Structure and vertical stratification of plant galler–parasitoid food webs in two tropical forests

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Abstract. 1. Networks of feeding interactions among insect herbivores and natural enemies such as parasitoids, describe the structure of these assemblages and may be critically linked to their dynamics and stability. The present paper describes the first quantitative study of parasitoids associated with gall-inducing insect assemblages in the tropics, and the first investigation of vertical stratification in quantitative food web structure.

2. Galls and associated parasitoids were sampled in the understorey and canopy of Parque Natural Metropolitano in the Pacific forest, and in the understorey of San Lorenzo Protected Area in the Caribbean forest of Panama. Quantitative host–parasitoid food webs were constructed for each assemblage, including 34 gall maker species, 28 host plants, and 57 parasitoid species.

3. Species richness was higher in the understorey for parasitoids, but higher in the canopy for gall makers. There was an almost complete turnover in gall maker and parasitoid assemblage composition between strata, and the few parasitoid species shared between strata were associated with the same host species.

4. Most parasitoid species were host specific, and the few polyphagous parasitoid species were restricted to the understorey.

5. These results suggest that, in contrast to better-studied leaf miner–parasitoid assemblages, the influence of apparent competition mediated by shared parasitoids as a structuring factor is likely to be minimal in the understorey and practically absent in the canopy, increasing the potential for coexistence of parasitoid species.

6. High parasitoid beta diversity and high host specificity, particularly in the poorly studied canopy, indicate that tropical forests may be even more species rich in hymenopteran parasitoids than previously suspected.

Key words. Apparent competition, canopy, coexistence, Cecidomyiidae, gall, Panama, parasitoid, quantitative food web, tropical forest, understorey.

Introduction

Food webs linking insect herbivores and their parasitoids comprise a major component of global biodiversity. Recent studies have moved from simply documenting the incidence of interactions among these species, to incorporate information on the frequency of each trophic interaction (Memmott & Godfray, 1994). These quantitative food webs have been used to describe the structure of host–parasitoid communities for a variety of insect

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feeding guilds, including leaf miners (Memmott *et al.*, 1994; Rott & Godfray, 2000; Valladares *et al.*, 2001; Lewis *et al.*, 2002), aphids (Müller *et al.*, 1999), and gall-inducing temperate Cynipidae (Schönrogge & Crawley, 2000). Furthermore, these webs provide a rich source of information for generating and testing hypotheses about the dynamic processes organising natural communities of herbivorous insects (Morris *et al.*, 2004), and the impacts of human actions, such as the introduction of alien species (Henneman & Memmott, 2001) and tropical forest habitat degradation (Tylianakis *et al.*, 2007).

While several quantitative food web studies have focused on species-rich tropical forest insect communities (e.g. Memmott *et al.*, 1994; Lewis *et al.*, 2002), our current understanding of

the structure of tropical insect communities (and indeed, tropical forest ecology more generally) is based almost entirely on studies limited to a small fraction of the forest biomass, accessible from the ground. The tropical forest canopy supports a diverse and poorly studied assemblage of plants and animals, and has been described as the 'last biotic frontier' (Erwin, 1982). For example, at least 20% of tropical arthropods, most of them insect herbivores, are confined to the upper canopy (the canopy surface and the volume of vegetation within a few metres below it: Basset *et al.*, 2003), but little is known about ecological interactions among these species, their host plants, and natural enemies. The canopy of tropical forests has biotic and abiotic conditions that contrast markedly with conditions in the understorey, and is the site of the vast majority of primary productivity (Ozanne *et al.*, 2003). Consequently, canopy arthropod assemblages are expected to show considerable differences in their composition, structure, and function, compared with those in the understorey. While an increasing number of studies have investigated vertical stratification in arthropod community composition (e.g. Stork *et al.*, 1997; Basset *et al.*, 2003), data are lacking entirely on food web interactions in these communities, limiting our ability to understand the factors structuring and maintaining tropical diversity. Furthermore, the extent to which the canopy and understorey act as discrete sub-communities or compartments in the forest food web is uncertain. Consequently, we do not know whether ground-based studies accurately reflect the processes operating within tropical forests as a whole (Basset *et al.*, 2003; Ozanne *et al.*, 2003). While much of the previous research on canopy arthropods has been descriptive, relying on indirect and often destructive methods such as insecticide fogging, new methodological advances, particularly the use of large construction cranes to provide safe and flexible access to the upper canopy, have enhanced the opportunity to carry out more extensive, selective, and replicated sampling (Basset *et al.*, 2003; Ozanne *et al.*, 2003). In particular, it is now possible to sample living insect herbivores from the canopy, allowing their trophic interactions with host plants and natural enemies to be documented in a systematic and quantitative fashion. This opens up the opportunity to construct the first quantitative food webs for the forest upper canopy, and to compare the composition and structure of food webs for both canopy and understorey.

The present paper describes the first study to quantify host–parasitoid interactions in the forest canopy, and the first quantitative study of parasitoid assemblages associated with gall-inducing insects in the tropics. We construct quantitative host–parasitoid food webs for the canopy and understorey of a Semideciduous Tropical Dry Forest, and for the understorey of an Evergreen Tropical Forest, both in Panama. We compare trophic web statistics, and other indices based on quantitative data across habitats and strata. Our overall objectives are to study the effect of forest type and vertical stratification on food web organisation, and to quantify the specificity of parasitoid–gall makers interactions. Specifically, we predict that

1 Host–parasitoid assemblages will show vertical and geographical stratification in composition and structure. The species composition of gall maker (host) communities shows strong horizontal (between forest) and vertical (within forest) stratification (Medianero & Barrios, 2001). If there is a close link between parasitoids and gall makers, the parasitoid community should also show stratification.

2 High host-plant and gall maker diversity will lead to parasitoid species showing a high degree of polyphagy, resulting in food webs characterised by high realised connectance and low levels of compartmentalisation. Patterns of connectance and compartmentalisation are likely to have consequences for the dynamics and stability of these communities (Tylianakis *et al.*, 2007).

3 Apparent competition (Holt, 1977) will structure gall maker–parasitoid communities in the tropical forest canopy and understorey. Apparent competition describes indirect antagonistic interactions between species at the same trophic level mediated by shared natural enemies (Bonsall & Hassell, 1998; Morris *et al.*, 2004), and has been suggested as an important structuring force linking the dynamics of networks of species that never compete directly for resources. Direct competition for resources is unlikely to be a widespread structuring factor in tropical gall maker assemblages, because of their high host-plant specificity (Hanson & Gómez-Laurito, 2005). On the other hand, indirect interactions such as apparent competition (indirect antagonistic interactions between species at the same trophic level mediated by shared natural enemies: Bonsall & Hassell, 1998; Morris *et al.*, 2004, 2005) can act as an important structuring force linking the dynamics of species that never compete directly for resources.

Methods

Study site

Galls were collected in the canopy and understorey adjacent to the canopy crane operated by the Smithsonian Tropical Research Institute (STRI) in Parque Natural Metropolitano (PNM) in the Pacific forest, and in the understorey of San Lorenzo Protected Area (SLPA) in the Caribbean forest of Panama, Central America. The two sites are separated by 80 km and differ markedly in their rainfall regime. As a result, there is an almost complete change in plant species composition between the two sites (Basset *et al.*, 2003).

Parque Natural Metropolitano is located in Panama Province (8°58′N, 79°35′W, 50 m above sea level) and is characterised as a Semideciduous Tropical Dry Forest, with a dry season from December to April, an annual average rainfall of 1740 mm, and an annual mean temperature of 28 °C. The crane has access to 0.85 ha of the forest canopy, within a plot of 1 ha where 316 trees have been recorded [diameter at breast height (d.b.h.) > 10 cm]. Canopy tree heights range from 30 to 40 m and the basal area is 26 m² ha⁻¹. The dominant species is *Anacardium excelsum* (Anacardiaceae), but more than 60 tree and vine species have been identified (Basset *et al.*, 2003). Gall maker diversity is estimated as Fisher's $\alpha = 6.11$ and 16 morphospecies for the understorey, and Fisher's $\alpha = 8.19$ and 31 morphospecies for the canopy (Medianero *et al.*, 2003).

San Lorenzo Protected Area, located in Colon Province (9°17′N, 79°58′W, 125 m above sea level) is categorised as an Evergreen Tropical Forest, with an annual average rainfall of 3400 mm and

an annual mean temperature of 27 °C. Sampling was carried out within a 6 ha plot, where more than 240 species of trees and vines have been recorded, with 22 400 individuals with d.b.h >1 cm. The forest has a density of 3338 stems (d.b.h. >1 cm) ha⁻¹ and a basal area of 32 m²ha⁻¹. The mean canopy tree height is 45 m, and the canopy is dominated by *Brosimun utile* (Moraceae) (Basset *et al.*, 2003). Gall maker diversity was Fisher's $\alpha = 6.45$ with 37 morphospecies in the understorey, and Fisher's $\alpha = 8.53$ with 20 morphospecies in the canopy (Medianero *et al.*, 2003).

Study system

Parasitoid species associated with gall-inducing insects (Diptera: Cecidomyiidae) were investigated. Galls are composed from plant tissue in which the gall makers shelter and feed (Price *et al.*, 1987). Although galls are formed from plant tissue, they represent the extended phenotype of the gall maker, with their structure and development determined by the genome of the gall maker (Stone & Cook, 1998). Gall maker species can be identified through a combination of the external morphology of the gall and the identity of the host plant. Larvae within the galls are attacked by a range of parasitoid species from the order Hymenoptera (Askew, 1980; Gagné, 1994), specifically from the superfamilies Ichneumonoidea, Chalcidoidea, and Platygastroidea. We chose to focus on gall makers, because they represent discrete microhabitats, which support relatively closed, specialised communities (Stone & Schönrogge, 2003). Thus, gall maker–parasitoid food webs represent discrete compartments within the overall forest food web. The investigation was limited to cecidomyiid galls, because the Cecidomyiidae are responsible for the majority of insect-induced galls in the Neotropics (Gagné, 1994) and represents 94% of the gall makers previously recorded in the study area (Medianero & Barrios, 2001).

Field collections

Galls were sampled from plant species identified as hosts at the same locations by Medianero and Barrios (2001). We also surveyed for galls on plant species where galls had not previously been recorded. In PNM, the sampling was carried out from August 2005 to May 2006 in both strata. In the canopy, galls were sampled within the canopy crane perimeter, while in the understorey sampling was carried out within a plot of 0.4 ha below the crane perimeter. Sampling area differed between strata at PNM, because part of the crane perimeter is close to a main road, and we restricted understorey sampling to the less disturbed sectors. Nonetheless, data for both strata were comparable after transformation to density values. In SLPA, the sampling period was from January to June 2006, and only the understorey was sampled. The collections were made in a plot of 0.37 ha within the 6 ha near the canopy crane. Ancillary data about the canopy of SLPA and other strata were taken from Medianero and Barrios (2001). Each plot area was searched comprehensively for galls every 2 weeks. All individual galls found were collected and placed in sealed plastic bags (Gagné, 1994). Bags were checked for emerging insects every 2 days for a minimum of 1 month. Emerging gall makers and

parasitoid adults were preserved in vials with 70% ethanol. Dissections of a fraction of each gall morphospecies collected outside the plots were carried out to (1) discriminate the gall makers and their associated parasitoid assemblages from other phytophagous insects feeding in gall tissue and their own parasitoid community; (2) investigate parasitoid life history (koinobiosis or idiobiosis, endoparasitism or exoparasitism) and (3) distinguish primary parasitoids from hyperparasitoids.

Identification

Gall makers were sorted to morphospecies level through the combination of host-plant species and gall external morphology (Gagné, 1994). However, when possible, morphospecies separation was confirmed using reared gall maker adults. Chalcidoidea were identified to genus and where possible, species using Schauff *et al.* (1997) and Hansson (1998, 2004, 2005). Entedoninae identifications were confirmed by C. Hansson (Lund University). Boucek (1993), Heydon (1994), Boucek and Heydon (1997), Heydon and Hanson (2005) were used to identify Pteromalidae; DiGiulio (1997) for Eurytomidae; Grissell (1997) for Torymidae; Hayat (1983) and Woolley (1997) for Aphelinidae; Gibson (1995, 1997) for Eupelmidae. Tetrastichinae (Chalcidoidea: Eulphidae) and Platygastridae (Hymenoptera: Platygastroidea), were sorted to morphospecies level, because of the paucity of taxonomic works for the Neotropical region. Braconidae were identified using Wharton *et al.* (1997).

Characterising host abundance

The number of viable chambers collected for each gall maker species varied depending on gall maker abundance in the sampling plots, and was estimated from the total number of adults reared (gall makers + parasitoids + hyperparasitoids) from each gall maker morphospecies. This assumes that for each viable chamber collected only one adult insect hatched, i.e. that parasitoids are solitary rather than gregarious, and that when two parasitoid individuals attack a single host or when one attacks the host and the other attacks its parasitoid, only one survives to maturity (Force, 1985). By using the number of viable chambers as our measure of abundance, we excluded other mortality factors such as entomopathogens, differing rearing methods or differing collecting periods. We chose the number of chambers over the number of individual galls, because oligothalamous and multithalamous galls shows intraspecific variation in their number of chambers.

Description of parasitoid communities

Gall maker and parasitoid abundance were transformed to relative density terms (number of individual collected per sampling area per sampling period). This standardisation allows comparisons between sites and strata, and also the construction of quantitative trophic webs expressing the trophic links and species abundance in the same units (Memmott & Godfray, 1994). Gall maker and parasitoid diversity for both strata and localities were

compared using *t*-tests for the Shannon index (Hutcheson, 1970; Magurran, 1988); and in terms of their similarity, with Chao's quantitative Jaccard index (Chao *et al.*, 2005) calculated using SPADE v 2.1 software (Chao & Shen, 2005).

Quantitative trophic webs

Quantitative trophic webs were built to describe graphically the structure of host–parasitoid communities. The trophic webs show the summary of all the interactions found during the sampling period, summing the absolute density of host, parasitoids and trophic links (Lewis *et al.*, 2002). Trophic webs statistics were calculated for each stratum at each site, including the host/parasitoid ratio (*H/P*) and realised connectance (*L/HP*), where *L* is the total number of trophic links, *H* is the number of host species, *P* is the number of parasitoid species and *HP* is the maximum possible number of trophic links (Lewis *et al.*, 2002). Trophic web compartmentalisation was measured calculating the number and diversity of independent sub-webs within each trophic web. Compartmentalisation was defined as the degree to which a trophic web is composed of groups of host and parasitoids with no connection to any other similar group. Variability in compartment size was estimated with the diversity measure proposed by Lewis *et al.* (2002), defined as $\exp - (\Sigma^n_{i=1} p_i \ln p_i)$, corresponding to the exponential form of Shannon diversity index. Following Tylianakis *et al.* (2007), we also calculated a series of quantitative food web statistics (Vulnerability, Generality, Linkage Density, and Interaction Evenness), using the formulae of Bersier *et al.* (2002) implemented in the Bipartite package for R (R Development Core Team, 2008). These statistics incorporate information on the frequencies of trophic interactions as well as their incidence, are much less sensitive to sampling biases than conventional binary food web statistics, and are becoming the metrics of choice in quantitative food web analyses (Albrecht *et al.*, 2007; Tylianakis *et al.*, 2007; van Veen *et al.*, 2008).

The potential for apparent competition

Parasitoid specificity was determined by calculating the interactions between every pair of gall makers through all the possible shared parasitoids in the community. The interaction (d_{ij}) represents the proportion of parasitoid species attacking gall maker (*i*) that also develop in gall maker (*j*); *i* and *j* can be the same species (d_{ii}) (Müller *et al.*, 1999). The magnitude of these interactions is defined as:

$$d_{ij} = \sum_k \left[\frac{\alpha_{ik}}{\sum_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right]$$

where α_{ik} is the absolute density of the trophic link between the host *i* and the parasitoid *k* in the trophic web. The first term in the parentheses is the fraction of the parasitoid assemblage from host *i* which belongs to species *k*, and the second term is the fraction of the individuals of parasitoid species *k* which develop on host *j*. The sum d_{ij} will tend to 1 when most of the parasitoid

species attacking host *i* also attack host *j*, and to 0 when the host pair do not share any parasitoid species (Müller *et al.*, 1999). The use of d_{ij} is based on the following assumptions: (1) parasitoids of each species move randomly through the community; (2) there are no races or biotypes associated with different host species (Lewis *et al.*, 2002); and (3) all the parasitoids attacking a host originate within the focal community (Müller *et al.*, 1999). The values of d_{ii} are defined as the probability that parasitoids attacking host *i* developed on hosts of the same species. This value was used as a parasitoid specificity measure. The probability that pairs of hosts interact through shared parasitoids was represented graphically using quantitative parasitoid overlap graphs (Müller *et al.*, 1999), where vertices represent the gall maker species, with their size proportional to host density, and the d_{ii} value is represented by the shaded portion of each vertex and d_{ij} by the width of lines joining vertices. The importance of shared parasitoids in the communities was assessed by comparing the sum of d_{ij} values ($\Sigma d_{i(j-i)}$) against the d_{ii} values for each gall maker species in the community, using the Wilcoxon test for related samples.

The overlap in resource use by parasitoids was calculated with the symmetric measure proposed by Pianka (1973):

$$O_{12} = O_{21} = \frac{\sum\limits_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum\limits_{i=1}^{n} \left(p_{2i}^{2}\right)\left(p_{1i}^{2}\right)}}$$

where $p_1 i$ and $p_2 i$ refer to the use of resource *i* by species 1 and 2. The resource overlap matrix was compared against a null model to determine if the overlap observed in the community is non-random (Gotelli & Graves, 1996). The null model was generated and simulated with EcoSim 7.0 (Gotelli & Entsminger, 2001) using the randomisation algorithm RA4 (Winemiller & Pianka, 1990), which allows the retention of 'zero' values (host–parasitoid interactions not observed in the field) and the amplitude of the resource use (parasitoid host range). It was assumed that the host–parasitoid interactions recorded correspond to the realised host range of parasitoids.

Results

The results are based on 1590 viable chambers reared to produce 468 gall makers and 1122 parasitoids (Table 1). Fifty-seven parasitoid morphospecies were reared, 25 from PNM understorey, 17 from PNM canopy, and 22 from SLPA understorey. The chambers correspond to 24 gall makers morphospecies associated with 28 host plants, six from PNM understorey, 14 from PNM canopy, and 11 from SLPA understorey. The parasitoids belong to the superfamilies Chalcidoidea, Platygastroidea, and Ichneumonoidea.

Vertical and horizontal stratification

There were no differences in the relative density of viable chambers reared between understoreys at the two localities ($U = 52.00$,

Table 1. Summary information for viable chambers for the different strata and sites sampled.

	PNM understorey	PNM canopy	SLPA understorey	Total
Total	1102	272	216	1590
Gall makers	384	44	40	468
Parasitoids	718	228	176	1122
Parasitism rate	0.65	0.84	0.81	0.7
Density	0.02755	0.0034	0.01167	0.04262

$n = 21$, $P = 0.541$), but density was higher in the understorey than in the canopy at PNM ($U = 29.50$, $n = 24$, $P < 0.05$). The SLPA understorey has higher gall maker and parasitoid diversity than the understorey and canopy of PNM (Table 2). In PNM, gall makers were more diverse in the canopy than in the understorey ($H't = 2.79$, d.f. $= 336$, $P < 0.001$), but parasitoid diversity shows the opposite pattern ($H't = 3.927$, d.f. $= 326$, $P < 0.001$).

Similarity between gall makers communities in PNM understorey and canopy was $J_{Chao} = 0.0697$, SE $= 0.1087$; but there was no overlap at all between the understorey assemblages at the two localities. Despite this, parasitoid communities were less similar between the PNM understorey and canopy ($J_{Chao} = 0.0715$, SE $= 0.0612$) than between understoreys at the two localities ($J_{Chao} = 0.1410$, SE $= 0.0886$).

The quantitative trophic webs are shown in Fig. 1, and their trophic web statistics in Table 3. The canopy trophic web is completely composed of sub-webs of species-specific parasitoids. In the understorey, the trophic webs comprise a small number of species-specific parasitoids and their hosts, and a larger group of gall makers interconnected through polyphagous parasitoids. In both cases, the sub-web size is homogeneous. The differences in compartmentalisation patterns between strata are caused by the small fraction of polyphagous parasitoids. These species were the same for both understoreys, but were absent from the canopy web. For completeness, we also present quantitative food web statistics in Table 3. These metrics were devised by Bersier *et al.* (2002), and were first applied as a more rigorous way of describing the quantitative structure of host–parasitoid networks by Tylianakis *et al.* (2007). The values calculated should be useful for authors carrying out future comparative work, but the absence of comparative data for other gall maker–parasitoid food webs precludes further discussion here.

Resource use overlap

Quantitative overlap graphs are presented for each strata and forest in Fig. 2. Overall, for each gall maker morphospecies, d_{ii} values were higher than the summation of d_{ij} (Wilcoxon related

Table 2. Diversity of gall maker–parasitoid communities.

	H'		
	PNM canopy	PNM understorey	SLPA understorey
Gall makers	1.5620	1.3210	2.0110
Parasitoids	2.0050	2.3380	2.5060

pair, $Z = 3.66$, $n = 19$, $P < 0.001$). The d_{ii} values were also higher than the summed d_{ij} values in the PNM understorey ($U = 51.00$, $n = 100$, $P < 0.001$), SLPA understorey ($U = 73.00$, $n = 121$, $P < 0.001$) and PNM canopy ($U = 455.00$, $n = 196$, $P < 0.001$). This suggests a low likelihood of indirect interactions mediated by shared parasitoids in these gall maker communities. The overlap in resource use for PNM and SLPA understoreys differs from the values simulated based on null models ($\chi^2 = 36.02$, $P < 0.001$ and $\chi^2 = 365.32$, $P < 0.001$), respectively. This implies that overlap patterns were non-random.

Parasitoid assemblage characteristics

Galls from different sampling sites did not differ in their d_{ii} values ($H = 0.637$, $n = 35$, $P = 0.727$). In PNM, parasitoid assemblage size was larger in the understorey than in the canopy ($H = 6.920$, $n = 35$, $P = 0.031$). Parasitoid assemblage size was similar between the understoreys of the two localities ($U = 46.500$, $n = 21$, $P = 0.557$). The differences in parasitoid assemblage size were influenced by a lower gall maker sample size and the lack of generalist parasitoids in the canopy.

Discussion

Food web structure

The tropical forest gall maker–parasitoid food webs show three main features: (1) high levels of compartmentalisation; (2) parasitoid assemblages characterised by host-specific species; and (3) very low potential for indirect interactions. Schönrogge and Crawley (2000) found similar patterns in cynipid gall maker–parasitoid food webs in temperate habitats, although in their system, parasitoids were a little more polyphagous, resulting in slightly higher realised connectance. Differences in host/parasitoid ratio for the system of Schönrogge and Crawley (2000) may be explained by the presence of non-native gall makers with few associated parasitoids.

We observed that in the tropical gall maker–parasitoid communities, the realised connectance was twice as high as in the tropical leaf miner–parasitoid community studied by Lewis *et al.* (2002). The trophic web statistics indicate that in the case of gall maker food webs, higher connectance is driven by the number of parasitoid species associated with each gall maker, and not by parasitoid species with wide host ranges, as in the

Table 3. Trophic web statistics.

	PNM canopy	PNM understorey	SLPA understorey
Number of host species (H_c)	14	10	11
Number of host species with parasitoids (H_p)	9	9	10
Number of parasitoid species (P)	17	25	22
Number of associations (L)	17	31	30
Host:parasitoid ratio (H_c/P)	0.824	0.400	0.500
Host:parasitoid ratio (H_p/P)	0.529	0.360	0.455
Realised connectance [$L/(H_c \times P)$]	0.111	0.138	0.136
Parasitoid assemblage size (L/H_p)	1.890	3.440	3.000
Chamber density (m^2 month^{-1})	0.003	0.028	0.012
Number of compartments	9	6	5
Diversity of compartments	8.404	4.033	2.396
Quantitative vulnerability	2.391	3.691	2.596
Quantitative generality	1.000	1.298	1.448
Quantitative linkage density	1.696	2.495	2.022
Quantitative interaction evenness	0.399	0.469	0.508

leaf miner community. Two other leaf miner–parasitoid food webs, described by Valladares *et al.* (2001) and Rott and Godfray (2000), show higher values of realised connectance and lower compartment diversity. This is probably because these food webs were restricted to a single taxonomic group within the leaf miner assemblage (Agromyzidae and Gracillariidae, respectively). Both the tropical and temperate gall maker–parasitoid communities have lower potential for indirect interaction via shared parasitoids than the leaf miner communities.

The parasitoid assemblages in the communities studied were dominated by host-specific species, following the pattern found by Cornell (1990) and Tscharntke (1992), but contradicting the theories of Askew (1980) and Hawkins and Goeden (1984) about the dominance of polyphagous parasitoids species in endophytic host communities. We found no evidence supporting the prediction of Tscharntke (1992) concerning the relationship between the availability of alternative hosts, and the dominance of polyphagous parasitoids within the parasitoids assemblages of gall makers. Rather, our results show that host specificity is a dominant characteristic in the parasitoid assemblages associated with gall inducing Cecidomyiidae in our study sites. Overlap in resource use follows a non-random pattern, indicating the existence of gall traits that determine the partitioning of hosts among parasitoid species. This suggests a role for interspecific competition among parasitoids in the understorey, involving both specialist and generalist species. In the canopy, the high specificity of parasitoids means that competition among parasitoid species is unlikely to be a significant contemporary structuring force, although current patterns may reflect the 'ghost of competition past' (Connell, 1980).

Vertical and horizontal stratification

Gall makers were more diverse in the canopy than in the understorey at PNM, in agreement with the pattern found by Medianero and Barrios (2001). In contrast, parasitoids show the reverse pattern, being more diverse in the understorey. This apparent contradiction is explained by the fact that gall makers

in the canopy have fewer associated parasitoid species than those in the understorey. Overall differences in parasitoid assemblage size were thus influenced by a lower gall maker density, and the absence of generalist parasitoids in the canopy. Assuming that dispersal is a key factor for species coexistence (Briggs & Latto, 2000), we suggest that high average distances between plant hosts of the same species, extreme weather conditions, and the asynchronous phenology of host plants (Mendonça, 2001) will limit parasitoid dispersal in the canopy, thus restricting parasitoid assemblage species richness. There was only one gall maker species shared between strata, associated with a vine (*Serjania mexicana* Willd. (Sapindaceae). In both strata, the parasitoid assemblage species composition was similar, except that the polyphagous species *Tropicharis cecivora* Hansson (Eulophidae: Entedoninae) seems to be restricted to the understorey. The other polyphagous parasitoid [*Cecidellis inflativena* Hanson (Pteromalidae: Coelocybinae)] was present in the canopy, but associated only with *Serjania mexicana* galls. The high specificity of parasitoids and the small number of gall makers shared between strata, suggest that canopy and understorey gall maker–parasitoids systems act as independent compartments in the tropical forest food web, although the frequency of dispersal of parasitoids between strata remains to be determined. Furthermore, these patterns of specificity, combined with the high specificity of the gall makers themselves and the marked turnover in gall maker composition between sites, indicate that the poorly studied assemblages of parasitic Hymenoptera associated with these hosts in tropical forests may constitute a very large contribution to global insect biodiversity. This is particularly the case in the context of the work of Ribeiro and Basset (2007), who suggest that the diversity and abundance of the galls themselves in the upper canopy of tall tropical forests is exceptionally high, because the harsh abiotic environment in the canopy is particularly favourable to insects in this guild.

Gall maker and parasitoid diversity was higher in the understorey of SLPA than in PNM. Taking into account the high host specificity of the gall makers and their parasitoids, higher gall
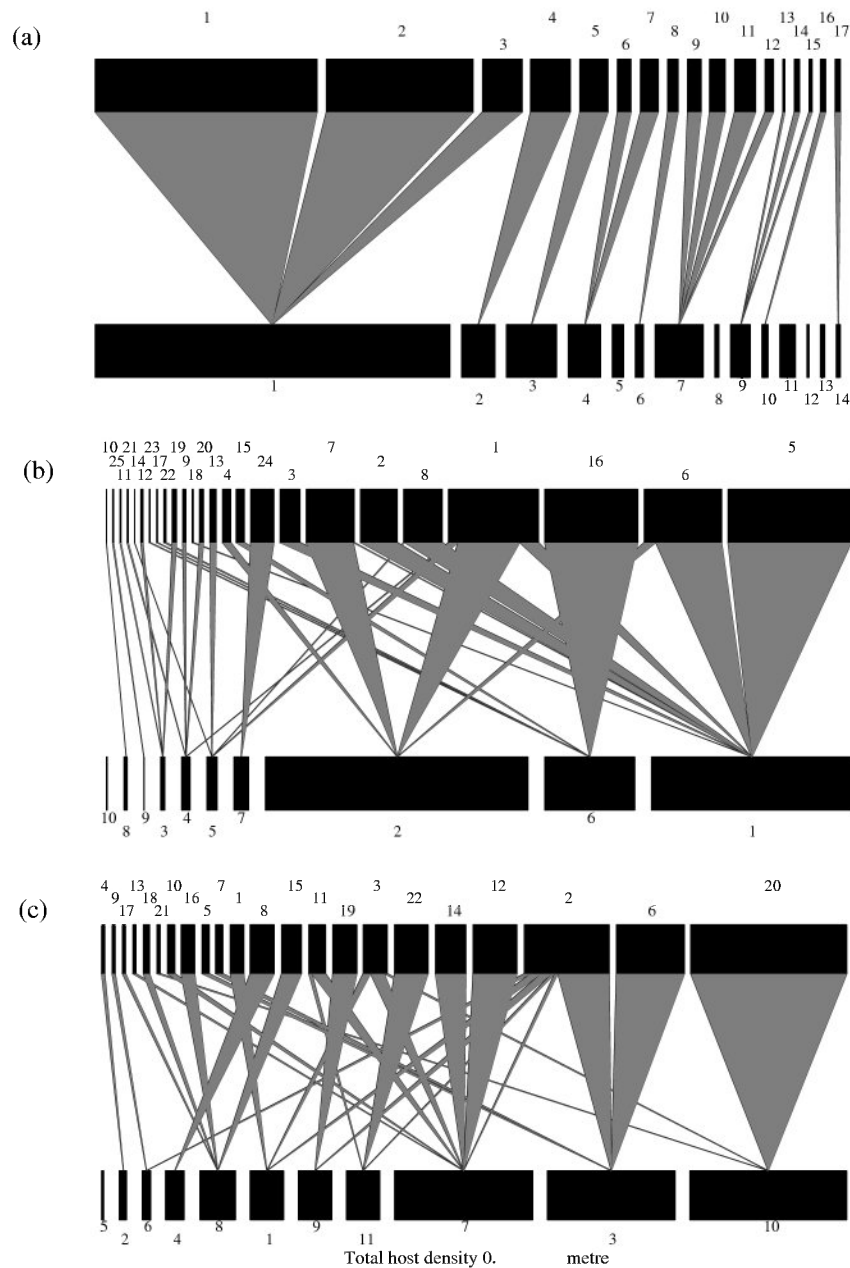
Fig. 1. Quantitative gall maker–parasitoid trophic webs for (a) PNM canopy, (b) PNM understorey, and (c) SLPA understorey. In each case, the lower bar shows the density of hosts (PNM canopy: 0.0034 m^{-2} month^{-1}, PNM understorey: 0.0276 m^{-2} month^{-1}, SLPA understorey: 0.0117 m^{-2} month^{-1}) and the upper bar the density of parasitoids (PNM canopy: 0.0028 m^{-2} month^{-1}, PNM understorey: 0.0179 m^{-2} month^{-1}, SLPA understorey: 0.0095 m^{-2} month^{-1}). Species are numbered according to Appendices 1–3.

maker and parasitoid species diversity may simply reflect higher plant diversity at this site (Novotny *et al.*, 2006). The set of polyphagous parasitoid species is similar in the understorey at both sites, despite non-overlapping assemblages of gall makers and host plants. These parasitoid species differed in the composition of their host range at the two sites. However, we cannot exclude the existence of cryptic species among our set of apparently polyphagous parasitoids (Smith *et al.*, 2006).

Potential sources of bias

We found that the species richness of parasitoids across gall maker species was positively correlated with host sample size. Thus, our study will underestimate the extent of the true parasitoid complexes for the less abundant gall makers. Furthermore, for polyphagous parasitoids, the host range recorded in this study will be a subset of the potential host range. In both cases, the quantitative trophic webs represent the direct (parasitism,
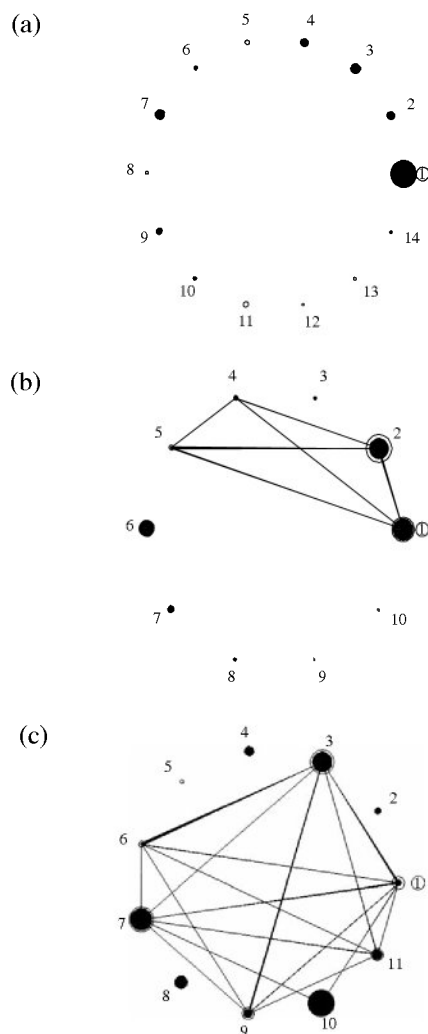
Fig. 2. Quantitative parasitoid overlap graph for (a) PNM canopy, (b) PNM understorey, and (c) SLPA understorey. The size of the circle for each host represents its abundance, and the extent to which each circle is shaded indicates d_{ii} (the fraction of parasitism on that host inflicted by parasitoids that developed on the same host species). Hosts that share parasitoids are linked, and the width of the linkage at host j indicates d_{ij}, the fraction of parasitism inflicted by parasitoids developing on the other host, j. Species are numbered according to Appendices 1–3.

competition) and indirect (apparent competition) interactions realised in field conditions, not all potential interactions. However, the trophic link density values have been used as an implicit estimate of the abundance of each species in the community (Müller *et al.*, 1999).

The galls remained active in the field, i.e. with the immature gall maker alive, for 2.81 ± 0.67 months (PNM understorey), 2.6 ± 0.42 months (SLPA understorey), and 3.08 ± 0.65 months (PNM understorey) (Medianero, 1999). These values are lower than the sampling periods in each site, so it is likely that our data represent a large fraction of the parasitoid species associated with the gall makers recorded during the sampling periods.

Quantitative trophic links represent gall maker mortality due to parasitoids, and the results could be influenced by other mortality factors present in the system (predators, pathogens, or birds) or by the rearing methods. There are three probable sources of error. First, variations in rearing success for both parasitoids and hosts may introduce biases (Memmott & Godfray, 1994; Müller *et al.*, 1999; Rott & Godfray, 2000; Lewis *et al.*, 2002). For gall makers, variations in rearing success make it difficult to describe completely the host–parasitoid community at each study site, but there was no evidence that parasitoid species associated with a particular gall differed in terms of ease of rearing. In general, failed rearing occurred mainly for galls in younger tissues, because these are more prone to dehydration and to fungal attack. Second, gall maker parasitoids can show preferences for particular developmental stages of galls (Force, 1974; Stone & Schönrogge, 2003). The collection of hosts could lead to an underestimate of those species attacking the more advanced developmental stages of the gall makers (Memmott & Godfray, 1994; Rott & Godfray, 2000; Valladares *et al.*, 2001; Lewis *et al.*, 2002). The impact of this source of error is likely to be minimal, because of the low rearing success for galls in their early stages of development, resulting in mortality of both gall makers and parasitoids, with these galls excluded from the analyses. Third, it was observed from the dissections that pathogens constitute a mortality factor affecting the gall-associated fauna. Pathogen incidence was not quantified, but our observations suggest that pathogens affect gall makers and their parasitoids to a similar extent.

Parasitoid assemblage characteristics

Given the high host specificity of gall makers (Hanson & Gómez-Laurito, 2005), resource competition is unlikely to play a significant role in structuring their communities. However, Morris *et al.* (2004) suggest that interactions mediated by shared natural enemies may be a significant factor in structuring assemblages of species in which ordinary competition is not pervasive, including many tropical host–parasitoid communities. However, the effects of apparent competition may be noticeable only over multiple generations of hosts and parasitoids (Morris & Lewis, 2002). Apparent competition is defined as a negative effect of one species on the population growth rate or abundance or another species, mediated through the action of shared natural enemies (Holt, 1977). A reduced potential for apparent competition could be a factor allowing the coexistence of a great diversity of taxonomically related species with similar feeding habits, as for the gall inducing Cecidomyiidae in tropical forests. This is assuming that two species cannot coexist if they share a natural enemy that treats them identically (Morris *et al.*, 2005). The predominance of specialist parasitoids over generalists, and the fact that some parasitoid species have differing host ranges at different localities, may reflect 'dynamic monophagy' (Holt & Lawton, 1993), with parasitoids coexisting with different hosts at different sites (Holt, 1984). The coexistence of gall-associated specialist parasitoids could be explained by the presence of different competitive strategies (Force, 1974), and

the trade off between the dispersal and competitive ability of the species in the assemblages (Briggs & Latto, 2000). These characteristics mean that parasitoid species respond in different ways to environmental conditions, so that the key to specialist parasitoid coexistence is the spatial variation in species responses (Amarasekare & Nisbet, 2001). Another factor in tropical forests is likely to be high spatial heterogeneity in environmental conditions (Hochberg & Hawkins, 1993) associated with the distribution of host plants, the presence of gaps, disturbances and asynchronous leaf phenology of conspecific host-plant individuals (Mendonça, 2001; Kushwaha & Singh, 2005). These factors could be responsible for the continuous presence of hosts, which is a prerequisite for specialist parasitoids (Hawkins & Goeden, 1984), and could also explain the size of the parasitoid assemblages associated with gall makers.

Recommendations for future research

The present study describes the first quantitative food web from the canopy, finding an almost complete vertical stratification in the gall maker–parasitoid community and a marked difference in parasitoid host specificity between strata. More research on canopy quantitative food webs is now needed to understand whether such differences are widespread across sites, and whether they are consistent for different focal herbivore guilds.

Currently, the best method for sampling the canopy is the use of canopy cranes. Cranes enable easy and safe three-dimensional access to the canopy, facilitating access to the whole forest column within reach of the crane (Basset *et al.*, 2003). These characteristics allow for continuous, intensive, and non-destructive sampling of insects feeding in foliage and other plant organs in the upper canopy. However, as noted by Basset *et al.* (2003), the use of canopy cranes can lead to problems in ensuring adequate replication, because the sampling area is restricted within the relatively small and fixed crane perimeter. Thus, the food webs in the current paper represent just three replicates (one of them from the canopy), and we cannot therefore be certain that the differences we identify between forest strata are a general phenomenon, or simply reflect the idiosyncrasies of the particular sampling locations. Future studies involving quantitative food webs of phytophagous insect–parasitoid communities in forest canopies should aim for enhanced replication in space or time. Furthermore, it will be informative to extend such studies to a variety of insect herbivore guilds at particular sites.

Acknowledgements

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Appendix 1. Hosts and parasitoids from the canopy of Parque Natural Metropolitano.

Hosts: **1**, *Serjania mexicana* gall 2; **2**, *Machaerium milleflorum*; **3**, *Vitis vitifoliae* gall 1; **4**, *Vitis vitifoliae* gall 2; **5**, *Enterolobium cyclocarpum*; **6**, *Amphilophium paniculatum*; **7**, *Mikania leiostochya*; **8**, *Cordia bicolor*; **9**, *Chrysophylum cainito*; **10**, *Spondias mombin*; **11**, *Combretum* sp. gall 1; **12**, *Combretum* sp. gall 2; **13**, *Cydista* sp.; **14**, *Doliocharpus* sp. **Parasitoids**: **1**, *Ablerus* sp.; **2**, *Chrysonotomya* 04; **3**, Tetrastichinae 07; **4**, *Holcaeus* sp.; **5**, Torymidae 01; **6**, *Eurytoma* 04; **7**, Torymidae 02; **8**, *Euritoma* 05; **9**, *Cecidellis inflativena*; **10**, Tetrastichinae 08; **11**, *Klyngon jimenezi*; **12**, Tetrastichinae 09; **13**, *Chrysonotomyia* 05; **14**, *Chrysonotomya* 06; **15**, Pteromalinae 01; **16**, Pteromalinae 02; **17**, Tetrastichinae 10.

Appendix 2. Hosts and parasitoids from the understorey of Parque Natural Metropolitano.

Gall-inducing insects are referred to by the names of their host plants. **Hosts**: **1**, *Serjania mexicana* gall 1; **2**, *Serjania mexicana* gall 2; **3**, *Serjania mexicana* gall 3; **4**, *Serjania mexicana* gall 4; **5**, *Phryganocydia coymbosa*; **6**, *Cydista* sp.; **7**, *Inga* sp.; **8**, *Copaeifera* sp. gall 1; **9**, *Copaeifera* sp. gall 2; **10**, *Chrysophylum cainito*. **Parasitoids**: **1**, *Tropicharis cecivora*; **2**, *Klyngon jimenezi*; **3**, *Brasema* sp.; **4**, *Ametallon gorgonaense*; **5**, Tetrastichinae 01; **6**, Tetrastichinae 02; **7**, *Pentastichus* sp.; **8**, *Cecidellis inflativena*; **9**, Platygastridae 01; **10**, *Eurytoma* 01; **11**, *Eurytoma* 02; **12**, *Chrysonotomyia* 01; **13**, Tetrastichinae 03; **14**, Tetrastichinae 04; **15**, Tetrastichinae 05; **16**, *Chrysonotomyia phenacapsia*; **17**, *Eurytoma* 03; **18**, *Chrysonotomyia* 02; **19**, *Allorhogas* sp.; **20**, *Lyrcus* sp.; **21**, Tetrastichinae 06; **22**, *Ametallon* 01; **23**, Platygastridae 02; **24**, *Chrysonotomyia* 03.

Appendix 3. Hosts and parasitoids from the understorey of San Lorenzo Protected Area

Hosts: **1**, *Inga* sp. gall 1; **2**, *Marila* sp.; **3**, *Smilax panamensis*; **4**, *Doliocarpus* sp.; **5**, *Tovomita* sp.; **6**, *Heisteria acuminata*; **7**, *Unonopsis* sp.; **8**, *Inga* sp. gall 2; **9**, *Dendropanax arboreum*; **10**, *Coccoloba* sp.; **11**, *Philodendron* sp. 12, **Parasitoids**: **1**, *Ametallon gorgonaense*; **2**, *Tropicharis cecivora*; **3**, *Brasema* sp.; **4**, Tetrastichinae 11; **5**, *Chrysonotomyia laeviscuta*; **6**, Tetrastichinae 12; **7**, Platygastridae 03; **8**, *Allorhogas* sp.; **9**, *Pentastichus* sp.; **10**, Tetrastichinae 13; **11**, *Cecidellis inflativena*; **12**, Platygastridae 04; **13**, Pteromalinae 03; **14**, *Eurytoma* 06; **15**, *Ametallon* 01; **16**, *Eurytoma* 07; **17**, Braconidae 01; **18**, Braconidae 02; **19**, Tetrastichinae 14; **20**, Platygastridae 05; **21**, *Chrysontomyia* 07; **22**, *Eurytoma* 08.