

# Compartments in insect–plant associations and their consequences for community structure

PAULO INÁCIO PRADO\*† and THOMAS MICHAEL LEWINSOHN†

\*Núcleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas, Campinas, Brazil; and

†Laboratório de Interações Insetos-Plantas, Departamento de Zoologia, Universidade Estadual de Campinas, Campinas, Brazil

## Summary

1. Compartmentation has been less explored than other forms of community structure. We assessed compartmentation of associations between insects and plants on a regional scale, and analysed some of its causes and consequences. The data set used was the host records of fruit flies (Diptera; Tephritidae) that breed in flowerheads of plants of the tribe Vernoniae (Asteraceae) in the Espinhaço Mountain range, Minas Gerais, Brazil. This data set was obtained with a consistent sampling protocol and is taxonomically fully resolved.

2. The binary association matrix had a total of 35 insect and 81 plant species. Most of the insects were specialized on plants of a single subtribe, genus or species group. Correspondence analysis showed that the association matrix is divided in six well-delimited compartments of insects specialized on subtribes or genera of plants.

3. Host dissimilarity among insects and insect dissimilarity among plants were expressed as Jaccard distances. Tests with a multi-response permutation procedure (MRPP) showed that both kinds of dissimilarities were higher among compartments than within them.

4. Monte Carlo randomizations were used to compare matrix parameters with values expected in the absence of compartments. In 4000 runs, the number of insect species that shared at least one host plant (ecological neighbours) was smaller than expected. Nevertheless, mean host similarity among insects, and the proportion of exclusive host plants used by each insect species did not differ from null model predictions. Host similarity of insects with their nearest neighbours in niche space was higher than expected by the null model. On the other hand, host similarity with farthest neighbours was lower than expected.

6. The observed compartmentation of insect/plant associations can be ascribed to the marked specialization of flowerhead tephritids, and allows the reduction of diffuse competition among insects. However, compartmentation did not decrease overall niche overlap among insects because reduction in number of neighbours is offset by increased overlap with species in the same compartment. Therefore, the pattern in this system cannot be derived from resource partitioning alone.

*Key-words:* Brazil, Campos Rupestres, niche overlap, null-models, Tephritidae, Vernoniae.

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## Introduction

One of the first principles of insect–plant ecology is that most phytophagous insects feed on only a minute

fraction of all the plant species in their surroundings (Brues 1924; Strong, Lawton & Southwood 1984; Jaenike 1990; Farrell & Mitter 1993; Bernays & Chapman 1994; Thompson 1994; Futuyma & Mitter 1996). The host ranges of most herbivorous insects are restricted to a few plant genera or families because the attributes that constrain insect usage are customarily similar among related plants (Strong *et al.* 1984; Jaenike 1990; Farrell & Mitter 1993; Ward & Spalding 1993; Futuyma & Mitter 1996). However, these constraints are not

Correspondence: Paulo Inácio Prado, Núcleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas, Caixa Postal 6166, Campinas – SP, CEP 13084–971, Brazil.  
Tel: + 55 19 37887631; Fax: + 55 19 37887690;  
E-mail: prado@unicamp.br

obligate correlates of plant taxonomy, and insects may use unrelated plants that share other key attributes, such as chemicals, microhabitat preferences or geographical distribution (Feeny 1992; Menken 1996; Becerra 1997; Becerra & Venable 1999).

At the community level, as a consequence of the specialization of phytophagous insects, the phytophagous assemblage may be split into compartments of insect species that use different plant subsets (Root 1973; Lawton & Pimm 1978). Compartmentation is possible if the rules that set host ranges are the same or are correlated for all herbivores, a reasonable condition for closely related insect species (Futuyma & Gould 1979; Straw 1989a; Denno, McClure & Ott 1995). Like the hypothesis of food-web compartmentation due to habitat segregation (Pimm & Lawton 1980; Pimm 1982), this is a biological explanation for the existence of compartments (Pimm 1982; Winemiller 1990; Jordano, Bascompte & Olesen 2003). Among theoretical hypotheses, the argument that compartments enhance the stability of food webs has been most extensively scrutinized (May 1973; McNaughton 1978; Rejmánek & Stary 1979; Yodzis 1980; Pimm 1982; Krause *et al.* 2003).

However, a different theoretical explanation also derived from competition theory remains largely untested. A compartment can be defined as a ‘subgroup of taxa in which many strong interactions occur within the subgroups and few weak interactions occur between subgroups’ (Krause *et al.* 2003; see also Yodzis 1980). Hence, in compartmented systems the overall number of interactions that can occur is reduced, but the strength of the ‘allowed’ interactions (within compartments) may increase (Pianka 1980; Joern & Lawlor 1981; Winemiller & Pianka 1990). This is in accordance with the classical argument that species that converge in using a particular resource subset escape from diffuse competition, but increase niche overlap among themselves; at least in theory, such reduction of diffuse competition can overcompensate the increase in niche overlap among species of the same compartment and thus reduce the net competitive effects in the community (MacArthur & Levins 1967; Pianka 1974). These models conceive compartmentation as an optimal configuration towards which communities will evolve by means of resource-partitioning and competitive exclusion (Pianka 1974; Inger & Colwell 1977).

Whatever their causes, compartments are a primary constraint on ecological and evolutionary processes, because they delimit the sets of species that can potentially interact (Root 1973; Yodzis 1980; Raffaelli & Hall 1992; Futuyma & Mitter 1996; Montoya & Solé 2002; Jordano *et al.* 2003; Krause *et al.* 2003). Therefore, compartments are often viewed as a basic structural property of communities and food webs, although there is as yet no consensus on procedures to detect them (e.g. Pimm & Lawton 1980; Winemiller 1990; Raffaelli & Hall 1992; Fonseca & Ganade 1996; Solow & Beet 1998; Montoya & Solé 2002; Krause *et al.* 2003).

The status of compartmentation in the literature on community structure is somewhat unclear. At first, compartments were apparently taken for granted. Based on two well-studied cases (Lawton & McNeill 1979), Pimm & Lawton (1980) adduced that compartments should be commonplace in plant–herbivore assemblages; however, they also stipulated that a community is compartmented only when compartments traverse demonstrably at least three trophic levels. This strict condition seems to be met only in food webs which span distinctive habitats whose spatial boundaries are impressed in food-web structure (Pimm, Lawton & Cohen 1991). Raffaelli & Hall (1992) found no such habitat imprint in a thoroughly documented large web, although they recognized compartment structures in some previously analysed webs. Since their study the subject has received less attention than other forms of community structure, until the recent application of innovative analytical approaches (Solow & Beet 1998; Montoya & Solé 2002; Krause *et al.* 2003). Some recent studies also have found evidence for compartmentation in plant–animal mutualistic assemblages (Fonseca & Ganade 1996; Dicks, Corbet & Pywell 2002).

In this paper we probe compartmentation structure in a plant–herbivore assemblage by means of correspondence analysis, followed by a permutation test to assess the distinctness of compartments. We also evaluate host overlap with a randomization procedure to test hypotheses on competitive structuring in this assemblage. The analysed data set comprises plants of the tribe Vernonieae (family Asteraceae) and the fruit flies (family Tephritidae), that breed in their flowerheads, in the highland vegetation of the Espinhaço Mountain Range in Brazil. To date, 35 insect species and 81 host-plant species were recorded in this system (Prado *et al.* 2002). This system is a suitable candidate for compartmentation because the insects belong to the same subfamily, use resources in a very similar way, and have narrow host ranges. This data set is fully and consistently resolved in taxonomic terms and does not suffer from the problem of taxonomic or trophic aggregation that troubles some analyses, especially those of multitrophic webs (Pimm 1982; Sugihara, Shoenly & Trombla 1989; Martinez 1991; Raffaelli & Hall 1992).

We address the following questions: (1) are there detectable compartments in this insect–plant matrix? (2) If compartments are detectable, can they be attributed solely to the trend of insects to use taxonomically related plants? (3) Do compartments influence the number of interactions among insect species, or their overlap in host use?

## Methods

### STUDY AREA

The Serra do Espinhaço is a chain of low mountains and plateaux (800–2100 m) composed mainly of Precambrian quartzitic rocks. It covers an area of about

6000 km<sup>2</sup>, extending from the central part of the state of Minas Gerais (20°35' S) to northern Bahia (about 10° S), a length of 1200 km in the N–S direction, centred at 43° W (Saadi 1995).

The *campos rupestres* (literally, rupestral fields) are a complex of highland savannas and grasslands that occur in this chain above altitudes of 900 m, where soils are sandy and poorly developed (Harley 1995; Giuliatti, Pirani & Harley 1997). Climate in the Espinhaço *campos rupestres* is mesothermic (Cwb of Köppen), with average annual temperatures between 17.4 °C and 19.8 °C, a summer rainy season, a dry 3–4-month winter season and approximately 1500 mm annual rainfall in the southern range, where our sites are located (Giuliatti *et al.* 1997). The vegetation has very high plant diversity and endemism (Harley 1995; Giuliatti *et al.* 1997). The Asteraceae rank among the three most important plant families, with local diversities ranging from 50 to more than 150 species (Leitão Filho & Semir in Giuliatti *et al.* 1987; Hind 1995).

#### STUDY SYSTEM

The plant and insect records used in the present study pertain to an extensive inventory of endophagous insects of flowerheads of Asteraceae in Brazil (Lewinsohn 1991; Prado *et al.* 2002). Tephritidae is the most diverse and abundant family among this group of endophages, and currently it is also the best known (Prado *et al.* 2002).

Asteraceae is the largest family of plants, and occurs worldwide, with highest diversities in open vegetation types (Barroso 1986; Bremer 1994). Vernoniaeae is one of the largest and more widespread tribes of Asteraceae in the Neotropics (Barroso 1986; Bremer 1994; Robinson 1999). It is especially important in the highlands of south-eastern and central Brazil (including the *campos rupestres*), to which an entire subtribe is endemic, the Lychnophorinae (Robinson 1999). In Brazil, flowerheads of Vernoniaeae are used by endophagous species of several dipteran and moth families. Tephritids comprise about two-thirds of the species and individuals recorded to date (Lewinsohn 1991; Prado *et al.* 2002).

Tephritids that breed in flowerheads of Vernoniaeae are a well-defined system. Among the 35 species reared from Vernoniaeae in the Espinhaço range, only six were also reared from plants of other tribes (Lewinsohn 1991; Prado 1999; Almeida 2001; Prado *et al.* 2002), and even these species tend to be specialized. Two of them (*Tomoplagia incompleta* (Williston) and *Dictyotrypeta* sp. 2) are associated primarily with Vernoniaeae, and occasionally with the tribe Mutisieae. *Dictyotrypeta* sp. 3 is also associated with these two tribes, but its Vernoniaeae hosts are all in the endemic subtribe Lychnophorinae. Conversely, *Trupanea* sp. 1, *Xanthaciura biocellata* (Thomson) and *X. chrysura* (Thomson) are specialists on the tribes Eupatorieae and Heliantheae, but were reared from Vernoniaeae only sporadically (5% of the samples and 2% of the individuals reared).

#### SAMPLING OF FLOWERHEADS AND INSECT REARING

Five localities of *campo rupestre* vegetation in the Espinhaço Range in Minas Gerais were surveyed: Grão Mogol (centroid coordinates of sampling sites: 16°34' S 42°42' W), Serra do Cabral (17°43' S 44°44' W), Diamantina Plateau (18°13' S 43°43' W), Serra do Cipó (19°15' S 43°43' W) and Ouro Branco (20°30' S 43°43' W). In order to cover flowering periods of most plant species, each locality was sampled five times between February 1995 and September 1996, in different seasons of the year. In each locality we inspected five to 10 sites with a minimum spacing of 500 m (usually more than 2 km) and sampled flowerheads in different developmental stages from all flowering species of Vernoniaeae found. The number of sampled capitula ranged from tens to several thousand depending on their individual size, plant fecundity and the commonness of the plant at each site; whenever possible samples were standardized to 500–1000 ml of fresh volume. Insects were reared from the flowerhead samples in the laboratory. Further details on rearing procedures, insect sorting and identification and vouchers can be found in Prado *et al.* (2002).

#### DETECTION OF COMPARTMENTS

The analysed matrix contained presence/absence data of species of tephritids recorded on each Vernoniaeae species, pooled over all sampling localities. Hence, this is a composite web which represents the regional pools of plants and tephritids that can use them.

A correspondence analysis (CA, Gauch 1982; ter Braak 1995), was used to distinguish clusters of plant species each used by a shared set of insect species. Although CA has been used commonly to represent patterns of gradual replacement of species along presumed environmental gradients it is also able to detect discontinuities, or blocks of species (ter Braak 1995). CA organizes a presence–absence matrix by maximizing the reciprocal association between its rows and columns, hence standard scores of insects on the CA axes will be similar to the standard scores of their host plants. Thus compartments can be identified as clusters of plant and insect scores. As noted by ter Braak (1995), CA axes can reveal matrix structures ranging from a continuous gradient (diagonal structure, or Petrie matrix) to complete compartmentation ('blocking'); the eigenvalue associated with each CA axis has the maximum value of one when there is perfect blocking, which provides a potential reference to assess degree of compartmentation. Compartments were therefore delimited as sets of insect species and plant species whose standardized scores formed distinct clusters along one of the first four CA axes. A cluster analysis (Ward method, Euclidean distances) was then used to outline the clusters. Due to its high sensitivity to rare species, CA can separate uninteresting blocks

formed by single species (Gauch 1982; ter Braak 1995). To avoid this, plants associated with a single insect species were excluded from the CA calculations, but their scores were then computed to include them in the cluster analysis.

#### STATISTICAL TESTING OF COMPARTMENTATION

Once outlined, compartments can be validated statistically by testing whether trophic similarity is significantly higher within than among compartments. For this we used the multiresponse permutation procedure (MRPP) (Biondini, Bonham & Redente 1985; McCune & Mefford 1999), a non-parametric test of differences among predefined groups. In MRPP the mean dissimilarity among pairs of elements within groups is compared to the mean value expected if groups were assembled at random. The ratio between observed and expected values is the ‘within-group chance-corrected agreement index’ ( $A$ ), whose maximum value is one when there is no difference among entities of the same group. The associated  $P$ -value is taken from an approximation to a Pearson type-III distribution (McCune & Mefford 1999). Further MRPP analyses tested host dissimilarities among species of insects and endophage dissimilarities among plant species, within compartments, with dissimilarity measured as Jaccard distance. Mean within-group dissimilarity was weighted by group size, according to Mielke (McCune & Mefford 1999):

$$p_i = n_i/N$$

where  $p_i$  is the weight for entities of group  $i$ ,  $n_i$  is the number of entities in the group, and  $N$  is the total number of entities.

#### COMPARTMENTS AND HOST OVERLAP AMONG INSECTS

Monte Carlo simulations were used to compare indices of niche overlap among insect species to values expected in the absence of compartments. We constructed 4000 randomized matrices by reassigning at random the host plants of each species of insect. Given that the columns of the matrix represent the host vectors of each insect, randomizations shuffled each vector independently. This algorithm, proposed by Sale (1974), was named RA3 by Lawlor (1980) or ‘scrambled zeroes’ by Winemiller & Pianka (1990). It is a null model that conserves the host breadth of insects, but disassembles compartments (Winemiller & Pianka 1990).

The following statistics were calculated from each randomized matrix:

1. Mean host Jaccard similarity among insect species. Host species similarity was calculated for each pair of insect species. Overall mean similarity was set as the sum of between-pair similarities, divided by total number of pairs:

$$\bar{X} = (\sum x_{ij})/N$$

where:  $x_{ij}$  = host similarity between insect species  $i$  and  $j$ ,  $N$  = total number of pairs. This index is the complement of the Jaccard distance used for MRPP analyses.

2. Mean number of neighbours of insect species: Inger & Colwell (1977) and Winemiller & Pianka (1990) termed ‘neighbours’ those species that share common resources, because they are in the same niche space. Insect species that shared at least one plant species were considered neighbours, and represent potentially interacting species. The number of neighbours of each insect species was counted, and then mean number of neighbours was computed across all insect species.

3. Similarity by neighbourhood ranking: the closeness of a neighbour is its degree of overlap in niche hyperspace. Resource overlap indices can be used to rank neighbours of a given species as the first, second, up to the furthest, and then the mean community overlap can be calculated at each rank (Inger & Colwell 1977; see Winemiller & Pianka 1990 for simple graphical and numerical examples). A plot of mean overlap by neighbour rank is very effective to detect whether assemblages are structured in well-defined guilds or compartments (Winemiller & Pianka 1990; Gotelli & Graves 1996), equivalent to compartmentation, by showing high mean overlap with close neighbours and very low overlap with distant ones (Inger & Colwell 1977; Winemiller & Pianka 1990). Neighbours of each insect species were ranked according to Jaccard host similarity, and means of host similarities at each rank were calculated.

The probability that each of these statistics was higher or lower than expected by the null model of no compartments was estimated as the proportion of randomized matrices that had more extreme values of the statistics than those of the observed matrix (Gotelli & Graves 1996; Manly 1998).

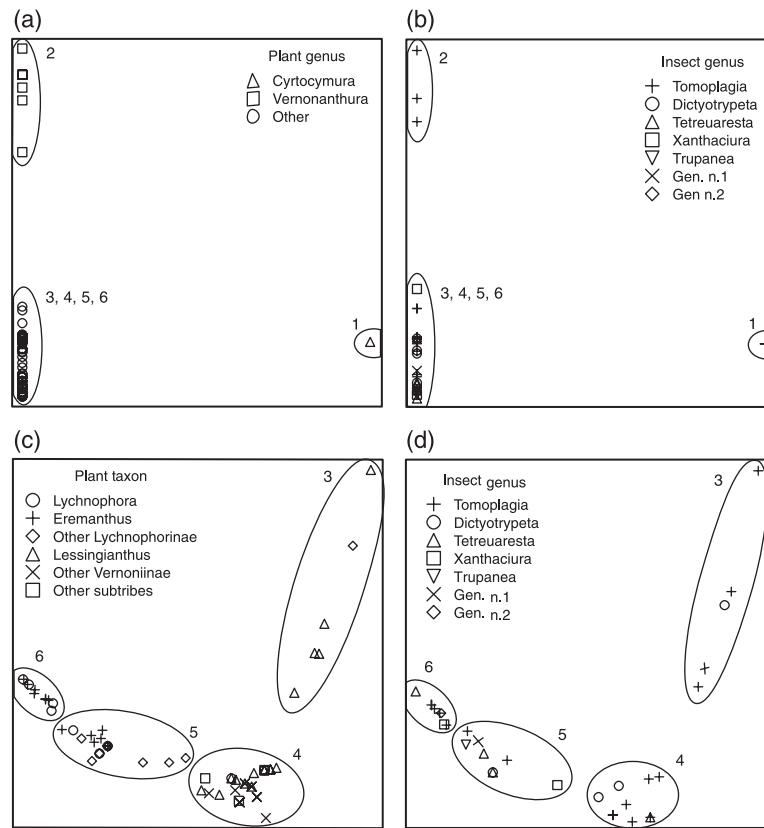
## Results

#### DETECTION OF COMPARTMENTS

The total number of insect records on plant species was 163, which is 5.8% of all possible interactions (35 insects  $\times$  81 plants = 2835 insect/plant combinations). This connectance value is related to the narrow host range of most tephritids. Twenty species (57%) were recorded on a single plant species or genus, seven (20%) were recorded on plants of a single subtribe and eight (23%) species were reared from plants of more than one subtribe or tribe.

Hence, interactions among many tephritids did not occur because they are restricted to different plant taxa. In the studied system, the oligophagy of tephritids makes this a very important constraint. From the 595 pairs that are possible with 35 tephritid species, 407 (68%) did not share any host simply because they use plants of different subtribes or genera. Only 88 pairs (15%) had at least one host species in common and





**Fig. 1.** Standard scores of plants and insects on the first four axes of a correspondence analysis (a, b: 1st vs. 2nd axis; c, d: 3rd vs. 4th axis). Plants and insects scores were plotted separately for clarity, but are standardized and at the same scale. Plants and insects with similar scores are closely associated, and their clustering is evidence of compartments. Compartments were outlined according to separate cluster analyses on the plant and insect scores. Compartment numbers correspond to those in Tables 1 and 2. Eigenvalues from the first to fourth axis are 1.0, 0.92, 0.90 and 0.76.

there were 100 pairs of species that use the same plant genus, but were not recorded in the same plant species.

Ordination on the first four axes of CA showed six compartments comprising host plants of the same subtribe or genus and the tephritid species specialized on them (Fig. 1, Table 1). From the 163 insect-plant records, only 14 are not in any compartment.

The first axis separated *T. argentiensis* Aczél and *T. pseudopenicillata* Aczél and their single host, *Cyrtocymura scorpioides* (Lam.) H. Rob. from all other plants and insects (Fig. 1a,b, Table 1). This is the only completely isolated compartment, as neither the insects nor the plant had any outside interaction. Given this isolation, the first CA axis had the maximum possible eigenvalue ( $\lambda = 1.0$ ).

The second axis also discriminated a sharp-cut block ( $\lambda = 0.92$ ), formed by *T. minuta* Hering, *T. reimoseri* Hendel and *T. fiebrigi* Hendel and their host plants, all in the genus *Vernonanthura* (Fig. 2a,b, Table 1). These three tephritid species are specialists on *Vernonanthura*, although *T. reimoseri* was recorded on occasion from other plant genera outside the Espinhaço (*Baccharis* spp. and *C. scorpioides*, Prado *et al.* 2002). The plants in this compartment were not used by other insect species, except for a single individual of the generalist *X. biocellata*, reared from *V. mariana* (Mart. ex Baker) H. Rob. (Table 1). The only *Vernonanthura* species not

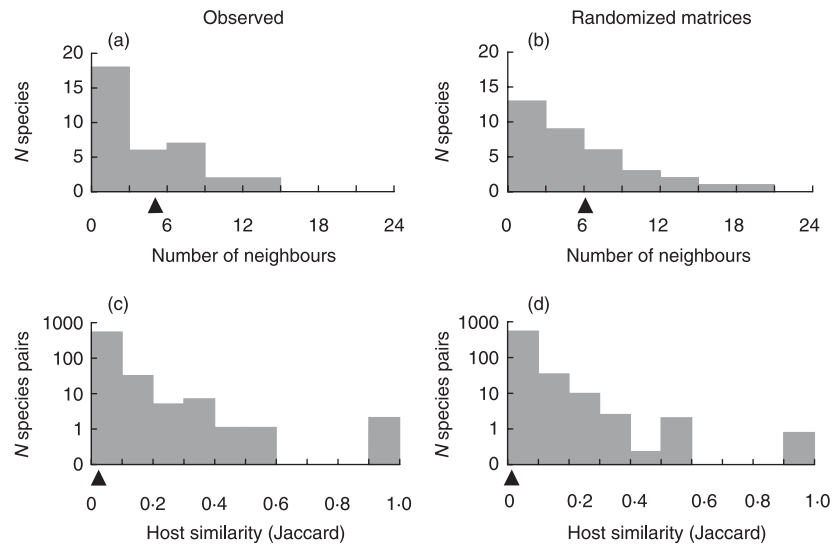
included in this compartment was *V. ferruginea* (Less.) H. Rob., which in the present study was used by only a generalist tephritid of the fourth compartment (see below); however, *T. reimoseri* and *T. minuta* have also been recorded from this plant species in São Paulo State (Adriana Almeida *et al.*, unpublished data).

The third axis separated other genera of Vernoniinae from the species of the subtribe Lychnophorinae, with their associated insects. These two groups are also well defined ( $\lambda = 0.90$ ), but scores on the fourth axis ( $\lambda = 0.76$ ) produced a further split in each (Fig. 2c,d, Table 1). These larger compartments are cross-linked by one tephritid species (compartments 3–4; 4–6), four species (5–6) or five species in common (3–5; 5–6). However, even these cross-linking tephritids were concentrated mainly in one compartment (Table 1) to which they were assigned by cluster analysis. Three species of Lychnophorinae clustered with the Vernoniinae, a placement that probably makes sense for only *Proteopsis* sp. 1, used by two tephritids specialized on *Lessingianthus* species from compartment three (Table 1). *Eremanthus erythropappus* (DC) MacLeish and *Eremanthus* sp. 3 did not cluster with the other Lychnophorinae as expected, due to their sporadic use by generalist tephritids associated to Vernoniinae.

Insect species did not cluster according to their taxonomic affinity as clearly as did the plants. Compartments

**Table 1.** Association matrix of species of Vernoniaceae (rows) and Tephritidae (columns), ordered by their scores in the CA axes. Compartments, as inferred through CA (see text and Fig. 1), are outlined and numbered. Subtribe of each plant species is indicated in the second column (C = Centratheriinae, H = Chrestinae, L = Lychnophorinae, V = Vernoniinae). For authorities names of plants see Robinson (1999), and of insects Norrbom *et al.* (1999) and Prado *et al.* (2004)

		1	2	3	4	5	6	Total																												
		<i>Tomoplagia argentinensis</i>	<i>Tomoplagia pseudopenicillata</i>	<i>Tomoplagia fiebrigi</i> <i>Tomoplagia reinoseri</i> <i>Tomoplagia minuta</i>	<i>Tomoplagia grandis</i> <i>Tomoplagia ochromopera</i> <i>Tomoplagia brasiliensis</i> <i>Dicycropyta atacta</i> <i>Tomoplagia cipoensis</i>	<i>Tomoplagia tripunctata</i> <i>Tomoplagia incompleta</i> <i>Xanthaciura biocellata</i> <i>Dicycropyta</i> sp.1 <i>Dicycropyta</i> sp.2 <i>Tomoplagia</i> sp.1 <i>Tomoplagia dimorphica</i> <i>Tomoplagia variabilis</i> <i>Tetreaesta</i> sp.1 <i>Tomoplagia formosa</i> <i>Tomoplagia punctata</i> <i>Tetreaesta</i> sp.2 <i>Dicycropyta</i> sp.3 <i>Tomoplagia bicolor</i> <i>Tetreaesta</i> sp.3 <i>Trupanea</i> sp.1 <i>Acrotaenini</i> n.gen.1 sp.1 <i>Tomoplagia interrupta</i>	<i>Tomoplagia aczelti</i> <i>Xanthaciura chrysur</i> <i>Tomoplagia voluta</i> <i>Acrotaenini</i> n.gen.2 sp.1 <i>Tomoplagia rupestris</i> <i>Tomoplagia</i> sp.2 <i>Tetreaesta</i> sp.4	Total																												
1	V	<i>Cyrtocymura scorpioides</i>	X X					2																												
	V	<i>Vernonanthura</i> aff. <i>lucida</i>	X X					2																												
	V	<i>Vernonanthura</i> aff. <i>laxa</i>	X					1																												
	V	<i>Vernonanthura glanduloso-dentata</i>	X					1																												
	V	<i>Vernonanthura membranacea</i>	X					1																												
	V	<i>Vernonanthura mucronulata</i>	X					1																												
	V	<i>Vernonanthura phosphorica</i>	X					1																												
	V	<i>Vernonanthura subverticillata</i>	X X					2																												
	V	<i>Vernonanthura westiniana</i>	X					1																												
	V	<i>Vernonanthura mariana</i>	X X					3																												
	V	<i>Lessingianthus buddleifolius</i>		X				2																												
	L	<i>Proteopsis</i> sp.01		X X				2																												
	V	<i>Lessingianthus coriaceus</i>		X X X	X			4																												
	V	<i>Lessingianthus roseus</i>		X X X	X			4																												
	V	<i>Lessingianthus linearis</i>		X X X	X			1																												
	V	<i>Lessingianthus vepretonum</i>		X X X	X X X			6																												
	V	<i>Lessingianthus rosmarinifolius</i>			X			1																												
	V	<i>Lessingianthus linearifolius</i>			X X			2																												
	V	<i>Lessingianthus carduoides</i>			X X			2																												
	V	<i>Lessingianthus brevipetiolatus</i>			X X			2																												
	V	<i>Lessingianthus pumillus</i>			X			1																												
	V	<i>Lessingianthus glabratus</i>			X			1																												
	V	<i>Lessingianthus simplex</i>			X			1																												
	V	<i>Lessingianthus</i> aff. <i>simplex</i>			X			1																												
	L	<i>Eremanthus</i> sp.03			X			1																												
	H	<i>Chresta</i> sp.01			X			1																												
	V	<i>Lessingianthus tomentellus</i>			X			2																												
	H	<i>Chresta sphaerocephala</i>			X	X X		4																												
	V	<i>Lessingianthus</i> sp.01			X			1																												
	L	<i>Eremanthus erythropappus</i>			X			1																												
	V	<i>Lessingianthus psilophyllus</i>			X X X			4																												
	V	<i>Lessingianthus warmingianus</i>			X X X			3																												
	V	<i>Lepidaploa spixiana</i>			X X X			3																												
	V	<i>Echinocoryne schwenkiaeifolia</i>			X X			3																												
	V	<i>Lessingianthus rubricaulis</i>			X			2																												
	V	<i>Lepidaploa lilacina</i>			X			2																												
	V	<i>Lepidaploa</i> aff. <i>rufogrisea</i>			X			2																												
	V	<i>Lessingianthus virgulatus</i>			X			2																												
	V	<i>Echinocoryne holosericea</i>			X			2																												
	V	<i>Stilpnopappus bicolor</i>			X			1																												
	V	<i>Lessingianthus hoveaeifolius</i>			X X	X X X		4																												
	V	<i>Lepidaploa rufogrisea</i>			X X	X X X		3																												
	V	<i>Chrysoaena herbacea</i>			X	X X	X	3																												
	C	<i>Centratherum punctatum</i>					X	2																												
	V	<i>Vernonanthura ferruginea</i>			X			1																												
	V	<i>Lepidaploa</i> sp.01			X			1																												
	V	<i>Lepidaploa salzmannii</i>			X			1																												
	V	<i>Lepidaploa aurea</i>				X		1																												
	L	<i>Minasia</i> sp.06			X			2																												
	L	<i>Proteopsis argentea</i>				X X X		3																												
	L	<i>Minasia</i> sp.02				X		2																												
	L	<i>Minasia</i> sp.04			X			1																												
	L	<i>Eremanthus polycephalus</i>				X		2																												
	L	<i>Minasia</i> sp.01				X X		2																												
	L	<i>Piptolepis</i> sp.02				X		1																												
	L	<i>Piptolepis</i> sp.01				X		1																												
	L	<i>Piptolepis</i> sp.03				X		1																												
	L	<i>Minasia</i> sp.05				X		1																												
	L	<i>Minasia scapigera</i>				X		1																												
	L	<i>Minasia alpestris</i>				X		1																												
	L	<i>Lychnophora tomentosa</i>				X		1																												
	L	<i>Lychnophora cipoensis</i>				X		1																												
	L	<i>Eremanthus crotonoides</i>				X		1																												
	L	<i>Lychnophora markgravii</i>				X X		2																												
	L	<i>Lychnophora pseudovillosissima</i>			X		X X	3																												
	L	<i>Anteremanthus hatschbachii</i>				X	X X	1																												
	L	<i>Lychnophora candelabrum</i>				X	X X	2																												
	L	<i>Lychnophora villosissima</i>			X	X	X X	5																												
	L	<i>Eremanthus bicolor</i>				X X X	X	4																												
	L	<i>Lychnophora passerina</i>				X		1																												
	L	<i>Eremanthus</i> aff. <i>glomerulatus</i>				X	X	3																												
	L	<i>Eremanthus elaeagnus</i>				X	X	3																												
	L	<i>Lychnophora</i> aff. <i>pohlil</i>				X	X X X	6																												
	L	<i>Lychnophora salicifolia</i>					X X	3																												
	L	<i>Lychnophora pohlil</i>					X	2																												
	L	<i>Lychnophora diamantinana</i>					X X	3																												
	L	<i>Lychnophora pinaster</i>					X	1																												
	L	<i>Eremanthus glomerulatus</i>					X	2																												
	L	<i>Lychnophora rosmarinifolia</i>					X	1																												
	L	<i>Lychnophora grammogolense</i>					X X	1																												
	L	<i>Eremanthus incanus</i>					X X X X	4																												
	Total	1	1	8	3	1	2	3	5	3	7	24	5	11	2	16	1	1	1	1	1	1	2	21	5	2	4	4	2	1	2	7	7	5	1	163



**Fig. 2.** Frequency distributions of number of neighbours of each tephritid species (a, b), and Jaccard host similarity of each pair of tephritid species (c, d). Left-hand graphs (a, c) show values of the observed association matrix, and on the right hand (b, d) are graphs for mean values, in each class, of 4000 randomized matrices. Arrows indicate the mean of each distribution.

**Table 2.** MRPP Analysis of compartment dissimilarities, showing mean host dissimilarity among insects and mean insect dissimilarity among plants in each compartment. The chance-corrected agreement index (A) expresses the within-group homogeneity and has a maximum of 1 when there is no dissimilarity among elements of any group. The *P*-value is the probability of obtaining by chance a value of A equal or larger than the observed

Compartment*	Intragroup mean Jaccard distance			
	Among insects according to their host plants		Among plants according to their associated insects	
	Group size	Distance	Group size	Distance
1	2	0.00	1	–
2	3	0.88	9	0.48
3	5	0.77	6	0.75
4	11	0.94	32	0.75
5	7	0.96	22	0.64
6	7	0.89	11	0.80
Intragroup Agreement (A)		0.129		0.236
<i>P</i>		< 0.0001		< 0.0001

\*Compartment number as in Fig. 1 and Table 1.

3–6, the largest ones, contained two to five genera of tephritids from at least three different subtribes (Table 1).

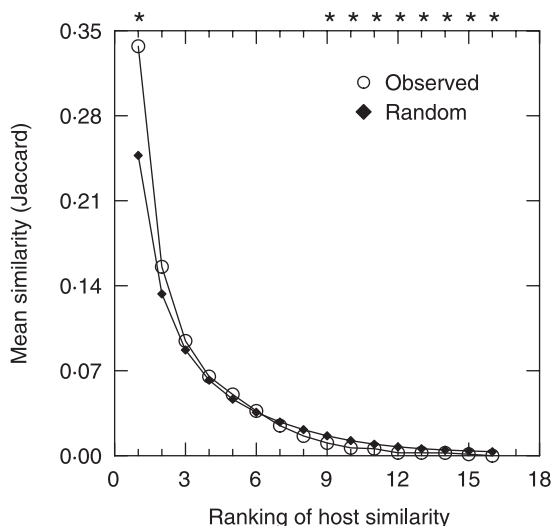
#### STATISTICAL TESTS OF COMPARTMENTATION

MRPP tests indicated that trophic dissimilarity is significantly higher among compartments than within them. Tephritid species of the same compartment had lower mean host dissimilarity among themselves than among species from other compartments ( $A = 0.129$ ,  $P < 0.0001$ , Table 2). The species of the first compartment (*T. argentiensis* and *T. pseudopenicillata*) have zero dissimilarity by virtue of their shared single host; whereas in the five other compartments dissimilarity

ranged from 0.77 to 0.96 (Table 2). Nevertheless, if species of the first compartment are excluded the result is still highly significant, despite the decrease in the index of within-group agreement ( $A = 0.075$ ,  $P < 0.0001$ ). Conversely, there was significantly lower dissimilarity of tephritid set among plant species of the same compartment than among plants of different compartments ( $A = 0.236$ ,  $P < 0.0001$ , Table 2).

#### COMPARTMENTS AND OVERLAP OF HOST USE BY INSECTS

Each tephritid species shared at least one host plant with one to 15 other species (neighbours). Most species had fewer neighbours than expected, with a mean



**Fig. 3.** Average host similarity (Jaccard) against neighbour rank of similarity for tephritid species, in the observed association matrix, and in mean values of 4000 randomized matrices. Host similarity declines both in observed and in randomized data as neighbour rank increases, but observed values are higher at initial ranks and lower at final ones. Ranks with a similarity value more extreme than obtained in less than 200 random matrices ( $P < 0.05$ ) are indicated by an asterisk.

number of 5.03 against a mean of 6.16 neighbours in randomized matrices (Fig. 2a,b). Only seven of 4000 random matrices ( $P = 0.002$ ) had a mean number of neighbours equal or lower than the observed value, and all of them had maximum number of neighbours higher than the observed ( $P < 0.00025$ ).

Jaccard host similarity from randomized matrices had a strongly skewed distribution, decreasing steeply from a maximum at zero similarity towards larger classes of similarity, much like the distribution of observed values (Fig. 2c,d). Observed mean host similarity was 0.0239; an equal or smaller mean was obtained from 3312 randomizations ( $P = 0.83$ ).

Insects had on average more hosts in common with close neighbours, and less with distant ones, than expected by the null model. Mean host similarity among insects was high among close neighbours but decreased steeply with neighbour ranking (Fig. 3). For random matrices, mean similarity was lower than the observed values for the five nearest neighbours (the difference being significant only for the first neighbour), and higher from the seventh onwards (significantly so from the ninth neighbour onwards, Fig. 3).

## Discussion

Most tephritid species used a small fraction of the pool of available host species, spanning in general either a single plant genus or a subtribe. The studied tephritids were widespread along the Espinhaço range, as were the plant genera and subtribes (Prado & Lewinsohn 2000; Prado *et al.* 2002). Also, there was no clear sep-

aration of insects or plants in discrete environments at each sampling site; thus, there is no indication that local habitat segregation could produce the observed patterns. Hence, we interpret the observed tephritid oligophagy as true ecological or evolutionary specialization, and not a side effect of geographical or environmental barriers.

Similar patterns of host specialization were found for tephritids that breed in flowerheads of other tribes of Asteraceae in Brazil (Lewinsohn 1991; Prado *et al.* 2002) and also in the Nearctic and Palearctic regions (Sobhian & Zwölfer 1985; Zwölfer 1987, 1988; Straw 1989a; White & Elson-Harris 1992; Goeden 1997; Headrick & Goeden 1998). Oligophagy on related plants seems to be a general trend among tephritids from flowerheads (and in tropical fruit-feeding tephritids as well; Novotny *et al.* 2004), and thus insect guilds that use distinct plant taxa are easily distinguishable. Correspondence analysis and multiple-response permutation tests showed that these insect guilds and their host plants form well-defined compartments wherein most insect–plant associations occur.

These results support the notion that the high degree of trophic specialization of herbivores is primarily responsible for compartmentation in plant–herbivore assemblages and that is ultimately driven by plant divergence in key attributes (Root 1973; Gilbert 1977; Lawton & Pimm 1978). For tephritids, plant chemistry, flowerhead morphology and plant phenology have all been shown to limit the use of novel hosts (Zwölfer 1988; Straw 1989a,b; Zwölfer & Romstöck-Völkl 1991).

The ensuing community pattern might be blurred by generalist species that link compartments (Futuyma & Gould 1979; Pimm & Lawton 1980). Within our study system, however, few species are generalists in terms of numbers of hosts, and even those had most of their hosts in a single compartment. Thus, host selectivity of polyphagous species (e.g. Fox & Morrow 1981) may reinforce compartmentation in insect–plant systems.

A second condition for compartmentation is that the constraints on host use must be the same, or must converge, among insect species (Futuyma & Gould 1979). Therefore the chances of finding compartments should be higher among closely related species. This is indeed the outcome for our study system, but the high degree of compartmentation found is far from preordained.

Conservatism and convergence in patterns of host use are highly variable among different insect lineages (Zwölfer 1987; Jaenike 1990; Gaston, Reavey & Valladares 1992; Thompson 1994; Menken 1996) and tephritids that breed in flowerheads have a remarkable constancy of taxonomic specialization; most tephritid genera and species are associated to the same plant taxa across regions and continents (Prado *et al.* 2002), suggesting the persistence of general rules for host ranges throughout the evolution of this clade.

Phylogenetic conservatism due to barriers imposed by plant traits is widely acknowledged as a key



determinant of host ranges of phytophagous insects (Gilbert 1977; Zwölfer 1987; Farrell & Mitter 1993; Thompson 1994; Futuyama & Mitter 1996; Janz & Nylin 1998). Once a barrier is crossed and a new set of plants colonized, a novel radiation of insect lineages will take place. This can be achieved by coevolution with the host clade (Ehrlich & Raven 1964; Thompson 1994) or by sequential evolution on pre-existing hosts (Jerny 1984; Farrell & Mitter 1993; Menken 1996). In either case related insects are expected to use related plants.

Although in the Espinhaço each tephritid species does tend to use related Vernoniae hosts, there are two lines of evidence that this system does not fit entirely predictions from coevolutionary or sequential–evolution models. First, each of the four largest compartments joined tephritids from different genera and subtribes, indicating independent colonization and convergence. Secondly, molecular data from *Tomoplagia* species provide several instances of species from the same compartment being less related among themselves than to species of other compartments (e.g. *T. argentinensis* and *T. pseudopenicillata*; *T. incompleta* and *T. tripunctata* Hendel), whereas in other cases (e.g. *T. interrupta* Prado *et al.* *T. voluta* Prado *et al.* and *T. rupestris* Prado *et al.* *T. tripunctata* and *T. cipoensis* Prado *et al.*) they are indeed genetically and morphologically close (Yotoko 2003; Prado, Norrbom & Lewinsohn 2004; Karla Yotoko and Vera Solferini, unpublished).

Thus, in evolutionary terms the compartments we found can be conceived as ‘radiation platforms’ (Zwölfer 1988) for tephritid lineages, but this does not preclude independent colonization or subsequent host-hopping among compartments.

The Monte Carlo simulations indicated that insects share host plants with fewer species than expected if there were no compartments. Moreover, mean host similarity with distant neighbours in niche space was lower than expected, whereas nearest neighbours were closer together in niche space. These results are similar to those found for many communities of lizards and of fishes analysed by Winemiller & Pianka (1990) and agree with the hypothesis that compartmentation reduces diffuse competition while raising the probability of interactions among those species that share resources (MacArthur & Levins 1967; Pianka 1974, 1980; Inger & Colwell 1977).

Compartments did not reduce total potential competitive effects, as average host similarity was not lower than expected from matrix randomization. Hence, contrary to some theoretical predictions (MacArthur & Levins 1967; Pianka 1974), we found no evidence that compartments in the studied system evolved to minimize overall competitive effects in the community. Other studies have shown similar results. Among published ecological studies that used Monte Carlo techniques, overall niche overlap was compared with the ‘scrambled zeroes’ null model for 22 communities with distinct guilds (those in Table 4.4 from Gotelli & Graves 1996; plus the results of Joern & Lawlor 1980;

Lawlor 1980; the communities of lizards of Winemiller & Pianka 1990). Mean overlap was higher than expected in 12 of these 22 assemblages (grasshoppers in Sale 1974 and in Joern & Lawlor 1980; newts in Griffiths 1987; four communities of lizards and four of fishes in Winemiller & Pianka 1990).

With some important exceptions (e.g. Yodzis 1980; Raffaelli & Hall 1992; Krause *et al.* 2003), published evidence for compartmentation in natural assemblages is still scarce, due probably to a variety of reasons. First, benchmark papers such as Pimm & Lawton’s (1980) study, may have convinced researchers that analysis of bitrophic assemblages was pointless. Secondly, most existing data sets are limited in their taxonomic resolution (see Martinez 1991) and this, combined with the common practice of aggregating species that share food resources and predators into single trophospecies, will tend to collapse compartments and make them less recognizable.

The recent upsurge of studies applying concepts and measures from complex networks to food webs has emphasized other features of community structure, such as connectance and degree distributions (e.g. Solé & Montoya 2001; Dunne, Williams & Martinez 2002; Williams *et al.* 2002; Jordano *et al.* 2003; Montoya & Solé 2003) or nestedness (Bascompte *et al.* 2003), rather than compartmentation. None the less, other fields already offer several tools to evaluate attributes related clearly to compartmentation (for instance the cluster coefficient, Newman 2003) which are now making their way into food-web analyses (Dunne *et al.* 2002; Montoya & Solé 2002; Krause *et al.* 2003). Indeed, social networks comprising two sets of entities, such as plants and insects in our case, can be analysed by correspondence analysis (Borgatti & Everett 1997), partly similar to our procedure. We expect that, in the near future, these analytical tools will help to bring compartmentation into ecological communities and its dynamic and evolutionary consequences into proper focus.

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