

Forest fragmentation leads to food web contraction

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Fragmentation and loss of habitat are critical components of the global change currently threatening biodiversity and ecosystem functioning. We studied the effects of habitat loss through fragmentation on food web structure, by constructing and analyzing plant–herbivore and host–parasitoid food webs including more than 400 species and over 120 000 feeding records, in 19 Chaco Serrano remnants of differing areas. Food web structure was altered by habitat fragmentation, with different metrics being affected depending on interaction type, and with all changes being driven by the reduced size of networks in smaller fragments. Only connectance varied in both quantitative and qualitative analyses, being negatively related to area. In addition, the interactions were represented by proper successive subsets, modulated mainly by resource availability (plant–herbivore) or consumer specialization (host–parasitoid), as forest size decreased. The results suggest that habitat loss has led to food web contraction around a central core of highly-connected species, for plant–herbivore as well as for host–parasitoid systems. The study provides new insights into the effects of human perturbations on complex biological systems.

Global loss and fragmentation of natural habitats are fast eroding terrestrial biodiversity (Fahrig 2003) and are expected to cause further unprecedented rates of species extinction in the near future (Sala et al. 2000). Since all species are connected through trophic relationships in complex food webs, the effects of species loss may propagate and even be magnified through secondary or cascading extinctions (Terborgh et al. 2001, Dunne and Williams 2009). Various studies have suggested that such extinction cascades, and thus the response of natural systems to species loss, depend on species extinction order and on the trophic structure of the system (Dunne et al. 2002, Staniczenko et al. 2010).

Increasing awareness of the intricacy of species interactions and their importance for ecosystem stability, persistence and functioning (Emmerson et al. 2005, Montoya et al. 2006, Cardinale et al. 2009) has revitalized food web study, which has also acquired new dimensions by adopting the framework and tools of network analysis taken from physics and social sciences (Bascompte 2009). In particular, bipartite interaction networks, which can be embedded as subwebs in more complex food webs (Kondoh et al. 2010), have become prominent (Dormann et al. 2009) and have already revealed effects of human-induced disturbances (Tylianakis et al. 2007). However, changes in foodweb structure due to habitat fragmentation have barely been addressed (Memmott 2009, Kaartinen and Roslin 2011) and how real multi-species food webs collapse following habitat reduction in a fragmented landscape remains largely ignored.

The negative effects of habitat loss and fragmentation on species diversity appear to be more pronounced for species

with particular food web-related traits, namely narrow trophic breadth and higher trophic levels (Holt et al. 1999, Davies et al. 2004, Cagnolo et al. 2009). Alterations in food web structure in fragmented systems could thus be expected either from allometric escalation due to reductions in species number, i.e. network size (Martinez 1994, Dunne 2006), or from altered interactions, e.g. loss of specialists leading to more connected systems (Melian and Bascompte 2002, Dunne 2006, Tylianakis et al. 2007), and extreme sensitivity of higher trophic levels, resulting in lower ratios of consumers to resources.

Despite the essentially spatial nature of habitat fragmentation, the spatial distribution of the actual feeding interactions has not yet been addressed. Biological assemblages in fragmented habitats frequently exhibit non-random nested patterns of species composition, in which communities in smaller remnants represent successive subsets of those found in larger remnants, probably as a consequence of differential extinction risks and dispersal abilities (Atmar and Patterson 1993). Since the spatial patterns of food web structure should reflect the non-random co-occurrence of resources and consumers (Brose et al. 2004), a spatially nested pattern of feeding interactions could arise through differential effects of specialization and ubiquity. Thus, the pattern might be driven by consumer trophic breadth, i.e. the capacity of consumers to use the existing resources, with generalist consumers defining a central subset of interactions from large to small habitats. Alternatively, resource availability may determine which consumers can be present, i.e. ubiquitous resources will dictate the composition of the central subset. In an intermediate scenario, interactions might be spatially ranked by a combination of

consumer specialization and resource availability, leaving a central core of generalist consumers on common resources.

In central Argentina, fragmentation of Chaco Serrano forest, currently reduced to about 6% of its original cover (Zak et al. 2004), has led to species loss in plant and insect communities involving leaf miners and their parasitoids, with particular traits like rarity, specialization and higher trophic level conferring higher extinction risk among those organisms (Cagnolo et al. 2009) and with negative effects on trophic processes such as herbivory and parasitism (Valladares et al. 2006). In this study, we examine the effects of habitat fragmentation on food web structure by analyzing bipartite plant–herbivore and host–parasitoid food webs that regionally include more than 400 species (Cagnolo et al. 2011), in 19 Chaco Serrano remnants of differing area. Using standardized methodology and sampling effort, both essential but frequently missing requisites for food web comparisons (Dunne 2006), we investigate whether the loss of Chaco Serrano habitat has resulted in changes in food web metrics, if such changes are related to the number of species involved, and whether host–parasitoid and plant–herbivore food webs are similarly affected. Finally, we investigate whether the feeding interactions themselves show a spatially nested organization, linked to the size of forest remnants and to feeding specialization of the species involved.

Material and methods

Study area and data collection

We studied 19 remnants of Chaco Serrano forest in central Argentina (31°10'S to 31°30'S and 64°00'W to 64°30'W), at an elevation of about 700 m, covering a wide range of areas while keeping the isolation and matrix characteristics as uniform as possible. Three of the sites represented continuous forests (>1000 ha), whereas the others spanned a size gradient from 117 to 0.13 ha. The remnants studied had been isolated for at least seven years, were separated by 75–200 m (119.69 ± 12.39 m on average) from the next nearest woodland, and were embedded in an agricultural matrix largely dominated by wheat in winter and soy or maize in summer. Isolation or spatial autocorrelation have been previously shown to lack significant effects on diversity and ecological processes within the system studied (Valladares et al. 2006, Cagnolo et al. 2009).

Sampling

Leafminer larvae feed and dwell inside a leaf, leaving internal tunnels (mines) easily detectable on the leaf surface. In each remnant, all mined leaves were collected along five transects (50 × 2 m each and up to 2 m high) in Nov–Dec 2002 and Feb–Mar 2003, within the peak period of leafminer activity (Valladares et al. 2001). Plant species cover was assessed in two 500-m² plots per site. The total area and the spread of sampling in space were kept constant in all sites to avoid sampling artifacts on the effects of habitat fragmentation (Hill et al. 1994).

We reared mining larvae in the laboratory to obtain leaf miner and parasitoid adults, in order to identify and quantify herbivore–plant and parasitoid–host feeding interactions. A list of the species involved can be found in the online Supporting information for Cagnolo et al. (2011).

Food web statistics

We have constructed plant–leafminer and leafminer–parasitoid bipartite networks for both qualitative (based on presence/absence of species and interactions) and quantitative (considering species abundance and interaction intensity) versions (Bersier et al. 2002), in an attempt to provide a better understanding of food web structure (Bersier et al. 2002, Dunne 2006).

We estimated qualitative food web indices (Dormann et al. 2009) as follows:

Link density: mean number of links per species, $LD = L / (I + J)$

where L = no. of realized links, I = no. of lower trophic level species (plants, leafminers), J = no. of upper trophic level species (leafminers, parasitoids).

Connectance: the realized proportion of possible links, $C = L / (I \times J)$

Vulnerability: mean number of consumers per prey, $V = L/I$

Generality: mean number of prey per consumer, $V = L/J$

Number of compartments, i.e. sub-sets of the web not connected to other compartments.

Quantitative food web statistics were calculated using the Bipartite package (Dormann et al. 2009) that runs in the R environment for statistical computing (R Development Core Team 2008). Besides quantitative versions of link density, connectance, vulnerability and generality, we calculated the evenness of interaction strength (interaction evenness) based on the Shannon index (Tylianakis et al. 2007, Dormann et al. 2009). These quantitative indices use weighted links by incorporating the strength of each trophic interaction, i.e. the number of individuals observed in each interaction. Full formulae and software details can be found in Bersier et al. (2002) and Dormann et al. (2009).

Quantitative food web graphs were constructed by using a function developed and provided by T. Hirao (Hirao and Murakami 2007) in R.

Interaction nestedness

We constructed matrices with forest remnants as columns and feeding links between pairs of species as rows. The free software BINMATNEST (Rodríguez-Gironés and Santamaría 2006), which employs a genetic algorithm to maximally pack the matrix, was used to determine the matrix Temperature T (Atmar and Patterson 1993) and the probability of finding the same value in 1000 null matrices of same size, number of presences and approximately same marginal sums (Bascompte et al. 2003). T measures the departure from a perfectly nested interaction matrix in which, when rows and columns are ordered by decreasing number of presences, the presences on each row and column coincide with the previous ones or represent a subset of them (Atmar and Patterson 1993, Dormann et al. 2009).

In order to test for the possible influence of consumer specialization and resource availability on the spatial arrangement of feeding interactions, we estimated consumer specialization as species degree (number of links in regional food

webs, Cagnolo et al. 2011), while the measure of availability was provided by the 'regional frequency' or number of sites where each resource species was present.

Statistical analyses

Linear regression analysis was used to evaluate the dependence of food web statistics on forest size (\log_{10} area). A second model evaluated the same relationship after allowing for the effects of food web size (number of species involved), by running for each metric a multiple regression with species richness entering before forest size (with type 1 sum of squares). All variables were log-transformed in order to achieve normality of residuals and facilitate the detection of linear relationships. As we were aiming to identify effects of habitat fragmentation on food web structure, we ran a large number of tests on potentially related food web metrics without unnecessarily conservative adjustments of significance levels, choosing not to incur the cost of false negatives which might hinder the identification of important questions and generation of new hypotheses (Roback and Askins 2005).

The role of remnant area in organizing the spatial interaction structure was assessed by correlating the area of the fragments with their position in the maximally packed matrix. In a significantly nested matrix, a statistical correlation between the ordinal position of each forest remnant in the matrix and remnant area can be interpreted as the latter influencing the nested arrangement of the food web (Wright et al. 1998). With a similar approximation, the importance of consumer specialization and resource availability on the spatial organization of feeding interactions was assessed by correlating the maximally-packed matrix position of each interaction to consumer degree, resource regional frequency, and the product of those variables for the pair of species in each interaction.

Results

At each remnant, between 73 and 134 species of plants + leafminers and 59–123 leafminers + parasitoids were involved in complex networks of interactions, in which over 120 000 interactions were recorded. A visual inspection of the food webs revealed a higher complexity within host–parasitoid than within plant–herbivore interactions, but no strikingly obvious changes throughout the area gradient (Fig. 1). However, web size was strongly related to forest area (Table 1), with about 40% fewer species interacting in small remnants than in continuous forest (Fig. 2).

Only connectance, which increased in smaller remnants, was affected in both herbivore and parasitoid qualitative food webs (Table 1, Fig. 2), albeit only marginally in the latter system. Other responses to habitat loss varied with interaction type (Table 1, Fig. 2): the number of compartments, which was noticeably higher in plant–herbivore than in host–parasitoid food webs, decreased with remnant size in the former only, whereas link density and vulnerability decreased in the latter (Table 1, model 1). All changes in qualitative food web structure were linked to species richness, since no relation to habitat area was detected after removal of variation explained by web size (Table 1, model 2). When quantitative statistics of food web structure were considered, only connectance varied with forest size (Table 1, model 1) for both the herbivory and parasitoid networks. This relationship also appeared to be mediated by changes in species richness (Table 1, model 2).

Plant–herbivore and host–parasitoid interactions in the forest remnants showed a spatially nested organization, with temperatures significantly lower than expected ($n = 19$ columns \times 231 rows, $T = 34.336$, expected 70.435 ± 2.146 , $p < 0.001$ for plant–herbivore interactions and $n = 19$ columns \times 915 rows, $T = 20.464$, expected 43.452 ± 1.47 , $p < 0.001$, for host–parasitoid interactions). The area of the

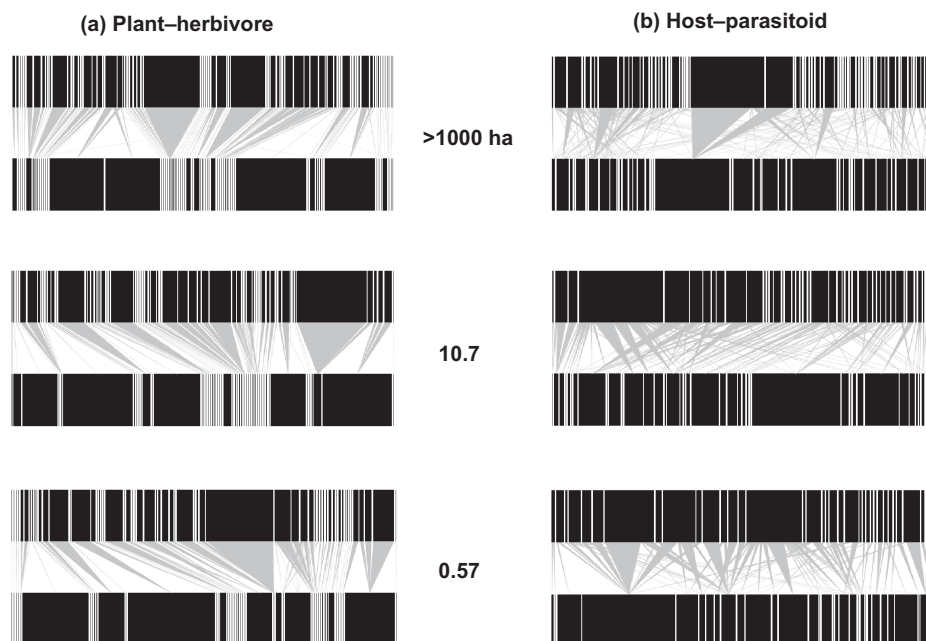


Figure 1. Quantitative plant–herbivore (left) and host–parasitoid (right) food webs in three forest remnants representing extreme and middle points from a gradient of decreasing area (top to bottom) involving 19 remnants. In each web, lower bars represent resource species and upper bars consumer species. Bar width is proportional to species density (at different scales). Grey triangles show feeding links and their width indicates interaction strength.

Table 1. Effects of habitat fragmentation on qualitative and quantitative statistics of (a) plant–herbivore and (b) host–parasitoid foodwebs. Model 1 shows results from simple linear regression of variables versus forest area; in Model 2, area effects have been corrected for variations in food web size by running a multiple regression with species richness entering before forest area (with type 1 sums of squares); r^2 are adjusted values and $n = 19$ in all cases. Significant relationships between forest area and food web metrics are shown in bold text.

(a) Plant–herbivore food webs						
Metric	Model 1			Model 2		
	<i>b</i>	r^2	<i>p</i>	r^2	<i>p</i>	<i>p</i>
<i>Qualitative</i>						
Species richness	0.043	0.49	<0.001	---	---	---
Link density	0.014	0.04	0.211	0.16	0.092	---
Connectance	−0.035	0.40	0.002	0.78	<0.001	0.836
Generality	0.025	0.02	0.262	0.20	0.064	---
Vulnerability	0.033	0.02	0.261	0.01	0.357	---
Compartments	0.033	0.35	0.005	0.70	<0.001	0.932
<i>Quantitative</i>						
Link density	−0.001	0.08	0.122	0.04	0.278	---
Connectance	−0.054	0.50	<0.001	0.87	<0.001	0.404
Generality	−0.004	0.00	0.861	0.00	0.818	---
Vulnerability	−0.010	0.00	0.629	0.00	0.665	---
Interaction evenness	−0.001	0.00	0.759	0.00	0.549	---
(b) Host–parasitoid food webs						
<i>Qualitative</i>						
Species richness	0.056	0.54	<0.001	---	---	---
Link density	0.069	0.23	0.021	0.40	0.007	0.984
Connectance	−0.026	0.147	0.059	0.30	0.022	0.876
Generality	0.078	0.062	0.156	0.05	0.258	---
Vulnerability	0.176	0.227	0.023	0.46	0.003	0.804
Compartments	0.019	0.00	0.670	0.00	0.802	---
<i>Quantitative</i>						
Link density	0.023	0.030	0.230	0.15	0.274	---
Connectance	−0.045	0.179	0.040	0.36	0.011	0.815
Generality	0.02	0.000	0.433	0.00	0.431	---
Vulnerability	0.191	0.041	0.207	0.03	0.304	---
Interaction evenness	−0.007	0.000	0.567	0.00	0.786	---

forest fragments was strongly correlated with their position in the maximally packed matrix (Fig. 3) in both, the herbivore ($r = -0.776$, $p < 0.001$) and the parasitoid networks ($r = -0.750$, $p < 0.001$).

Interaction position within the maximally packed matrix was most strongly correlated to plant regional frequency in the herbivory web (leafminer degree: $r = 0.070$, $p = 0.281$; plant frequency: $r = -0.466$, $p < 0.001$; leafminer degree \times plant frequency: $r = -0.1832$, $p = 0.005$). Instead, the product of parasitoid degree and leaf miner frequency showed the strongest correlation with interaction position in the parasitoid food web, albeit the effect of parasitoid degree doubled that of host frequency (parasitoid degree: $r = -0.269$, $p < 0.001$; leaf miner frequency: $r = -0.1393$, $p < 0.001$; parasitoid degree \times leaf miner frequency: $r = -0.341$, $p < 0.001$).

Discussion

Fragmentation of Chaco Serrano forest has resulted in impoverished plant–herbivore and host–parasitoid food webs and

alterations in various qualitative metrics, with these changes being strongly linked to those in species numbers. Different indices were affected depending on interaction type. Nonetheless, in comparison with their plant–herbivore counterparts, the host–parasitoid food webs did not show any evidence of the increased sensitivity expected at higher trophic levels (Holt et al. 1999, Solé and Montoya 2005, Cagnolo et al. 2009), either in terms of the number of metrics affected or the strength of relationships with forest size. Different network architectures seem to favor stability depending on the type of interaction (Thebault and Fontaine 2010), and in this case the remarkably wide trophic breadth of the parasitoids, feeding on up to 72 hosts within the study area (Salvo et al. 2011), might have buffered trophic position effects.

Connectance showed the most consistent changes, being the only quantitative metric affected by forest area. Its increase as forest area and species richness decreased suggests poorer but apparently more interactive food webs in smaller remnants. Even though this trend might reflect scale-dependent effects (Martinez 1994, Banasek-Richter et al. 2009), changes in connectance might also result from changes in the prevalence of specialists or generalists (Dunne 2006), and we have previously shown habitat fragmentation effects being more intense for specialized consumers (Cagnolo et al. 2009). Since connectance may affect resistance to species removal and consequent changes in ecosystem properties (Dunne et al. 2002, Thebault et al. 2007, Gilbert 2009), its increase in smaller remnants may buffer the effects of habitat fragmentation, thus delaying further species loss in the already impoverished food webs (but see Thebault and Fontaine 2010).

All other changes reported here were limited to qualitative indices and also driven by the number of interacting species. Local plant–herbivore food webs were more compartmentalized than their host–parasitoid counterparts, as observed at a regional level (Cagnolo et al. 2011), and they sustained fewer compartments as woodland area decreased. A compartmentalized structure may isolate the cascading effects of a perturbation, thus reducing its propagation through the food web (Melián and Bascompte 2002). Given the high specificity of leaf miners and the differential extinction risks already mentioned, compartment loss likely reflects local disappearance of rare plants and their specialized consumers.

On the other hand, host–parasitoid food webs showed decreased vulnerability, i.e. fewer parasitoid species attacking each host species as fragments become smaller, which is consistent with a greater loss of higher trophic levels (Holt et al. 1999, Rantalainen et al. 2005, Cagnolo et al. 2009). They also showed lower linkage density, which frequently scales with web size (Dunne 2006, Banasek-Richter et al. 2009) and was predicted to scale also with area in a theoretical model based on co-occurrence patterns and simultaneous consideration of species richness, area and trophic links (Brose et al. 2004).

Besides these changes in metrics, a new aspect of spatial organization of food webs has been revealed in this study by the nested structure of feeding interactions in relation to habitat area. Nested structures have frequently been reported for the species composition of biotas in fragmented habitats (Martínez-Morales 2005) and for interactions within ecological networks (Bascompte and Jordano 2007, Kondoh et al. 2010). Nestedness has also been linked to ecologically plausible rankings of species extinction risks (Srinivasan et al.

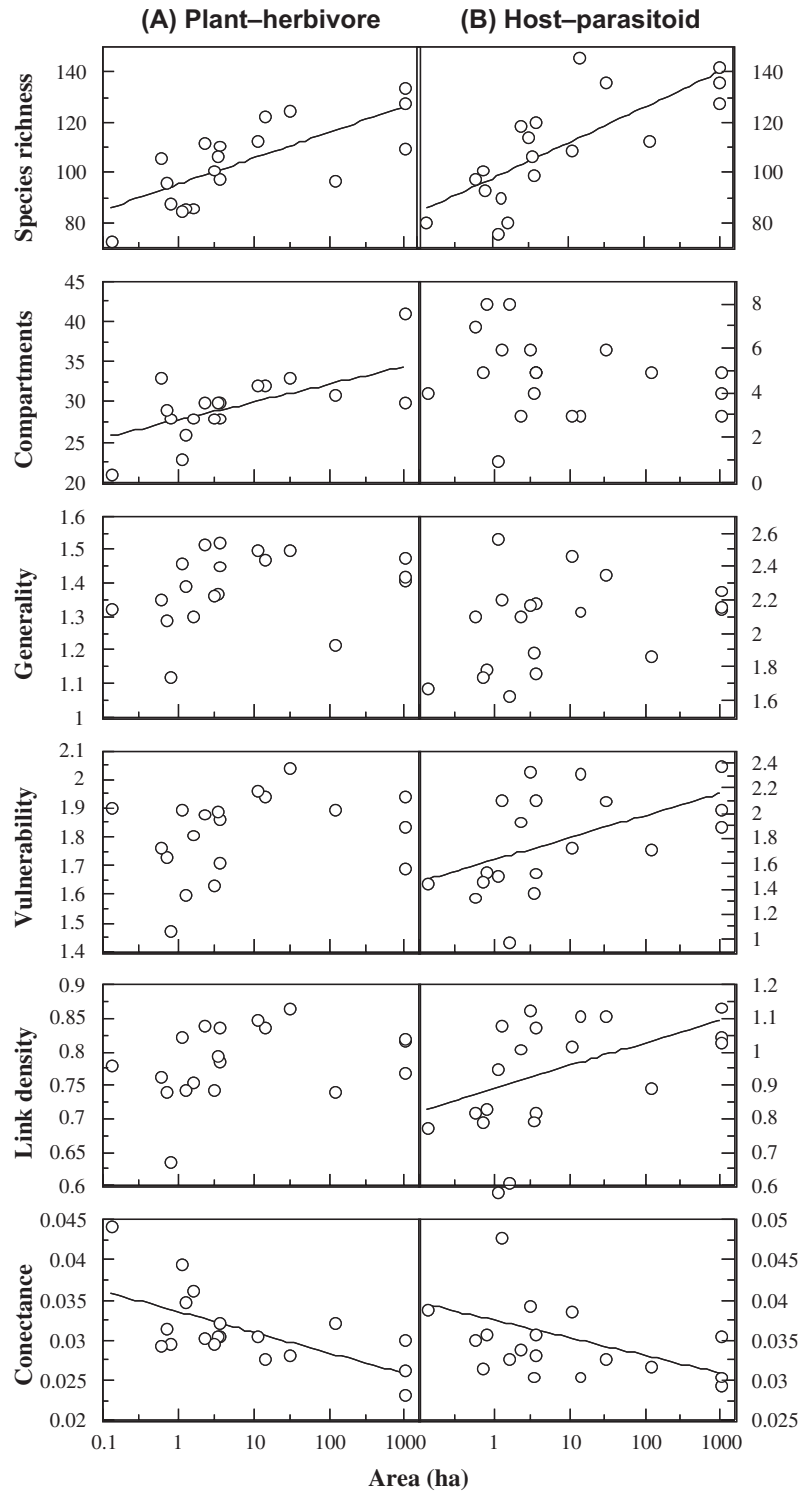


Figure 2. Variations in qualitative food web statistics as a function of forest area. (A) plant–herbivore food webs; (B) host–parasitoid food webs.

2007). In the Chaco Serrano remnants, increasingly smaller subsets of plant–herbivore and host–parasitoid interactions were found as forest area decreased, suggesting that a stable core of common interactions, maintained throughout the area gradient, might underlie the structure of these foodwebs.

Given the increased connectance of food webs in smaller remnants here reported, in addition to our previous findings of specialists being lost faster than generalists (Cagnolo et al.

2011), we expected core interactions to be defined by generalist species, i.e. consumer trophic breadth to be associated to the position of trophic interactions within the nested matrix. This was true for host–parasitoid webs, and fitting in with the extreme vulnerability of specialized parasitoids due to synergistic effects of specialization and trophic level (Cagnolo et al. 2011). Moreover, although host availability showed only a weak influence by itself, its combination

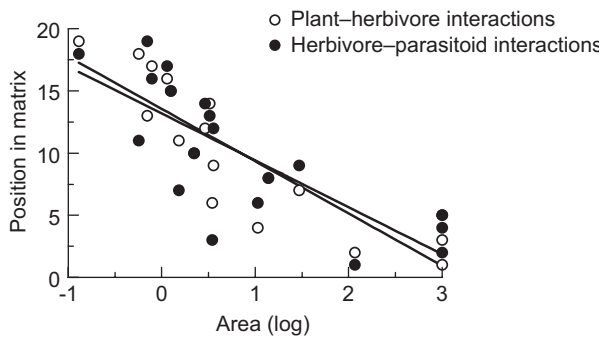


Figure 3. Relationship between area of 19 forest remnants and their ranking position in the nested interaction matrix, for plant-herbivore interactions and host-parasitoid interactions. Each point represents a remnant, and their position in the maximally packed interaction x site matrix resulting from nestedness analysis.

with parasitoid trophic breadth provided the best fit for the spatially nested pattern, suggesting that the central subset of interactions remaining through the area gradient involved generalist parasitoids feeding on relatively common hosts.

The spatial arrangement of interactions in plant-herbivore food webs was, instead, strongly underlined by resource availability. Being highly host specific, leafminers are constrained to use habitats where their host plants occur; hence such spatial interaction pattern may arise from bottom-up defined resource-consumer co-occurrence probabilities. Ubiquitous resources and their consumers, independently of the latter's trophic breadth, appear to define the core plant-herbivore interactions.

These results suggest that a spatially nested pattern could be driven by resource availability in systems with tightly established interactions (e.g. herbivore insects and their host plants), whereas in systems with looser interactions a similar arrangement might be driven by consumer trophic breadth and a weaker effect of resource distribution.

Further analyses and studies from other systems are needed to answer the questions raised by this pattern and to assess its applicability to other fragmented food webs. For example, the permanence of such core interactions suggests a rather limited scope for 'rewiring' (predators switching to food items not previously consumed following species removal), a mechanism proposed by Staniczenko et al. (2010) as an ecosystem buffer against environmental change. In any case, rewiring appears more likely to occur in host-parasitoid food webs, with their interaction spatial arrangement largely defined by a nucleus of generalist parasitoid species, probably concentrating on the most common resources as rarer ones disappear.

Food webs appear to be structured in ways that promote community stability and reduce species vulnerability to extinction (Dunne et al. 2002, Thebault et al. 2007, McCann and Rooney 2009). In this context, connectance (Thebault et al. 2007, Dunne and Williams 2009) and nested network configurations (Fortuna and Bascompte 2006) seem to play fundamental roles. Increased connectance and spatial nestedness, driven either by trophic breadth or by resource availability, may have mitigated species loss in the fragmented Chaco Serrano forest, thus allowing half of the species to remain after their habitat had been reduced by several orders of magnitude, whilst a single order of magnitude decline in habitat

size could drive 50% of species extinct according to estimates from species-area curves (Dobson et al. 2006). These observations highlight the importance of a food web approach in the context of conservation ecology, restoration ecology or habitat management (Mommott 2009, Tylianakis et al. 2010).

Summing up, the results of this study offer new insights into the effects of habitat fragmentation on complex biological systems and an improved understanding of the interactions between habitat fragmentation, species loss and food web structure, thus providing valuable information to allow more accurate predictions to be made about the consequences of human modifications to ecological systems.

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