Those species in the lower and upper third of the resulting list were, respectively, classified as specialists (leaf miners, 1 host; parasitoids, 1–5 hosts) and generalists (leaf miners,  $\geq 3$  hosts; parasitoids,  $\geq 15$  hosts). Only species with at least 10 individuals recorded were included in the analyses.

We assigned species to one of the following “trophic levels”: basal (plants), medium (leaf miners), or top (parasitoids). We took data on plant species richness from Cagnolo et al. (2006), in which a comprehensive analysis of plant traits in relation to habitat fragmentation was conducted.

### Data Analysis

We calculated species–area relationships for plants, leaf miners, and parasitoids with ordinary least-squares regression. We used the slope of the regression between the area of a forest remnant and species richness ( $z$  value) as a measure of the sensitivity of a species to habitat fragmentation. We compared the sensitivity to fragmentation among different categories of life-history traits within each trophic level ( $t$  test) and within the full data set (analysis of covariance [ANCOVA]). In the ANCOVA species richness was the response variable, trait categories were fixed factors, and fragment area was the continuous variable. Interaction terms were left in the model as tests for homogeneity of slopes. We evaluated possible synergistic effects between trophic level and life-history traits by leaving the corresponding interaction term (trophic level  $\times$  trait  $\times$  remnant area) in the models. A significant interaction including the remnant area indicates different slopes for the groups considered (Zar 1996).

All variables were  $\log_{10}$ -transformed to achieve residual normality or homoskedasticity. Despite the extreme range in area values of the study sites (0.13–10,514 ha) the exclusion of the largest and the smallest sites did not change our results qualitatively. Another potential source of bias in our results is the presence of spatial autocorrelation, which could create false-positive results (Legendre 1993). To test for spatial autocorrelation problems we evaluated spatial correlograms for raw variables (dependent and independent) and regression-model residuals and calculated Moran's  $I$  coefficients and their respective probability values with the spatial analysis in macroecology program (SAM; Rangel et al. 2006). Neither raw variables nor regression residuals showed significant autocorrelation according to the criteria proposed by Diniz-Filho et al. (2003).

## Results

Across all study sites we recorded 630 species (241 plants, 135 leaf miners, and 254 parasitoids). Large and small species appeared to be equally affected by changes in habitat area (Fig. 1a) for plants (small,  $r^2 = 0.62$ ,  $z = 0.07$ ,  $p < 0.001$ ; large,  $r^2 = 0.68$ ,  $z = 0.06$ ,  $p < 0.001$ ) and leaf miners (small,  $r^2 = 0.29$ ,  $z = 0.03$ ,  $p = 0.018$ ; large,  $r^2 = 0.31$ ,  $z = 0.04$ ,  $p = 0.013$ ). Parasitoid species richness followed the general tendency to decrease with habitat area only for small species (small,  $r^2 = 0.51$ ,  $z = 0.06$ ,  $p < 0.001$ ; large,  $p > 0.1$ ). Nevertheless, the slope of species–area relationships did not show differences in relation to body size, either in general (Table 1) or within each trophic level ( $p > 0.05$  in all cases).

When species abundance was considered we observed steeper species–area curves for rare species in every group (Fig. 1b). Regression slopes of rare species were, at least, three times larger than those of common species for plants (rare,  $r^2 = 0.69$ ,  $z = 0.25$ ,  $p < 0.001$ ; common,  $r^2 = 0.45$ ,  $z = 0.03$ ,  $p = 0.001$ ), leaf miners (rare,  $r^2 = 0.56$ ,  $z = 0.19$ ,  $p < 0.001$ ; common,  $p = 0.259$ ), and parasitoids (rare,  $r^2 = 0.32$ ,  $z = 0.10$ ,  $p = 0.011$ ; common,  $r^2 = 0.23$ ,  $z = 0.03$ ,  $p = 0.037$ ). This result was corroborated by the formal comparison of regression slopes, indicating that natural abundance significantly affected species response to habitat area across all trophic levels (Table 1) and within each trophic level ( $p < 0.1$  in all cases).

On average leaf miners (mean [SE] = 2.01 hosts [0.18]) were more specialized than parasitoids (mean [SE] = 4.75 hosts [0.47]) in their larval host use. The loss of species with decreasing habitat size was more pronounced for specialists (Fig. 2) in leaf miners (specialists:  $r^2 = 0.53$ ,  $z = 0.05$ ,  $p < 0.001$ ; generalists:  $r^2 = 0.21$ ,  $z = 0.02$ ,  $p = 0.05$ ) and parasitoids (specialists:  $r^2 = 0.24$ ,  $z = 0.09$ ,  $p = 0.03$ ; generalists:  $r^2 = 0.25$ ,  $z = 0.02$ ,  $p = 0.03$ ). Species–area slopes were steeper for specialists than for generalists (Table 1), which suggests a differential susceptibility to habitat size effects relative to trophic breadth. This result was mainly due to the almost three times higher slope for specialist than for generalist parasitoids ( $t = 219.01$ ,  $df = 34$ ,  $p = 0.001$ ) because specialist and generalist leaf miners slopes were not different ( $t = 3.20$ ,  $df = 34$ ,  $p = 0.08$ ).

All three trophic levels we considered showed significant and positive species–area relationships (Fig. 3). Decreasing habitat area resulted in nearly 50% reduction in plant diversity ( $r^2 = 0.67$ ,  $z = 0.05$ ,  $p < 0.001$ ), whereas leaf miner diversity decreased by 30% ( $r^2 = 0.49$ ,  $z = 0.04$ ,  $p < 0.001$ ), and almost half of the parasitoids were lost in the smallest remnants ( $r^2 = 0.44$ ,  $z = 0.06$ ,  $p = 0.001$ ). Although according to these results the effect of habitat area appeared to be most pronounced for the group at the top of the food web (parasitoids), the slope

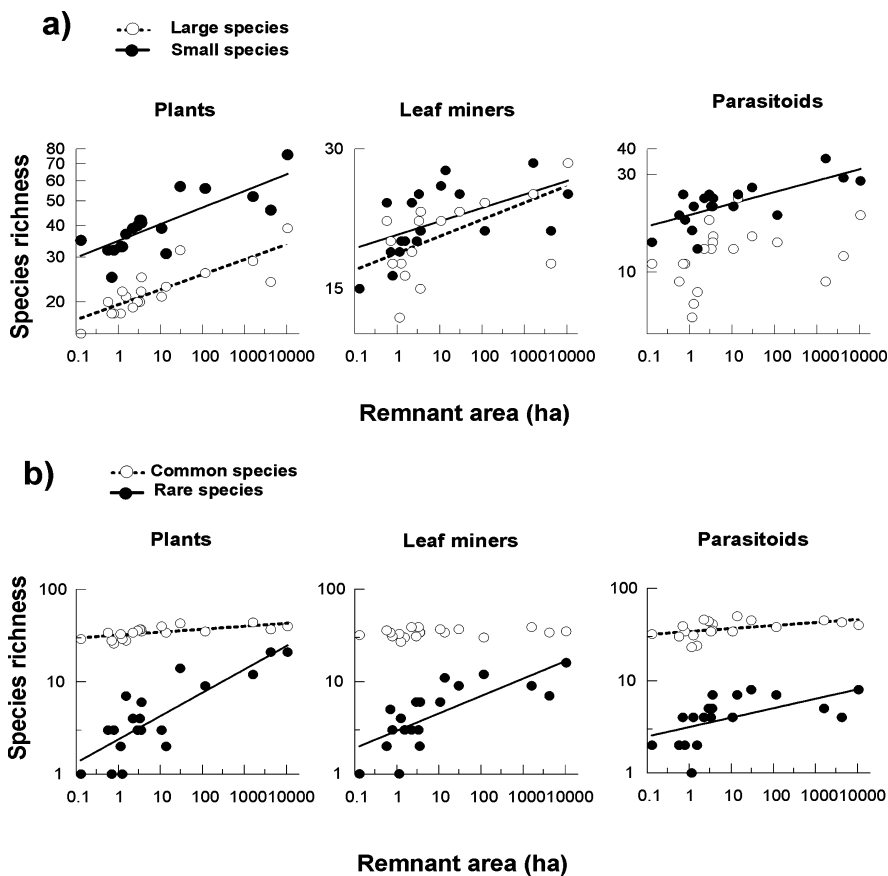


Figure 1. Species-area relationships for (a) large and small and (b) rare and common plants, leaf miners, and parasitoids in 19 Chaco Serrano remnants (Argentina).

of species-area relationships was not different among trophic levels ( $F_{2,51} = 1.09, p = 0.343$ ).

We predicted that species sharing traits such as low abundance or high specialization would have steeper species-area slopes at higher positions in the trophic chain. We found significant interactions between trophic level and other specific traits (Table 1), although not always following the expected trends. Surprisingly, the

slope of rare species relationships with area decreased gradually and by nearly one-third of its magnitude (from 0.25 in plants to 0.10 in parasitoids) with increasing trophic position (Fig. 4). On the other hand, our prediction was supported by the interaction between trophic breadth and trophic position: the slope of the species-area relationship was highest for specialists at the top of the trophic chain (Fig. 4).

Table 1. Test of homogeneity of slopes (analysis of covariance) from species-area relationships for plant, leaf miner, and parasitoid species sharing particular life-history traits and considering their interaction with trophic level.

Source of variation	df	Mean square	F	p
Body size × area	1	0.002	0.250	0.620
Body size × trophic level × area	2	0.003	0.400	0.672
Error	102	0.007		
Natural abundance × area	1	1.242	44.494	<0.001
Natural abundance × trophic level × area	2	0.104	3.711	0.028
Error	102	0.027		
Trophic breadth × area	1	0.045	4.027	0.048
Trophic breadth × trophic level × area	1	0.394	11.410	0.001
Error	68	0.011		

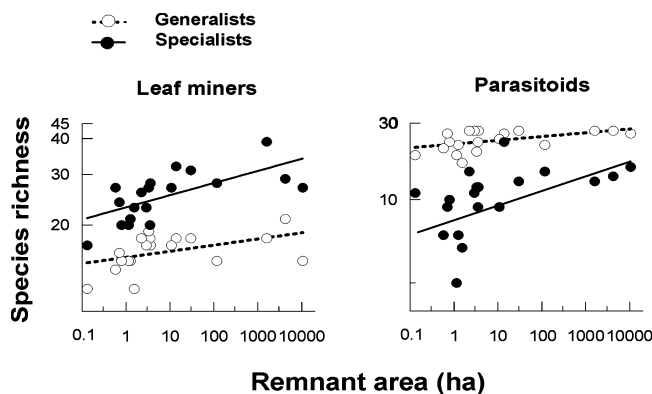


Figure 2. Species-area relationships for leaf miners and parasitoids with different trophic breadths (as larval host-use specialization) in 19 Chaco Serrano remnants (Argentina).

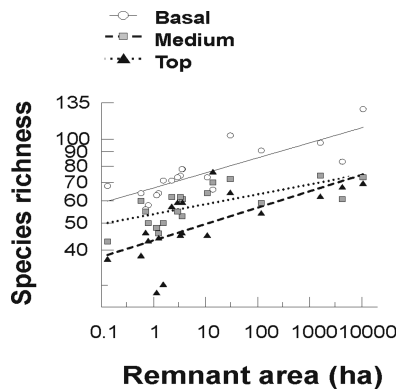


Figure 3. Species–area relationships for basal (plants), medium (leaf miners), and top (parasitoids) trophic levels in 19 Chaco Serrano remnants (Argentina).

## Discussion

Habitat fragmentation is a major threat to biodiversity, and its effects may reach farther and deeper than previously acknowledged because they may spread to different interacting species through direct and indirect paths (Terborgh et al. 2001). Our results illustrate the pervading effects of reductions in habitat area, an inevitable consequence of fragmentation, in a network of hundreds of species in three linked trophic levels.

Area effects did not seem to apply to all species groups uniformly. Body size was unrelated to species sensitivity to changes in remnant area. Notwithstanding the positive relationship between body weight and  $z$  values reported across a wide spectrum of organisms (Drakare et al. 2006), our results are not entirely surprising because body-size effects are predicted to be nonexclusively negative (given that larger species need more habitat) or positive (given that smaller species may have limited dispersal abilities) (Laurance et al. 2000; Drakare et al. 2006). Only parasitoids showed a trend in size-related differences in their response to remnant size. Larger species were not affected by habitat area, and fewer small species were found as forest remnants became smaller, which may be

explained by the limits their shorter wing span places on recolonization (Kruess & Tschardtke 2000).

Rare species were lost remarkably faster than common species as remnant area decreased, and this result was consistent across the three trophic levels. Our data supported the view of natural abundance of species as a characteristic related to extinction risk (Henle et al. 2004). Plant data, albeit processed in a slightly different way than in a previous paper (Cagnolo et al. 2006) and rendering different magnitudes of slopes for the species–area relationships, confirmed the link between rarity and vulnerability to fragmentation previously reported. Small populations are more vulnerable to stochasticity (Henle et al. 2004), and because local abundance and geographic distribution are frequently linked, they may also be less prone to be rescued by migrants from nearby populations (Johnson 1998; Hanski 1999; Lozada et al. 2008). Although relevant from a conservation perspective, the relationship between population size and extinction probability is still under discussion (Honnay et al. 1999) because rarity can be related to life-history traits such as specialization or lower reproductive output, which may confer a higher sensitivity to fragmentation (Kolb & Diekmann 2005).

The “specialization–disturbance” hypothesis (Vázquez & Simberloff 2002) predicts that specialist species are more vulnerable to disturbance than generalists because when facing the absence of a resource or the extinction of a prey, generalists can switch to consume alternative items. There is evidence of specialists being more sensitive to fragmentation of their habitat than generalists (Jonsen & Fahrig 1997; Steffan-Dewenter & Tschardtke 2000; Krauss et al. 2003), which can even thrive in fragments (Krauss et al. 2003; Sumerville 2004). Our analysis of niche breadth supports the specialization–disturbance hypothesis because area-related loss of specialists was nearly twice (for leaf miners) or nearly four times (for parasitoids) faster than that of generalists.

The trophic rank hypothesis holds that fragmentation effects are larger the higher a species is on the food chain (Holt et al. 1999) because consumers must face the direct effects of fragmentation on their populations and spatial

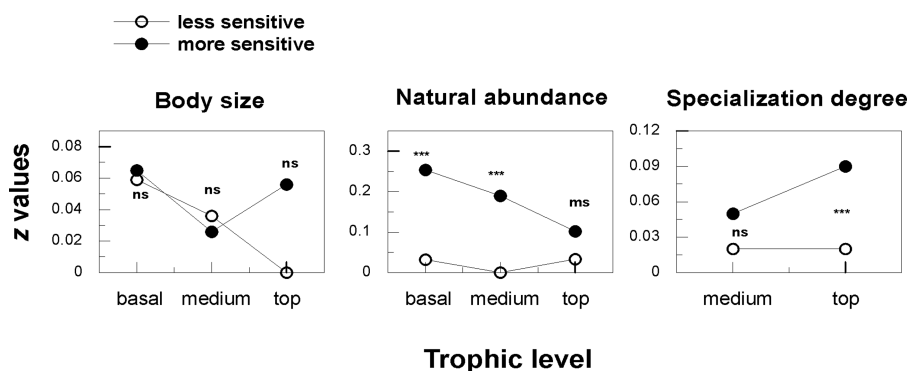


Figure 4. Relationship between species–area slopes ( $z$  values), trophic level (basal, plants; medium, leaf miners; top, parasitoids), and predicted sensitivity to habitat fragmentation on the basis of life-history and food-web traits. Symbols in the graph refer to differences within trophic levels (t test; ns,  $p > 0.1$ ; ms,  $0.1 < p < 0.05$ ; \*\*\*  $p < 0.001$ ;  $n = 19$ ).

constraints impinging on their food sources (Tscharntke & Brandl 2004). Thus, carnivores should be most affected by fragmentation because of their larger habitat requirements, small populations, and dependence on prey presence (Holt et al. 1999; Solé & Montoya 2006). This hypothesis was not supported by our results, which did not reveal significant differences among trophic levels, in concordance with the results of a meta-analysis made by Drakare et al. (2006). Although parasitoids may not require more space than leaf miners, their populations were lower in smaller fragments, but their capability to attack different hosts (Valladares et al. 2001) could prevent them from becoming disconnected from the food web following extinctions of particular leaf miners.

If consequences of species loss are mediated by species position within the interaction network (Petchey et al. 2004; Montoya et al. 2006), synergistic effects between trophic level and life-history traits could lead to steeper species-area relationships for rare or specialized species at the top of the food web. We found a significant interaction between natural abundance and trophic level, but contrary to our expectations, species loss in smaller habitats was more pronounced for rare plants and gradually decreased at higher trophic levels. Asymmetric interactions, as proposed for mutualistic networks (Vázquez & Simberloff 2002; Ashworth et al. 2004; Bascompte et al. 2007), could buffer the effect of habitat reduction at higher trophic levels because rare parasitoid and leaf miner species were usually associated with abundant hosts (data not shown).

Although bottom-up extinction cascades in this system remain to be tested, the hypothesis of synergistic effects between trophic breadth and trophic level was supported because the most pronounced area effects were observed in specialist parasitoids. The fast decrease in the diversity of specialist parasitoids with habitat reduction could have occurred because plants are a more stable and predictable resource for leaf miners than leaf miners are for parasitoids. This result is consistent with the mechanism of “stacked specialist” model (Holt et al. 1999), whereby species at higher trophic levels are present only if their preys at lower levels are also present, which suggests that linear food chains are more likely to be broken by disturbance (e.g., Komonen et al. 2000; Thébault et al. 2006; Petchey et al. 2008).

How the observed changes affect food-web structure, function, and stability upon further extinctions remains to be assessed, but weak interactions, such as those involving rare and specialized species, may promote community persistence and stability (McCann et al. 1998). Moreover, the synergistic effects we found suggest that local extinctions of plant species in Chaco Serrano remnants (Cagnolo et al. 2006) could lead to cascading effects on herbivores and their natural enemies, with the potential to disrupt basic ecological processes that could exacerbate fragmentation effects (Tilman et al. 1994).

Our results show that habitat area effects are consistently more intense for species with low abundance and narrow trophic breadth in food webs of organisms as different in size and biological profile as plants and insects. Moreover, we found that two food-web traits (trophic level and trophic breadth) interacted synergistically, whereas trophic level and natural abundance did not. These results, based on species presence-absence data, offer a coarse-grain approximation of the phenomenon, but changes in species abundance and interaction intensities (Ives & Cardinale 2004) could amplify fragmentation effects in the future (Tilman et al. 1994).

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