

# Network topology: patterns and mechanisms in plant-herbivore and host-parasitoid food webs

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## Summary

1. Biological communities are organized in complex interaction networks such as food webs, which topology appears to be non-random. Gradients, compartments, nested subsets and even combinations of these structures have been shown in bipartite networks. However, in most studies only one pattern is tested against randomness and mechanistic hypotheses are generally lacking.
2. Here we examined the topology of regional, coexisting plant-herbivore and host-parasitoid food webs to discriminate between the mentioned network patterns. We also evaluated the role of species body size, local abundance, regional frequency and phylogeny as determinants of network topology.
3. We found both food webs to be compartmented, with interaction range boundaries imposed by host phylogeny. Species degree within compartments was mostly related to their regional frequency and local abundance. Only one compartment showed an internal nested structure in the distribution of interactions between species, but species position within this compartment was unrelated to species size or abundance.
4. These results suggest that compartmentalization may be more common than previously considered, and that network structure is a result of multiple, hierarchical, non-exclusive processes.

**Key-words:** abundance, body size, compartmentalization, food webs, leafminers, nestedness, network topology, parasitoids, phylogeny

## Introduction

Biological communities are organized in complex interaction networks such as food webs, which in their basic form are graphs showing who eats whom in a community. The topology of ecological networks has received attention from ecologists and evolutionary biologists because species position within these networks could affect their vulnerability to disturbance (Montoya, Pimm & Solé 2006) and their co-evolutionary dynamics (Bascompte, Jordano & Olesen 2006). There is evidence that ecological network topologies depart from randomness, showing regularities that are not yet fully understood.

Recently, Lewinsohn *et al.* (2006) proposed four alternative models of network organization: gradient, compartmented, nested and a combination of the latter two structures. Gradients are structures where species and interactions are gradually replaced. A compartment can be defined as a group of species interacting more often with species within the group than with the rest of the species in the network. Nested patterns apply to networks in which the interaction partners

of the more specialist species are proper subsets of those species interacting with the more generalists (Bascompte *et al.* 2003). Finally, combined patterns involve compartments with internal nestedness. Nested patterns have received most attention, possibly because of the availability of concepts and tools provided by the study of meta-communities (Leibold & Mikkelsen 2002), and were found mainly in mutualistic interaction networks (Bascompte *et al.* 2003). In turn, compartments have been reported mostly in antagonistic networks (Krause *et al.* 2003; Prado & Lewinsohn 2004; Rezende *et al.* 2009). Nevertheless, a weak point in the study of ecological network topology is that usually only one pattern is tested against randomness, ignoring alternative structures (Lewinsohn *et al.* 2006) and thus precluding attempts to link particular topological patterns to particular kinds of interactions (e.g. mutualisms and nestedness).

Although searching for causes and consequences seems the natural step following pattern recognition, few studies have evaluated the factors underlying network organization (Vázquez, Chacoff & Cagnolo 2009). Proposed mechanisms include body size (Cohen *et al.* 2005; Rezende *et al.* 2009), phylogeny (Cattin *et al.* 2004; Rezende *et al.* 2009), habitat heterogeneity constraints (Pimm & Lawton 1980; Rezende

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*et al.* 2009) and also encounter probability based on species spatiotemporal co-occurrence or natural abundance (Vázquez, Chacoff & Cagnolo 2009).

Body size imposes restrictions to species interactions, thus different network patterns could arise depending on whether species prefer a particular range of body sizes (Stouffer *et al.* 2007) as predicted by the niche model (Williams & Martinez 2000), or whether they interact with all partners beyond a particular threshold, as predicted by the cascade model of food webs (Cohen & Newman 1988). Evidence indicates that large plant species, offering more apparent targets, tend to recruit more insect herbivores (Strong, Lawton & Southwood 1984). In animal–animal interactions consumer and resource size are frequently correlated, so that predators tend to consume smaller preys than themselves and larger predators have a wider range of prey sizes (Cohen *et al.* 2005).

Phylogenetical constraints on interactions can also be expected as related species may share characteristics to which partners have to be adapted, sometimes leading to co-evolutionary ‘arm races’ (Agrawal 2007). It has been shown that phytophagous insects are more likely to switch between closely related plants (Brandle & Brandl 2001). Moreover, plant species within the same genus or family tend to share similar herbivore faunas (Novotny *et al.* 2004; Weiblen *et al.* 2006). Although originally proposed for plant–herbivore interactions, the same predictions can be made for host–parasitoid (Hawkins 1988), host–parasite (Krasnov *et al.* 2004) or other types of antagonistic interactions.

Under a scenario of no restrictions to interactions, species natural abundance may determine interaction probability (Janzen 1968), leading to network topologies associated with species abundance distribution. The mechanism behind this prediction involves the occurrence of interactions resulting from the random encounter of individuals leading to an accumulation of interaction partners in a site by locally abundant species, and across localities or habitats by regionally widespread species (Vázquez *et al.* 2009). Moreover, sampling artefacts could arise because abundant species may receive more attention by researchers than rare species (Vázquez *et al.* 2009).

Here we examine the topology of regional, coexisting plant–herbivore and host–parasitoid food webs, in an attempt to discriminate between the network models proposed by Lewinsohn *et al.* (2006). If phylogeny or body size imposes restrictions to interactions between species, we expect to find compartments in the studied food webs; on the other hand, if there are no restrictions, networks would show nested patterns with interaction probabilities mainly given by species frequency and abundance. Finally, gradient patterns would be found if there are environmental gradients across study sites.

## Materials and methods

### STUDY AREA

The Chaco Serrano District, belonging to the most extensive dry forest in South America, covers an area between 16° and 33°30'(S), rang-

ing in elevation from 400 to 1300 m above sea level. The annual rainfall of 750 mm is concentrated mostly in the warm season (October–April), with mean maximum and minimum monthly temperatures of 26 and 10°C respectively.

The characteristic vegetation is a low, open woodland, with a tree layer (8–15 m high) dominated by *Aspidosperma quebracho-blanco* Schltdl., *Prosopis* spp., *Zanthoxylum coco* Gillies ex Hook. f. & Arn. and *Lithrea molleoides* (Vell.) Engl.; shrubs (1.5–3 m) dominated by *Celtis pallida* Torr. and *Acacia* spp.; herbs and grasses (0–1 m) and many vines and epiphytic bromeliads (Cabido *et al.* 1991).

Nineteen woodland sites in an area between 31°10'–31°30'S and 64°00'–64°30'W were sampled. The woodlands are mainly used for cattle grazing, and are embedded in an agricultural matrix largely dominated by wheat in winter and soy or maize in summer.

### STUDY SYSTEM AND SAMPLING

Herbivores in this study were represented by leafminer insects, whose larvae feed and dwell inside a leaf, leaving internal tunnels (mines) easily detectable on the leaf surface (Connor & Taverner 1997). Mines offer an unmistakable record of herbivory, and rearing mining larvae to adults allowed us to establish plant–herbivore and host–parasitoid interactions accurately.

At each site, we collected all mined leaves detected along five 50 m long, 2 m wide and 2 m high transects (100 m<sup>2</sup>) in two occasions (November–December 2002 and February–March 2003) within the peak period of leafminer activity. We took mined leaves to the laboratory and reared adult leafminers and parasitoids, which were identified and counted. A vegetation assessment was also carried out on April–May 2003. At each sampling site, complete floristic composition was recorded 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).

Regional plant–herbivore and host–parasitoid networks were built by organizing data in a matrix form in which resource species were placed as rows and consumer species as columns. The number (sum across sites and dates divided by the number of square meters sampled) of leaf mines (herbivory food web) or adult parasitoids reared (parasitoidism food web) was placed on each intersection of row and column. To have a list of species and interactions as complete as possible, additional sampling transects from a previous season on 10 of the 19 sites studied were included. We excluded all interactions involving only one insect individual to avoid sampling mistakes or accidental interactions.

### SPECIES DATA

Plant, leafminer and parasitoid species were characterized according to the following traits:

#### Size

We calculated specific average leaf area as leaf length × width (assuming that all leaves were ellipse shaped), by using data extracted from literature when available or measuring herbarium specimens when not. Leafminer and parasitoid body length was measured on at least five adult specimens per species.

#### Local abundance

The local abundance of each species was calculated as its average abundance across the sites where it was present (i.e. excluding zero

values). Abundance data referred to the midpoint of the cover category on each site (in the case of plants) and to the number of mines (leafminers) or adults reared (parasitoids) per square meter sampled.

To be confident that our abundance estimation reflects species' natural abundance values, the densities registered in this study were validated with those from independent sources. For plant species, we found a correlation of 73% ( $P < 0.001$ ,  $n = 74$ ) with the data presented in Cabido *et al.* (1991). For insects we used a previous survey of ours in the same area and found a correlation of 70% for leafminers ( $P < 0.001$ ,  $n = 91$ ) and 56% for parasitoids ( $P < 0.001$ ,  $n = 97$ ).

### Regional frequency

As the geographical range of the studied insects is unknown, we derived the regional frequency of species by counting the number of sites it was detected in the present study. According to this methodology, the most common species was detected on 19 sites while the rarest one was restricted to a single site.

### Taxonomic distance

We followed the logic of the STD index of Poulin & Mouillot (2003) by constructing taxonomic trees of plants, leafminers and parasitoids. First, we assigned all species into hierarchically organized taxonomic nodes. Then we measured the taxonomic distance between a pair of species by counting the number of steps necessary to reach a common node. In the case of plants we used species, genus, tribe, family, class and order; for leafminers and parasitoids we used species, genus, sub-family, family, super-family, sub-order and order. According to this, if a pair of species has a taxonomic distance of one, differ only at species level; if they have a distance of two, differ at genus level, and so on.

The usage of taxonomic trees instead of phylogenetic distances has the disadvantage of underestimating evolutionary distances, as all steps are considered equal (i.e. a jump from species to species has the same value as jumping from order to order) (Weiblen *et al.* 2006). Nonetheless, considering the differences in availability and quality among insect and plant phylogenies, we decided to use rough but comparable taxonomic distances instead of phylogenetic distances of different reliability among groups.

## DATA ANALYSIS

### Identification of patterns in network topology

Leibold & Mikkelsen (2002) proposed a methodology for metacommunity analysis (species  $\times$  sites matrix) to evaluate the fit of an incidence matrix to some known patterns of matrix organization: nested, compartmented ('Clementsian' gradient) and gradient ('Gleasonian' gradient). The analysis begins by performing a Reciprocal Averaging ordination (Legendre 1998) that rearranges the matrix to place close together those species that have similar interaction partners. This procedure maximizes the accumulation of interactions along the main diagonal of the matrix reducing the number of interruptions (empty cells) in the species' interaction ranges (Lewinsohn *et al.* 2006).

The rest of the analysis is divided in three consecutive steps: the evaluation of 'Coherence', 'Species turnover' and 'Boundary clumping'. The Coherence of a matrix is related to the interruptions in contiguous sequences of species interactions that are called 'embedded absences'. A matrix is coherent if the number of embedded absences in a matrix is lower than that found in 95% of a large enough number

of null matrices (here 500) in which size, marginal sums and connectance are equal to those of the observed matrix.

The second step evaluates interaction range turnover by examining the number of 'checkerboard' units (Gotelli & McCabe 2002) in the matrix, and comparing this number with those of 500 null matrices of equal size, marginal sums and connectance. Checkerboard units can be found when adjacent species in the interaction matrix do not interact with the same partner indicating a high turnover in the interaction ranges. Instead of the raw number of checkerboards, we report the normalized *C*-score which represents the average number of checkerboard units for each unique species pair (Stone & Roberts 1990). If the *C*-score is lower than those found in 95% of the null matrices then the target matrix is considered to be nested. This analysis was repeated for the consumer and the resource side of each matrix.

If species interaction ranges turnover higher than expected by chance, the third step ('Boundary clumping') is carried out to evaluate the degree to which the boundaries of species host ranges in the matrix are clustered together. The method calculates the Morisita Similarity index (Morisita 1971) between interaction ranges of species pairs in the matrix, and then evaluates their independence with a Chi-squared test. If the species interaction ranges were independent of each other, the matrix may present a gradient structure, otherwise it is said to be compartmented. Moreover, this methodology was applied separately for resource and consumer species.

If a matrix appeared to be nested in the Turnover step, it was reanalysed to determine its degree of nestedness by calculating the nestedness metric based on overlap and decreasing fill (NODF) index (Almeida-Neto *et al.* 2008) which varies between 0 (non-nestedness) and 100 (perfect nestedness). We also calculated the probability of finding the same NODF value in 1000 null matrices with the same size, marginal sums and connectance using bipartite package (Dormann, Gruber & Fründ 2008) of R statistical software (R Development Core Team 2007). On the other hand, if a matrix resulted to be modular, we identified compartments (and species therein) using the Modularity Analysis method presented by Guimerà, Sales-Pardo & Nunes Amaral (2007). The algorithm of this software maximizes a modularity value (*M*) using Simulated Annealing as a way to simplify the search of combinations (Olesen *et al.* 2007). In its calculation of *M* for a network, the algorithm excludes small isolated compartments without any links to the main network. We calculated the probability of finding similar or higher *M* values in 1000 null matrices with the same size and connectivity distribution as the observed networks. After that, large enough compartments (at least  $3 \times 3$  species) were reanalysed with the described techniques to search for patterns in their internal structure.

### Exploring the role of size, abundance and phylogeny on network topology

Once determined which one of the network patterns more likely resembles the observed interaction matrix, we explored association between species positions within the network and life-history traits (size, local and regional abundance and taxonomic distance) in the following way:

**Compartmented pattern.** We performed Multiresponse Permutation Procedure (MRPP), a nonparametric test of dissimilarity between predefined groups, to test whether species within compartments showed more similar trait values than expected by chance. MRPP calculates the mean (group size weighted) of pairwise dissimilarity (Jaccard distance) of elements within groups (*d*), then

calculates the expected dissimilarity  $[E(d)]$  by reassigning randomly all the elements to equally sized groups. After that it calculates the within group chance of corrected agreement ( $A$ ), defined as  $1-[d/E(d)]$ , which varies between 1 (when there is no dissimilarity between the elements of any group) and 0 (when the dissimilarity is maximal). Finally, it calculates the  $P$ -value of obtaining an equal or smaller value of  $A$  from an approximation to a Pearson type-III distribution. MRPP analysis was performed using PC-ORD software (McCune & Mefford 1999). The taxonomic relatedness of species within compartments was examined using the raw taxonomic categories described before as variables in the MRPP analysis. The agreement of taxonomic categories to the predefined groups was then interpreted as an indicator of shorter taxonomic distances of species within compartments. As environmental boundaries are suggested to be responsible for compartment formation in interaction networks (Pimm & Lawton 1980; Rezende *et al.* 2009), we performed MRPP analysis using sites and species occurrence within them as predictor variables to test its agreement with possible network compartments in our data.

Finally, we performed permutation tests to evaluate if species within compartments showed average values of size, abundance and taxonomic distances significantly different from those of 1000 randomly assembled, equally sized species groups (Manly 1998). While MRPP analysis provided a measure of the general agreement between compartment classification and biological traits, permutation tests allowed us to discriminate to what extent and in which compartments species traits differ from randomness.

**Gradient or nested pattern.** We used correlation analysis to explore the relation between the position of species in the network (after conducting Reciprocal Averaging ordination in the case of gradients or maximally packing the matrix in the case of nestedness) and life-history traits.

**No pattern.** If no structure was recognized, we explored the role of life-history traits as determinants of species degree (number of different interaction partners) through correlation analysis.

## Results

We recorded a total of 423 species, of which 27% were plants, 31% were leafminers and 42% were parasitoids (species

names in Appendix S1–S3 in Supporting Information). We observed 142 615 and 14 934 trophic interactions corresponding to 250 and 662 different trophic links, in the plant-herbivore and host-parasitoid food webs respectively.

### IDENTIFICATION OF PATTERNS IN NETWORK TOPOLOGY

Both food webs showed to be coherent and presented higher interaction turnover than expected by chance, allowing us to discard nestedness as the most reliable pattern. The boundary clumping analysis indicated that the interaction ranges of plants, leafminers and parasitoids were not independent, meaning that species tend to share interaction partners more frequently than expected by chance (Table 1). These results suggest that both plant-herbivore and host-parasitoid food webs are organized as compartments in which the internal connectivity is higher than in the rest of the network.

The Modularity analysis confirmed a compartmented structure in both webs (Table 1). The herbivory food web showed the highest modularity value (Table 1), with 26 isolated pairwise interactions and 29 compartments ranging in size from 3 to 21 species (Fig. 1). The host-parasitoid food web showed three isolated pairwise interactions and seven compartments comprising 3–90 species (Fig. 2). Moreover, only one compartment in the herbivory network showed an internal nested structure (observed NODF = 55.56, expected NODF = 47.46,  $P = 0.02$ ; Table S1 in Supplementary Information and Fig. 1), out of those large enough to be individually analysed (more than three rows and three columns: eight and five compartments in the herbivory and parasitoidism food web, respectively).

### EXPLORING THE RELATION OF SIZE, ABUNDANCE, FREQUENCY AND PHYLOGENY WITH NETWORK TOPOLOGY

From all traits evaluated through MRPP, we found that on average, species taxonomy was the factor showing best agreement with the identified compartments (Table S2 in Supple-

**Table 1.** Network topology analysis results for plant-leafminer and leafminer-parasitoid food webs from the Chaco Serrano in Central Argentina

| Analysis          | Statistic                    | Herbivory            | Parasitoidism     |
|-------------------|------------------------------|----------------------|-------------------|
| Coherence         | Embedded absences            | 961*                 | 5155**            |
|                   | Null expectation ( $\pm$ SD) | 1350.17 $\pm$ 132.79 | 9505 $\pm$ 973.41 |
| Turnover          | C-score (consumers)          | 0.96*                | 0.75***           |
|                   | Null expectation ( $\pm$ SD) | 0.94 $\pm$ 0.01      | 0.47 $\pm$ 0.04   |
|                   | C-score (resources)          | 0.98***              | 0.88***           |
|                   | Null expectation ( $\pm$ SD) | 0.89 $\pm$ 0.02      | 0.60 $\pm$ 0.03   |
| Boundary clumping | Morisita Index (consumers)   | 2.01                 | 9.14              |
|                   | Chi-square (d.f.)            | 349.96 (127)***      | 1625.86 (177)***  |
|                   | Morisita Index (resources)   | 1.30                 | 2.19              |
|                   | Chi-square (d.f.)            | 185.40 (110)***      | 508.68 (88)***    |
| Modularity        | $M$                          | 0.67*                | 0.46**            |
|                   | Null expectation ( $\pm$ SD) | 0.58 $\pm$ 0.01      | 0.41 $\pm$ 0.005  |

Probability to find the same value in null matrix: \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ .

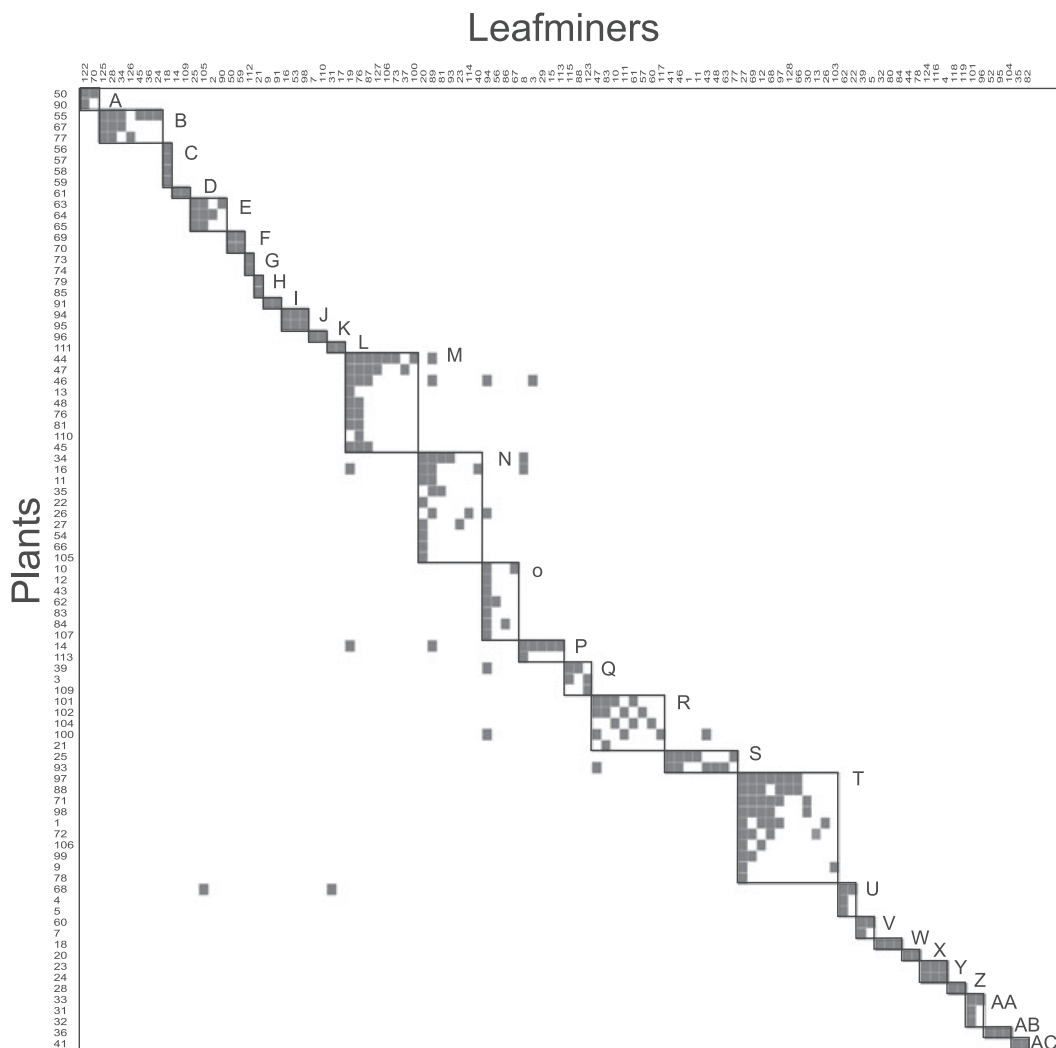
mentary Information). This was particularly true for the resource side of each network, i.e. plants in the herbivory food web ( $A = 0.75$ ,  $P < 0.001$ ) and leafminers in the parasitoidism food web ( $A = 0.36$ ,  $P < 0.001$ ). On the other hand, consumer species affiliation to compartments appeared to be guided by their co-occurrence in the studied sites in the herbivory food web ( $A = 0.12$ ,  $P < 0.001$ ) and by body size in the case of parasitoids ( $A = 0.1$ ,  $P < 0.001$ ).

Within plant-leafminer compartments, most plant species showed shorter taxonomic distances than expected by chance (Fig. 3). Compartments tend to encompass plants of the same genus, according to the average taxonomic distance (2.11) among species. Besides the major effect of taxonomic distance, other significant departures from randomness were observed: two compartments showed larger leaf area, two showed higher local abundance and one higher regional frequency than expected (Fig. 3).

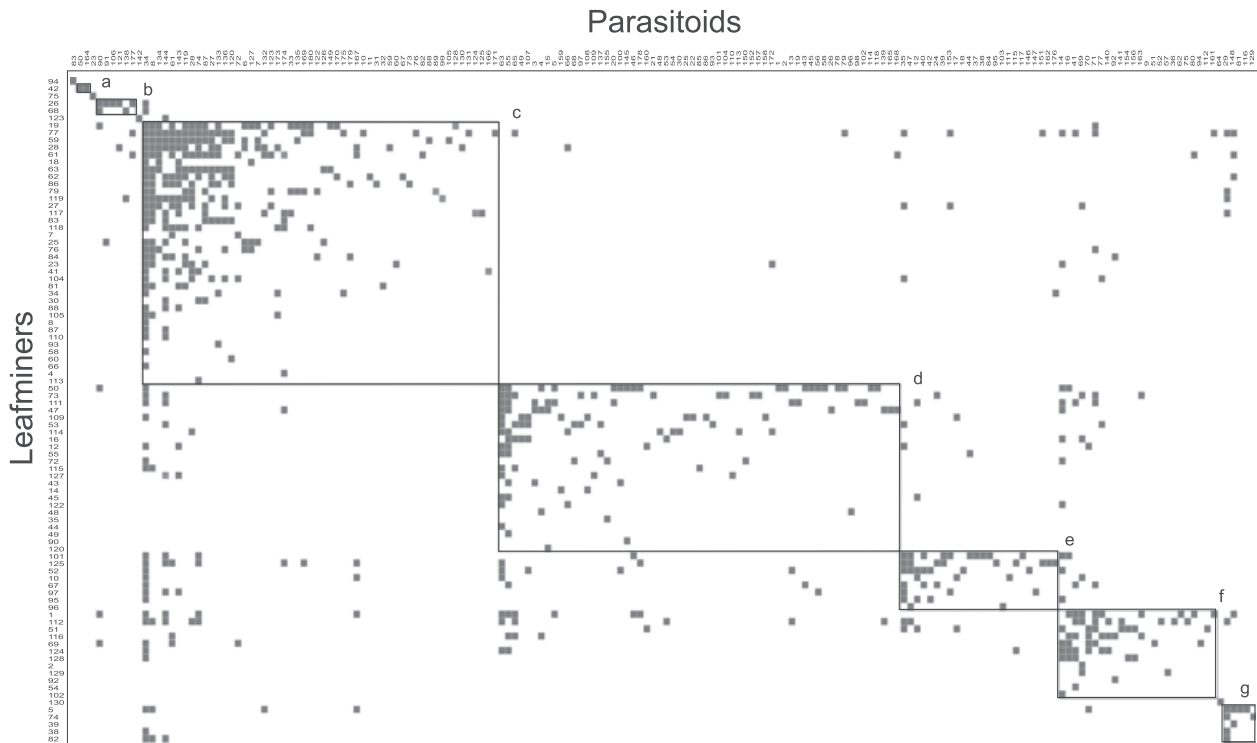
The consumer side of the herbivory food web (leafminers) showed less consistent patterns (Fig. 3). Only two compart-

ments (Z and W) had shorter taxonomic distances than expected by chance; both represented agromyzid (Diptera) species from a single genus (*Phytomyza* and *Liriomyza*) feeding on single plant species (*Clematis montevicensis* and *Bromus unioloides* respectively). Leafminers in three compartments showed higher local and regional abundance than expected. Only one compartment (S) showed a consistent pattern for consumers and resources, enclosing leafminers as well as plants with higher abundance and frequency than expected (Fig. 3).

In the parasitoidism food web, leafminers in three compartments showed shorter taxonomic distances than expected (Fig. 4). Their average taxonomic distance was higher than in the herbivory web, with compartment boundaries operating at the family level: two compartments were composed mainly by lepidopteran leafminers of Nepticulidae (compartment e) and Gracillariidae-Gelechiidae (compartment d), and the other one (compartment c) by agromyzid flies. Host species in the latter



**Fig. 1.** Plant-leafminer food web of the Chaco Serrano forest from Central Argentina. Row and column numbers are codes for species names given in Supporting Information. Compartments are outlined and uppercase letters are compartment names. Isolated pairwise interactions were removed from the figure for clarity.



**Fig. 2.** Leafminer-parasitoid food web of the Chaco Serrano forest from central Argentina. Row and column numbers are codes for species names given in Supporting Information. Compartments are outlined and lowercase letters are compartment names.

compartment were also smaller, had higher regional frequency and sustained parasitoids that were more closely related, smaller and abundant than expected by chance (Fig. 4). In the Gracillariidae-Gelechiidae compartment hosts and parasitoids were larger than expected, the latter being also rarer at regional level.

The internal structure of interactions within compartments was mostly explained by species regional frequency and local abundance. In general, species degree within compartments was positively associated with their abundance or frequency, meaning that common species tend to have more interaction partners than rare species (Table 2). Nevertheless, in the particular case of the only significantly nested compartment (O) we found no relationship between species position in the compartment matrix, arranged as to maximize nestedness and the studied traits (in all cases  $P > 0.05$ ).

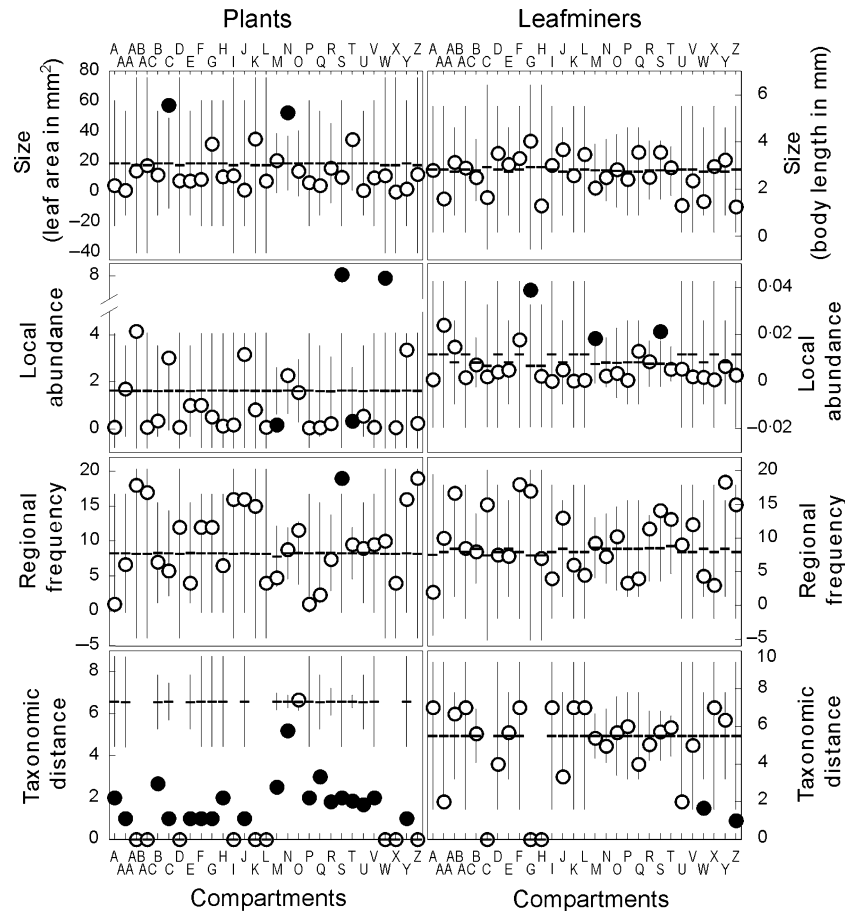
## Discussion

Food webs are paradigmatic examples of complex systems in nature (Montoya, Pimm & Solé 2006). Despite their complexity, several patterns of organization have been recognized among interaction networks, ranging from highly connected to compartmentalized structures (Lewinsohn *et al.* 2006). This is, to our knowledge, the first study assessing the fit of different patterns against the structure of two networks intimately related but resulting from different feeding modes, while also analysing possible ecological and phylogenetical correlates for the observed topologies.

Most studies evaluating the structure of ecological networks have focused on detecting one particular pattern against a randomly assembled network (Lewinsohn *et al.* 2006). The methodology here employed (Leibold & Mikkelson 2002) allowed us to discriminate whether the studied interaction matrices presented a nested, gradient or compartmented pattern. For both herbivory and parasitoidism food webs, the best fit proved to be a compartmented structure, with species organized in groups where the internal connectivity is higher than in the rest of the network.

The observed compartmented structure agrees with the expected relation between interaction intimacy and network structure (Guimarães *et al.* 2007), as leafminers as well as many parasitoids develop inside host bodies. Nevertheless we also expected that parasitoids here studied to conform to a nested network of interactions considering their high diversity and low specificity (Salvo & Valladares 2004). On the other hand, interactions between herbivores and plants showed higher compartmentalization than those between parasitoids and hosts, with more and smaller compartments. As a compartmented structure derives from restrictions to host ranges, such differences could be expected from the contrasting habits of highly specialist leafminers and generalist parasitoids.

The search for highly connected groups has long attracted ecologists but it was the development of powerful compartment detection algorithms that allowed scientists to find this kind of structure across a wide range of networks with different interaction types (Olesen *et al.* 2007). Through different



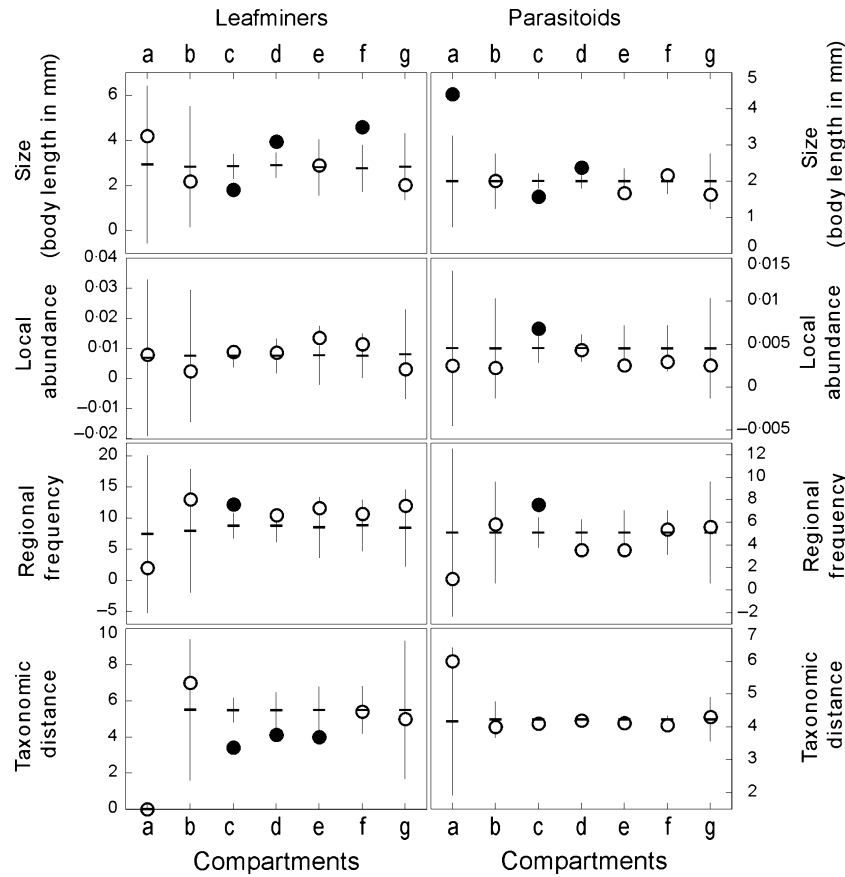
**Fig. 3.** Average values of species traits within compartments and average values obtained for same size groups of species randomly selected from the plant-leafminer food web from the Chaco Serrano forest in central Argentina. Horizontal lines are trait random expected values, vertical lines are 95% percentile confidence intervals (Manly 1998) of random expectations, empty circles are observed trait values not different from random expectations ( $P > 0.05$ ), and black circles are observed trait values different from random expectations ( $P < 0.05$ ).

methodological approaches compartmentalization has been found in pollination (Dicks, Corbet & Pywell 2002; Olesen *et al.* 2007), ant-plant (Fonseca & Ganade 1996; Guimarães *et al.* 2007), plant-fungus (Vacher, Piou & Desprez-Loustau 2008), multitrophic level food webs (Krause *et al.* 2003; Rezende *et al.* 2009) and plant-herbivore (Prado & Lewinsohn 2004) interaction networks. This study is the first report of compartments in plant-leafminer and leafminer-parasitoid food webs.

Compartmented and nested patterns are not mutually exclusive, as compartments can have an internal nested structure (Lewinsohn *et al.* 2006). Compartments that were large enough for an internal nested organization actually showed it in only one case in the herbivory web, nevertheless, the small size of most compartments could prevent the identification of nestedness in their internal structure (Guimarães *et al.* 2006). Nested patterns are characterized by highly asymmetrical interactions (high degree species interacting with low degree species) and a central core of highly interconnected species (Bascompte *et al.* 2003). They have been more frequently shown for mutualistic interactions such as pollination and frugivory (Bascompte *et al.* 2003),

although antagonistic examples are also known (Krasnov *et al.* 2005).

Despite the advances in the identification and description of network patterns, relatively little is known about the mechanisms behind these structures (Vázquez, Chacoff & Cagnolo 2009). As an attempt to explore those mechanisms, we evaluated the probability of species within compartments showing non-random average values of abundance, size or taxonomic distance. Compartments may arise through lineage divergence via escape-and-radiate or simply by tight co-evolution, as expected for plant-herbivore interactions (Thompson 1999). This hypothesis predicts that clades of plants and herbivores will mirror each other in their patterning of speciation events. Our results indicate that species within compartments had shorter taxonomic distances than expected by chance, although only when resource species were considered. The trophic interaction with closely related species is a widely demonstrated pattern in different systems including fleas and mammals (Krasnov *et al.* 2004), pathogens and plants (Gilbert & Webb 2007), predation (Cattin *et al.* 2004), parasitic fungus and plants (Vacher, Piou & Desprez-Loustau



**Fig. 4.** Average values of species traits within compartments and average values obtained for same size groups of species randomly selected from the leafminer-parasitoid food web from the Chaco Serrano forest in central Argentina. Horizontal lines are trait random expected values, vertical lines are 95% percentile confidence intervals (Manly 1998) of random expectations, empty circles are observed trait values not different from random expectations ( $P > 0.05$ ), and black circles are observed trait values different from random expectations ( $P < 0.05$ ).

**Table 2.** Correlation between life-history traits and species degree within compartments. Only significant and higher correlation coefficients are shown

| Food web      | Compartment | Number of species | Variable           | <i>R</i> | <i>P</i> |
|---------------|-------------|-------------------|--------------------|----------|----------|
| Herbivory     | M           | 19                | Regional frequency | 0.70     | < 0.001  |
| Herbivory     | T           | 21                | Regional frequency | 0.44     | 0.008    |
| Herbivory     | W           | 4                 | Local abundance    | 0.98     | 0.01     |
| Herbivory     | AA          | 5                 | Local abundance    | 0.91     | 0.03     |
| Parasitoidism | b           | 8                 | Regional frequency | 0.87     | 0.003    |
| Parasitoidism | c           | 90                | Regional frequency | 0.80     | < 0.001  |
| Parasitoidism | d           | 85                | Regional frequency | 0.88     | < 0.001  |
| Parasitoidism | e           | 32                | Regional frequency | 0.76     | < 0.001  |
| Parasitoidism | f           | 36                | Regional frequency | 0.88     | < 0.001  |

2008) and specially herbivores and plants (Strong, Lawton & Southwood 1984; Weiblen *et al.* 2006). Declining interaction range similarity with increasing phylogenetic distance between resource species could have two non-mutually exclusive explanations. One involves the tracking of chemical, morphological or ecological host traits (Cornell & Hawkins 2003) usually shared by related species (Agrawal 2007). The other involves the phylogenetic conservatism of host choice because of offspring feeding on the same host lineages as their parents (Barron 2001).

Despite the concordance between results of herbivory and parasitoidism food webs, host taxonomic distances within compartments were different for both food webs. While leafminer species within compartments tended to consume plants of a common genus, in agreement with other studies on host use by phytophagous insects (Novotny *et al.* 2004; Ødegaard, Diserud & Østbye 2005), host taxonomic distances were longer for parasitoids, which concentrated on leafminers belonging to the same order or family. These results could reflect differences in the evolutionary time of critical taxo-



nomnic events for host utilization: while leafminers seem to be affected by recent taxonomic branching, host selection by parasitoids could reflect ancient events. Nevertheless, we are not aware about how comparable are taxonomical categories across taxa.

Although phylogenetic factors appeared to be key determinants of compartment species composition, according to MRPP analysis, other traits like species size and abundance were also relevant. Particularly interesting examples are compartments c (agromyzid flies) and d (mostly Gracillariidae and Gelechiidae moths) in the parasitoidism food web, suggesting host and parasitoid species size matching. According to the cascade model of food web assembly based on body size, large predators should consume equal or smaller sized preys (Cohen *et al.* 2005) whereas the niche model predicts that predators should consume prey in a particular size range (Williams & Martinez 2000). The apparent size matching in the mentioned compartments suggest an agreement with the niche model prediction, which implies a reasonable balance between energetic input and host manipulation difficulties. The weakness of host phylogeny matching with compartment structure in the parasitoidism food web could be related to other characteristics that have been proved to be important in herbivore-parasitoid interactions, such as enemy free space (Nyman, Bokma & Kopelke 2007), species behaviour (Connor & Taverner 1997) or mine appearance (Salvo & Valladares 2004).

Finally, interaction structure within compartments, as indicated by species degree, was associated with species regional frequency and local abundance. Explanations derived from Island Biogeography Theory (MacArthur & Wilson 1967) could apply to this result. Encounter probability between species may increase as abundance increases, as originally proposed to explain variations in the number of associated herbivores to a particular plant species (Janzen 1968). Regional and local abundance may operate in a slightly different way: while regionally frequent species may capture consumer beta diversity, locally abundant species may be more efficient at sampling consumers within a community (Strong, Lawton & Southwood 1984). At the same time, sampling artefacts could be involved as abundant species receive more sampling effort than rare species (Vázquez *et al.* 2009). Our results support neutrality as a network assembly mechanism (Krishna *et al.* 2008) as the combination of resource and consumer abundance resulted in the observed internal configuration of some compartments.

In this study, we have evaluated the structure of two linked food webs that, taken together, compose the largest plant-leafminer-parasitoid food web studied until now. We found that both networks are compartmented and by the same reason: host phylogeny, with structure within compartments being determined by species abundance and frequency. These results suggest that network structure may be the result of multiple, hierarchical, non-exclusive processes (Vázquez *et al.* 2009). We expect this study to be a step forward in a way to predict the conditions under which certain network patterns are to be expected and, at the same time, the realiza-

tion that such configurations may be indicative of co-evolutionary and ecological processes.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Plant species names and compartment affiliations.

**Appendix S2.** Leafminer species names and compartment affiliations.

**Appendix S3.** Parasitoid species names and compartment affiliations.

**Table S1.** Nestedness analysis for all compartments in both food webs.

**Table S2.** Multiresponse permutation procedure analysis results for all studied traits.

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