



British Ecological Society

---

Structure of a Diverse Tropical Forest Insect-Parasitoid Community

Author(s): Owen T. Lewis, Jane Memmott, John Lasalle, Chris H. C. Lyal, Caroline Whitefoord, H. Charles J. Godfray

Source: *Journal of Animal Ecology*, Vol. 71, No. 5 (Sep., 2002), pp. 855-873

Published by: **British Ecological Society**

Stable URL: <http://www.jstor.org/stable/1555799>

Accessed: 06/05/2011 00:15

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=briteco>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology*.

<http://www.jstor.org>

# Structure of a diverse tropical forest insect–parasitoid community

OWEN T. LEWIS<sup>\*†</sup>, JANE MEMMOTT<sup>¶</sup>, JOHN LASALLE<sup>†\*\*</sup>,  
CHRIS H.C. LYAL<sup>‡</sup>, CAROLINE WHITEFOORD<sup>§</sup> and  
H. CHARLES J. GODFRAY<sup>\*</sup>

<sup>\*</sup>NERC Centre for Population Biology and <sup>†</sup>CABI Bioscience, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK; <sup>‡</sup>Department of Entomology and <sup>§</sup>Department of Botany, The Natural History Museum, London SW7 5BD, UK; <sup>¶</sup>School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

## Summary

1. Quantitative host–parasitoid food webs are descriptions of community structure that include data on the abundance of hosts and parasitoids, and the frequency of links between them, all expressed in the same units.
2. Quantitative host–parasitoid food webs were constructed describing the community of leaf-mining insects (Diptera, Coleoptera and Lepidoptera) and their parasitoids (Hymenoptera) in an 8500-m<sup>2</sup> area of moist tropical forest in Belize, Central America, over a 1-year period.
3. The summary food web, containing data for the whole year, is we believe the most diverse quantitative host–parasitoid web yet described. It contains 93 species of leaf-miner, 84 species of parasitoid and 196 links between hosts and parasitoids.
4. Most parasitoids were generalists, with individual parasitoid species recorded as parasitizing up to 21 host species. In contrast, most leaf-miners were specialists, with 114 links documented between leaf-miners and their host plants.
5. A robustness analysis was used to reveal the effects of different sampling intensities on food web statistics. The results suggest that the sampling had revealed most of the species of host and parasitoid in the community, but further interactions among species would continue to be detected with additional sampling. Measures of the ratio of hosts to parasitoids and of realized connectance were relatively insensitive to sampling intensity.
6. Three seasonal webs were constructed, revealing temporal changes in the structure of the community. There was greater turnover in host species composition than parasitoid species composition among seasons, but most web statistics remained relatively constant across seasons.
7. Both the summary web and the seasonal webs show low levels of compartmentalization, suggesting that the host–parasitoid community is not divided into relatively discrete subwebs with largely independent dynamics.
8. The extent of potential indirect interactions between pairs of hosts was assessed by constructing quantitative parasitoid overlap graphs. These suggest that abundant species are likely to have greater indirect effects on less abundant species than *vice versa*, and that species in the same taxonomic order are more likely to interact indirectly. The graphs do not support the hypothesis that species sharing the same host plant are more likely to interact via shared parasitoids.

**Key-words:** apparent competition, biodiversity, food web, rain forest, leaf miner.

*Journal of Animal Ecology* (2002) 71, 855–873

## Introduction

Tropical herbivorous insects, their host plants and parasitoids may account collectively for over 50% of the earth's species (Strong, Lawton & Southwood 1984; LaSalle & Gauld 1991). Understanding the enormous diversity of tropical insect faunas is one of the major challenges facing ecologists today. Accurate species inventories are becoming increasingly available for certain taxa, but we still know very little about the community-level processes generating and maintaining tropical insect diversity (Godfray, Lewis & Memmott 1999).

Food webs provide a means of investigating the factors structuring and maintaining diversity. Ideally, a food web should include quantitative information on trophic interactions for all trophic levels, involving all species in the community. The practical difficulties of constructing such an inclusive food web may be insurmountable, particularly in highly diverse ecosystems like tropical forests. An alternative is to focus on a more restricted form of food web, based around subsets or guilds of strongly interacting species. Attractive candidates for such analyses are guilds of insect herbivores and their parasitoids (Memmott & Godfray 1992, 1994). Because of the simple trophic relationship between hosts and parasitoids, strictly quantitative food webs in which all species and associations are measured in the same units can be constructed relatively simply. This allows numerically important and frequent associations to be distinguished from those that are casual and rare, providing a more robust insight into how communities are structured than traditional binary food webs where links are classified as either present or absent. Furthermore, quantitative webs can be constructed using similar methods in different systems, facilitating comparisons among communities.

In this study, we describe a quantitative host-parasitoid food web for leaf-mining insects and their parasitoids in an area of moist tropical forest in Belize, Central America. In doing this, we have a long-term and a short-term objective. Our long-term objective is to add to a growing database of quantitative host-parasitoid webs, collected in a consistent way. Reviews of the empirical database for food web studies have emphasized the need to use a common methodology when collecting food web data, and to incorporate quantitative information into measures of community structure (Cohen *et al.* 1993). Four quantitative host-parasitoid webs are now available for temperate communities (Müller *et al.* 1999; Rott & Godfray 2000; Schönrogge & Crawley 2000; Valladares, Salvo & Godfray 2001), and two for tropical communities (Memmott, Godfray & Gauld 1994; Henneman & Memmott 2001) and we know of several more in preparation in a variety of environments. Collectively, we hope that these webs will allow us to look for patterns and differences across communities, in the same way that analysis of the

first compilations of binary webs led to a wealth of generalizations and hypotheses about community patterns and processes (Cohen, Briand & Newman 1990).

Our more immediate short-term aim, and the focus of this paper, is to answer a series of particular questions about the structure of the present community. We want to know, first, how many species of host and parasitoid constitute a natural host-parasitoid assemblage, and what fraction of the possible host-parasitoid associations are actually realized in the field. Secondly, we investigate the degree to which the community is compartmentalized (divided into strongly interacting subcommunities). There is a huge body of theory on host-parasitoid dynamics, but most studies consider only pairs or small sets of interacting species (Hassell 2000). If a community is highly compartmentalized, then it might be possible to study its dynamics as a series of loosely coupled modules whose behaviour can be investigated using established theory. A more uniformly connected community would require a different approach. Thirdly, we ask how the structure of the web, and different web statistics, vary among seasons. Fourthly, we are interested in the extent to which host species that do not interact directly, typically because they feed on different host plants, might nevertheless influence each other's population dynamics through shared natural enemies. Such effects were termed apparent competition by Holt (1977) and are widely thought to be important in structuring insect communities (Jeffries & Lawton 1984; Holt, Grover & Tilman 1994). A definitive proof of apparent competition requires an experimental approach, or at least a long time-series of data, but we are able to use our food web data to assess the potential for such indirect effects. Fifthly, we explore the factors that determine the number of hosts per host plant, parasitoids per host, and the host range of parasitoids. These questions have been investigated normally at larger geographical scales (Strong *et al.* 1984; Hawkins 1994) but more detailed studies at a smaller geographical scale may be particularly informative about how a community is structured. We explore the robustness of our conclusions by re-analysing the web after omitting successively rarer species interactions, and by comparing properties of the full web with three seasonal subwebs. Finally, and more specific to this web, we investigate the extent to which our forest edge community is influenced by species that live in the forest interior or the forest canopy.

## Methods

### STUDY SYSTEM

The leaf-miners in our study area are insects from the orders Diptera (flies), Coleoptera (beetles) and Lepidoptera (moths) which feed as larvae in tunnels or chambers within the leaves of their host plants, creating

distinctive lines or blotches ('mines') on the leaf surface. Hespenheide (1991) provides a useful review of leaf-miner biology. The parasitoids of leaf-miners are Hymenoptera (wasps) and to a much lesser extent Diptera, which lay eggs on or within the leaf-miner larvae and whose larvae develop on the host tissue. We chose leaf-miners for our study for a number of reasons. First, leaf-miners form a distinct feeding guild whose parasitoids rarely attack hosts in other guilds (Askew 1994). Secondly, leaf-miners are relatively simple to sample and rear, and the permanent, normally species-specific feeding marks that they produce facilitate the association of parasitoids with their correct hosts. Thirdly, because leaf-miners are quite static (almost all species in this study completed their larval development within a single leaf) it is much easier to obtain quantitative estimates of host abundances and rates of parasitism, compared with more mobile hosts. Finally, parasitoids are a major source of mortality for leaf-miners, with typically 30–60% parasitism across species in previous studies (Askew & Shaw 1974, 1979; Memmott *et al.* 1994; Rott & Godfray 2000). Thus, the dynamic interactions among hosts and parasitoids are likely to be important in structuring the community (Hawkins, Thomas & Hochberg 1993).

Our field site was in moist tropical forest near the Las Cuevas Research Station in the 170 000 ha Chiquibul Forest Reserve, Cayo District, in south-west Belize. This forest was classified by Wright *et al.* (1959) as Deciduous Seasonal Forest and Deciduous/Semi-Evergreen Seasonal Forest. The research station is the only permanent settlement in the forest, although much of the area would have been under cultivation during the Mayan period (up to approximately 700 years ago), and the vegetation of the area may still reflect their impact (Johnson & Chaffey 1973). The climate in this area is seasonal, with a humid season typically from June to January and a dry season from February to May. The Chiquibul Forest is affected by hurricanes, and much of the vegetation in the study area has grown up following extensive wind and fire damage resulting from Hurricane Hattie in 1961. Preliminary surveys showed that leaf-miner abundance was low in the forest understorey and in the forest canopy (see below), whereas leaf-miners were abundant along trail edges, which were probably artificial analogues of forest gaps. For our plot, we chose the margins of a trail (known as the Monkey Tail Track) running east from the research station through the forest, an area 1700 m long and 5 m wide.

#### WEB CONSTRUCTION

To build the web we must obtain (i) quantitative estimates of the densities of all hosts in the site and (ii) quantitative information about the parasitoids attacking each host. Combining information on host density with that on the fraction of each host species successfully parasitized by different parasitoid species

allows the densities of all hosts, parasitoids and trophic links to be expressed in the same units ( $\text{m}^{-2}$ ).

To estimate host densities we divided the plot into four sectors and then 34 'sections': a length of trail 100 m long and 2.5 m wide incorporating the vegetation on either the north or south side of the track. Every 10 days a section was chosen for quantitative sampling. We stratified the plot by sector and north/south orientation, and on each sampling occasion chose a section at random from a new sector on an 8-week rotation. Sampling of miners was carried out between September 1997 and September 1998, in all months except December, January and May. All vegetation up to a height of 2 m in the sampled 100 m  $\times$  2.5 m section was searched carefully and all occupied mines and their host plant recorded. Our rearing records confirmed that almost all leaf-miner species could be recognized in the field by the combination of host plant and mine morphology (see Results).

Quantitative information on parasitism was obtained by rearing samples of each host. We collected and reared all the occupied mines found in the host density surveys described above, and supplemented these with additional mines from stratified collecting throughout the site (avoiding areas within and close to sections scheduled to be sampled in the next 4 weeks); on a further 2 km of the track further east along the Monkey Tail Track; and in similar habitat on a trail known as the San Pastor Track (0.5–4 km away). To rear hosts and parasitoids in the laboratory, individual leaves containing leaf-miners were placed in airtight plastic pots lined with absorbent paper until adult leaf-miners or parasitoids hatched. In some cases, leaves were kept fresh by placing their petioles in water. Depending on species, leaf-miner larvae may pupate either inside or outside the mine, and parasitoids may emerge either directly from the mine or from the host pupa.

#### TAXONOMY

Identification of over 4000 specimens of plants, leaf-miners and parasitoids from a diverse and poorly studied tropical ecosystem presented a considerable taxonomic challenge. To build a food web it is necessary only that species are recognized as distinct ('morphospecies'), although clearly a precise taxonomic identification increases the long-term value of the information obtained. Plants (largely sterile material) were identified to species by CW and voucher specimens are preserved in the Department of Botany at The Natural History Museum, London. Insects were identified to species or morphospecies with assistance from a network of taxonomic collaborators with expertise in different taxa (see Acknowledgements). Few of the insect species represented described species, and at least one parasitoid was a representative of a previously undescribed genus (Delvare & LaSalle 2000). Insect voucher specimens are preserved in the Department

**Table 1.** Tree and palm species investigated to assess the abundance of leaf-miners in the forest canopy. Five individuals of each species were searched for occupied and unoccupied mines

Plant species	Family	Approximate canopy area of searched plants ( $m^2$ )	Leaf-miner species recorded	Total unoccupied mines	Total occupied mines
<i>Stemmadenia donnell-smithii</i>	Apocynaceae	33	1	1	1
<i>Protium copal</i>	Burseraceae	31	1	12	0
<i>Sebastiana longicuspis</i>	Euphorbiaceae	29	1	1	0
<i>Pimenta dioica</i>	Myrtaceae	50	1	9	1
<i>Hesiteria media</i>	Olaceae	64	2	31	0
<i>Chryosiphila stauracantha</i>	Arecaceae	24	0	0	0
<i>Coccoloba belizensis</i>	Polygonaceae	28	1	178	0
<i>Pouteria campechiana</i>	Sapotaceae	36	0	0	0
<i>Pouteria reticulata</i>	Sapotaceae	20	1	201	0
<i>Vitex gaumeri</i>	Verbenaceae	59	0	0	0

of Entomology at The Natural History Museum, London.

#### ADDITIONAL SAMPLING

We surveyed the abundances of both mined and unmined plant species in the plot, to determine whether plant abundance influenced the number of leaf-miner species recorded per plant species. The large area of the plot combined with its high plant diversity made it impossible to carry out a comprehensive plant inventory. Instead, 14 10 m  $\times$  2.5 m subplots were chosen by stratified random sampling, and within each of these sections we recorded all plant species (individuals  $> 5$  cm high), and estimated their abundance on a scale of 1 (rare) to 5 (abundant). For each plant species, our measure of abundance was the sum of abundance values across the 14 subplots, and thus potentially varied from 0 to 70. To investigate their influence on the number of leaf-miner species associated with different plants, a variety of plant characteristics were also recorded. Plants were divided into six growth form categories (monocotyledonous herbs, dicotyledonous herbs, vines/lianas, shrubs, palms and trees). Mean leaf length was calculated from a sample of 5–15 leaves from each species. Two measures of plant taxonomic isolation were calculated, using data from Balick, Nee & Atha (2001): the number of plant species in Belize in the same genus, and the number of plant species in Belize in the same family. Finally, data on the geographical range occupied by each plant species were extracted from the literature (Croat 1978; Standley & Steyermark 1946–83) and from the Tropicos database (<http://mobot.mobot.org/W3T/Search/vast.html>). Plants were placed into one of four geographical range categories: (1) confined to Belize, Guatemala and Mexico; (2) range extending to other countries within central America; (3) range extending to South America and/or the southern United States; and (4) pantropical.

If the forest canopy and interior understorey support large populations of leaf-miners, then the food web may be influenced by immigration of parasitoids

from adjacent habitats. To assess the magnitude of this effect, we surveyed leaf-miner abundance in these two habitats. Understorey leaf-miner abundance was estimated by searching five randomly selected 2.5 m  $\times$  100 m sections parallel to the main plot but 50 m inside the forest. Canopy leaf-miner abundance was assessed by felling a sample of canopy trees and palms. The species selected included nine trees and one palm (representing nine plant families in total, see Table 1), and were among the 20 most abundant canopy species in the Las Cuevas area (Bird 1998). Five individuals of each species were felled, the area of canopy space occupied by each plant's crown was estimated, and their foliage was searched for occupied and unoccupied mines.

#### ANALYSIS

##### *Food webs*

We use quantitative food webs to provide a visual description of the structure of the host-parasitoid community. To create a summary web we summed the densities of hosts, parasitoids and trophic links over the 9 months of the study. We also present webs for the three main seasonal periods (i.e. the dry season, February–April inclusive; the early wet season, June–August; and the late wet season, September–November).

##### *Web statistics*

Connectance in food webs is usually calculated as  $2L/N(N - 1)$  where  $N$  and  $L$  are the total number of species and trophic links in the web. This measure is less suitable for host-parasitoid webs, as it allows the possibility of hosts feeding on hosts (which is not possible) and parasitoids feeding on parasitoids (hyperparasitism). Obligate hyperparasitoids are absent from our web, while facultative hyperparasitism is likely to be common but was not quantified. Given  $H$  hosts and  $P$  parasitoids the maximum possible number of host-parasitoid associations is  $HP$  and thus we define  $L/HP$  as an alternative measure of the fraction of realized links.

The number of compartments in a food web is defined as the number of subwebs with no connection to any other subweb. To calculate the number of compartments, we consider only subwebs that include both hosts and parasitoids, so that a single host species attacked by no parasitoids is not considered a separate compartment. We found that the size of different subwebs was highly variable (see Results) and to represent this calculated a measure we called compartment diversity,  $\exp - (\sum_{i=1}^n p_i \ln p_i)$ , where  $p_i$  is the fraction of all host and parasitoid species in the  $i$ th of  $n$  compartments. This is the exponential form of the Shannon–Wiener diversity index (Magurran 1988). Compartment diversity equals  $n$  when the number of species in each compartment is the same and becomes smaller as the asymmetries in subweb size increase.

We use the Jaccard index (Magurran 1988) to compare the similarity of species composition in seasonal webs. If two seasonal webs share a species, while  $b$  and  $c$  species occur uniquely in each of the two seasonal webs, then the Jaccard coefficient is defined as  $a / (a + b + c)$ .

#### *Robustness analysis*

The most informative web statistics are those that are robust to changes in sampling intensity (Martinez *et al.* 1999). We assessed robustness by recalculating different statistics in webs that omitted rarer associations and species. To do this, we defined 18 threshold link frequencies spaced equally on a log scale between the observed maximum and minimum link frequencies. The statistics were calculated for webs containing only links above the threshold link frequency, and the results displayed by plotting the three-point running average of the statistics against the threshold.

#### *Potential for indirect interactions*

We assess the extent to which hosts are likely to be dynamically linked by shared parasitoids using quantitative parasitoid overlap diagrams (Müller *et al.* 1999). For each leaf-miner species we calculate the probability ( $d_{ij}$ ) that a parasitoid attacking species  $i$  developed on species  $j$  (where  $j$  may be the same species:  $d_{ii}$ ). We assume that parasitoids of each species move randomly through the community, and that there are not races or biotypes associated with different host species; making these assumptions:

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

where  $\alpha_{ik}$  is the absolute density of the trophic link between host  $i$  and parasitoid  $k$  (and hence the summations in  $k$  and  $l$  are over all parasitoids and in  $m$  over all hosts).

#### *Structuring factors*

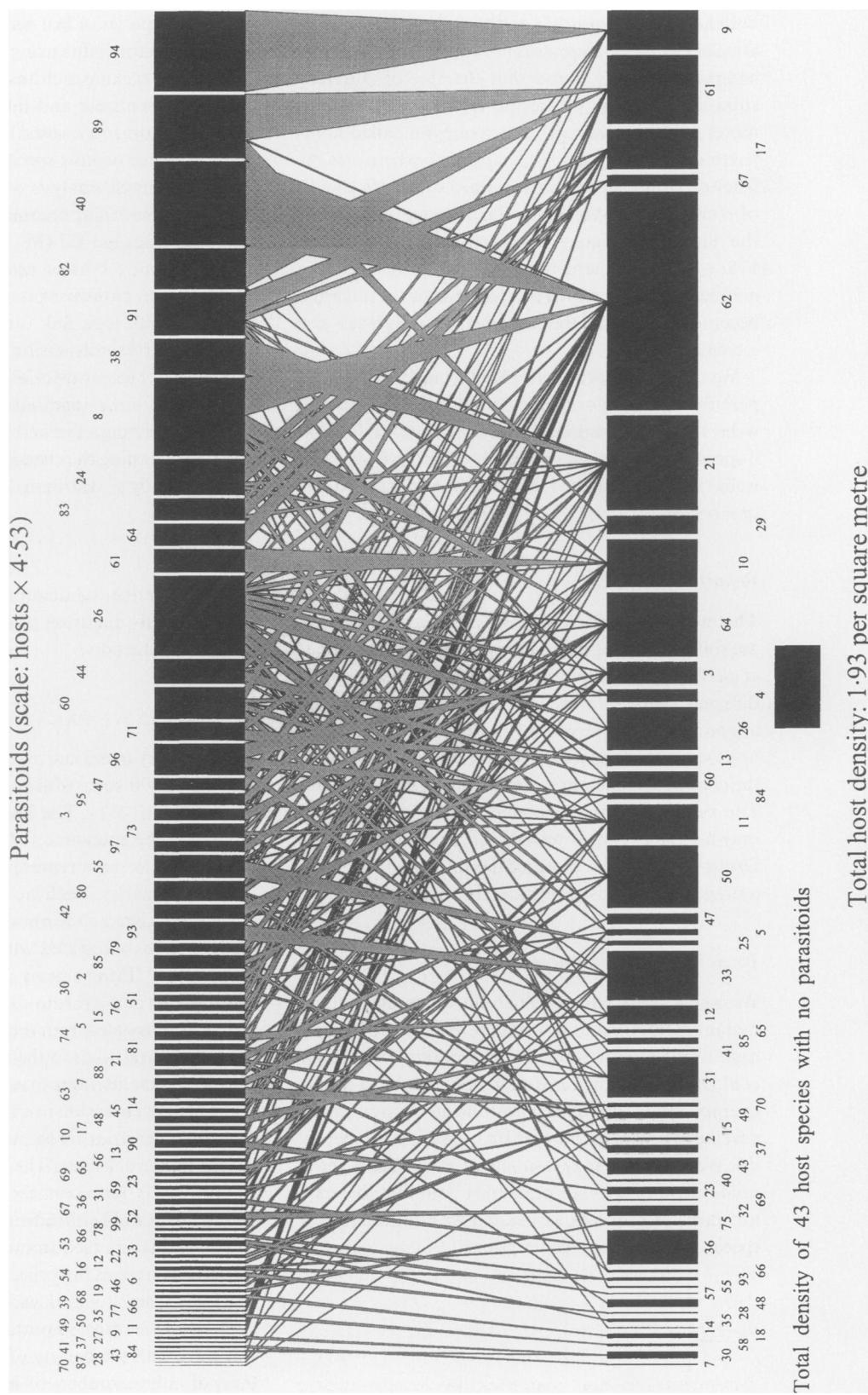
We investigated three classes of factor that might affect the structure of the web: (i) factors influencing the number of species of leaf-miner attacking a particular plant; (ii) factors influencing the number of species of parasitoid attacking each host and the fraction of hosts that are parasitized; and (iii) factors influencing the number of host species used by each parasitoid species, and the degree of host specificity. The data were analysed by stepwise analysis of deviance using generalized linear modelling techniques, implemented in the statistical package GLIM. The analyses of species counts assume a Poisson error distribution and those of proportion parasitism assume a binomial error distribution (with logit link function); in both cases we corrected for overdispersion where necessary using a heterogeneity factor (McCullagh & Nelder 1989). For non-normal error distributions, the significance of adding or deleting a factor from the statistical model is assessed by testing the change in the deviance, which is asymptotically  $\chi^2$  distributed.

#### **Results**

We first describe the quantitative food web and then address the six questions posed in the final paragraph of the Introduction.

#### QUANTITATIVE PARASITOID WEBS

Our summary quantitative web is shown in Fig. 1. It is based on 3470 successful rearings of hosts (1989) or parasitoids (1481). The lower series of black bars represents the abundance of the leaf-miners, and the upper series of bars represents the abundance of the parasitoid species. Each host and parasitoid species has an associated code number, and the species-level identifications associated with each code are listed in Appendix 1. Information on interactions between hosts, plants and parasitoids used to draw the webs is available on request from the authors. The ordering of hosts and parasitoids in the webs is determined by an algorithm that attempts to minimize overlap, and thus makes the web easier to interpret. For clarity, the parasitoid densities are shown at a larger scale relative to leaf-miner densities. The ‘wedges’ linking the two trophic levels represent the host–parasitoid associations. For example, all individuals of parasitoid species 94 (far right) emerged from host species 9; similarly, the most abundant host species 62 was attacked by 27 species of parasitoid, of which species 8 and 40 were numerically the most important. Webs can be drawn in two ways with the density of parasitoids measured in units of either numbers of individuals or numbers of mines attacked (Rott & Godfray 2000). The two differ only when more than one parasitoid emerges per host, and in our data a minority of parasitoid species (25) were gregarious. Here we have chosen the second



**Fig. 1.** Summary quantitative web, combining data for the whole year. The two series of black bars represent the abundance of leaf-miners (below) and parasitoids (above), drawn at different scales. The species associated with each code number are listed in Appendix 1. Links between the two trophic levels illustrate the relative frequency of each host-parasitoid association.

option, expressing parasitoid densities in terms of the number of mines attacked.

There were two exceptions to our ability to identify hosts in the mine and hence two host groupings in the web are in fact aggregates of pairs of species. Host taxon 50 is an aggregate of two hispine beetles, *Pentispa fairmairei* (Chapuis) and *Baliosus lineaticollis* Baly (feeding on several species of Asteraceae); taxon 30 consists of two lepidopterans, Gracillariinae sp.4 and Lepidoptera sp.1 (feeding on *Psychotria nervosa* Sw.). Although the lepidopterans were rare ( $0.013 \text{ m}^{-2}$  over the year), the hispine beetles in combination represent the fourth most abundant ‘host’ in the web ( $0.11 \text{ m}^{-2}$ ). Our data suggest that host taxon 50 is largely composed of *P. fairmairei* which accounted for 101 of 112 (90%) successful rearings of adult beetles from this pair of species.

In Fig. 2 we display three seasonal webs, representing the dry season (February–April, inclusive), the early wet season (June–August) and the late wet season (September–November). These webs are drawn using the same conventions as for the full web and we retain the same ordering of host and parasitoid taxa.

#### WEB SIZE AND LINKAGE

The summary web contains 93 species of leaf-miner and 84 species of parasitoid, with a total of 196 host–parasitoid links. Of the 93 hosts in the web, parasitoids were reared from 50; the absence of parasitoids from the other 43 species almost certainly reflects their rarity in the study site and hence the small number of individuals collected: with the exception of one species, all host species with greater than 11 rearings produced parasitoids. A further 20 species of parasitoid and 55 species of host were recorded in additional collections in or near the plot (72 additional host–parasitoid associations); all of these were rare and their absence from the quantitative web reflects sample size or the absence of particular host plants within the plot. The ratio of the numbers of host and parasitoid species was 1.11 (including hosts with no recorded parasitoids) or 0.60 (excluding these hosts). The realized connectance was 0.025 or 0.047 (with or without hosts with no parasitoid records).

Robustness analysis reveals which of these statistics is most susceptible to sampling intensity. As expected, the number of species and trophic links declines as the threshold for inclusion increases (Fig. 3a). However, the decline in the numbers of hosts and parasitoids is initially shallow, indicating that our sampling may have detected most species. The decline in the number of trophic links is much steeper, suggesting that a smaller proportion of links have been detected. In Fig. 3b the robustness of the host : parasitoid species ratio and the realized connectance are shown (in both cases calculated using only hosts from which parasitoids were recorded). The host : parasitoid ratio and realized connectance increase as weaker links are excluded, though

the increase is initially very shallow: by the time half the parasitoid species have been lost from the web, the host : parasitoid ratio has increased from 0.60 to 0.86 and the realized connectance has increased from 0.047 to 0.061 (in both cases hosts with no parasitoids are excluded).

For clarity, host plants are not shown in the webs, but host plant identifications and associations are available on request from the authors. Most leaf-miners were highly host plant-specific: the 93 herbivorous insects were recorded as using 71 host plants, with a total of 114 links between host plants and leaf-miners. A further 204 plant species were recorded in our plots, but no living miners were recorded on them.

#### COMPARTMENTALIZATION

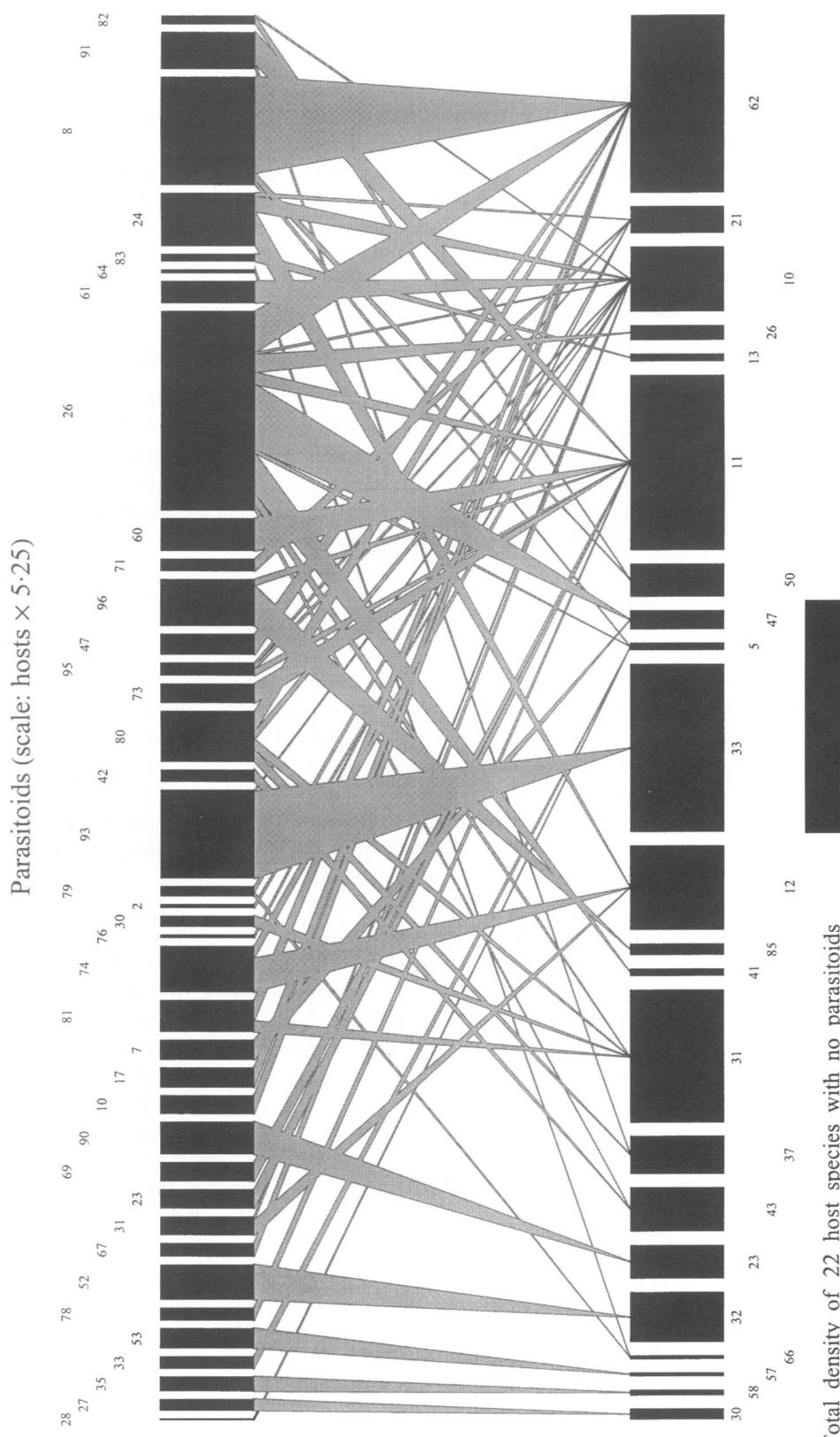
The full web consists of eight disconnected subwebs or compartments, but they are of radically different sizes: one contains 118 species of host and parasitoid while the others contain only three or two species. Our measure of compartment diversity, 1.81, is thus much nearer one than eight.

The robustness of these two measures (the number of compartments, and their diversity) is shown in Fig. 3c. As progressively weaker links are excluded, the number of compartments rises slowly until, when over half the species have been lost from the web, it peaks at about 12 representing a series of common hosts with their most abundant parasitoids, which appear to be monophagous at this level of resolution. Compartment diversity on the other hand remains approximately constant at ~2 until half the species are lost, when it rises to a value only a little lower than the number of compartments.

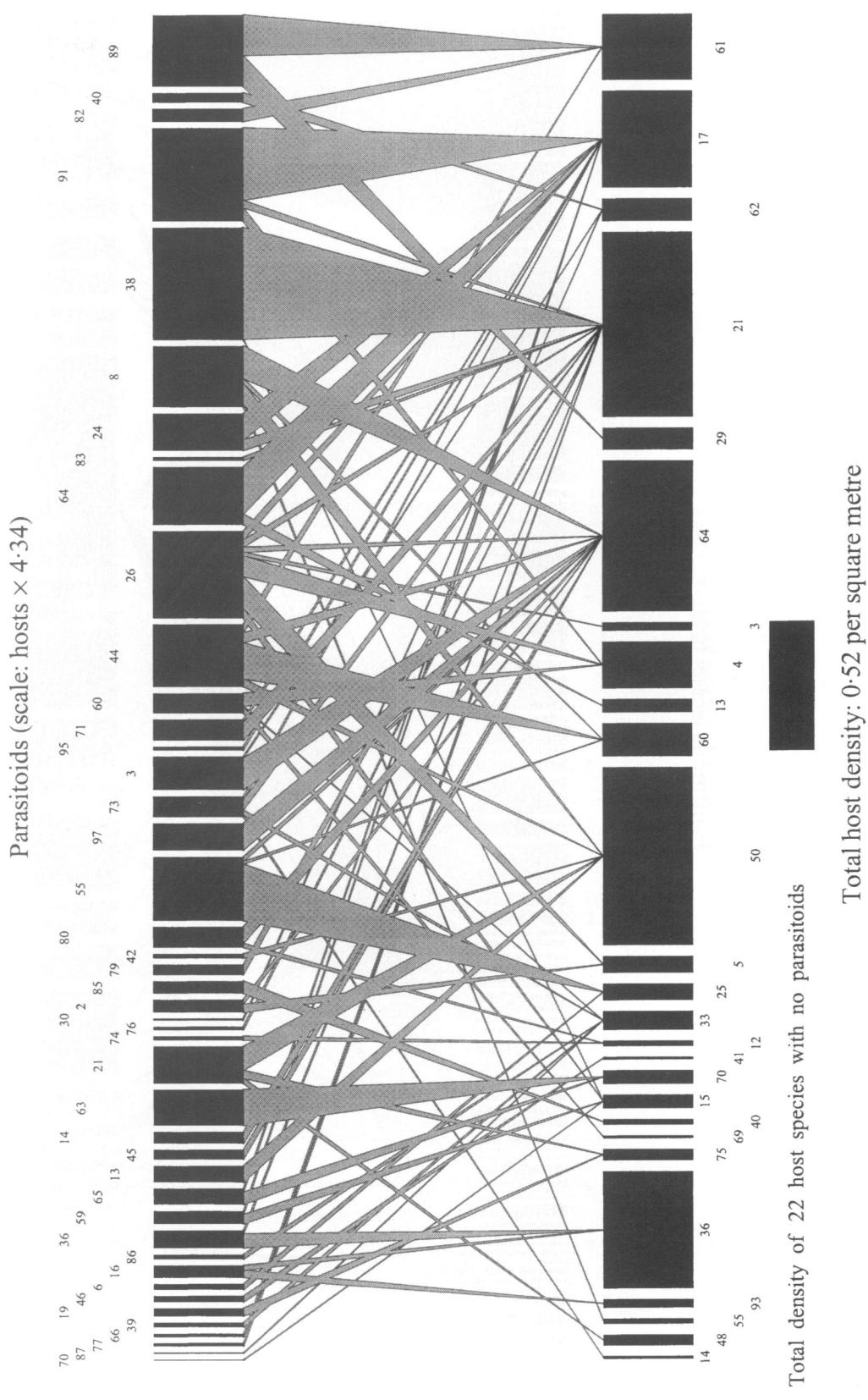
#### SEASONALITY

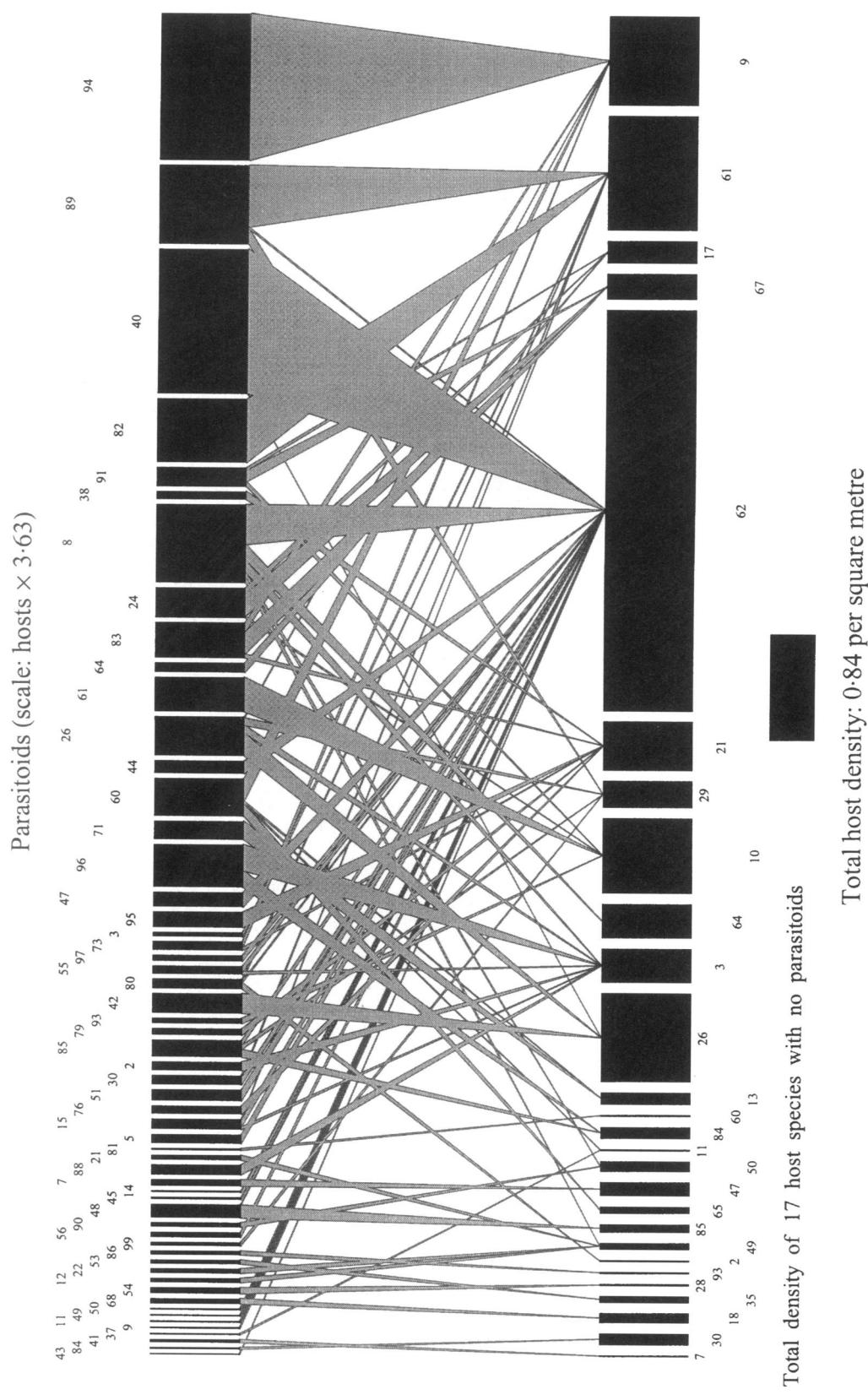
Comparisons of the statistics of three seasonal webs (Fig. 2) with those from the full web can, like the robustness analysis, suggest constant patterns in community structure. In Table 2 we summarize these statistics, and in Fig. 3b,c, which displays the robustness analysis, we also plot at the right hand side of the graphs the equivalent values from the seasonal webs.

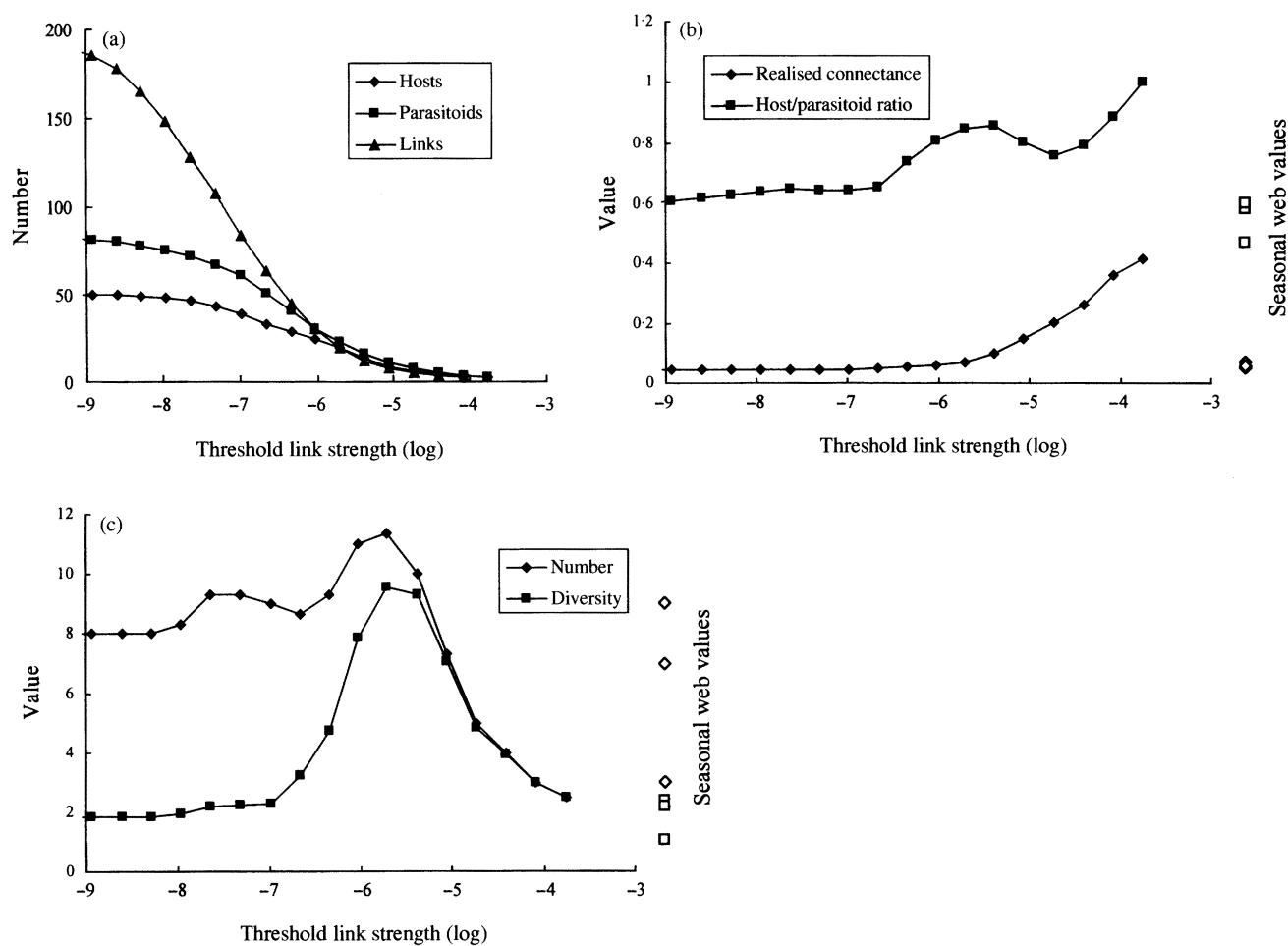
Approximately half the species in the full web appear in each of the three seasonal webs (82, 92 and 101 species in the dry, early wet and late wet season webs, respectively). Although there was substantial overlap of species between seasons there was less overlap of associations, with the large majority occurring in only one web. The mean between-season Jaccard similarity coefficient is 0.27 (s.e. = 0.02, n = 3) for hosts and 0.35 (s.e. = 0.04, n = 3) for parasitoids. The host : parasitoid species ratio (excluding the mostly rare hosts with no parasitoids) was relatively constant among webs (Fig. 3b) but realized connectance was consistently higher in the seasonal webs. The probable reason for this is that in the full web some potential host–parasitoid links were not realized because of the



**Fig. 2a.** Seasonal webs for (a) dry season (February–April), (b) early wet season (June–August) and (c) late wet season (September–November). The webs are drawn using the same conventions as Fig. 1, and the ordering of species is maintained.







**Fig. 3.** The effects of changing sampling intensity on food web statistics. Sampling intensity decreases from left to right along the horizontal axis, as progressively less frequent host-parasitoid interactions are dropped from the data set. (a) Recorded host species, parasitoid species and number of links. (b) Recorded connectance and ratio of hosts to parasitoids, with the values for the three seasonal webs plotted on the same axis. (c) Recorded number and diversity of compartments (see text for details), with the values for the seasonal webs plotted on the same axis.

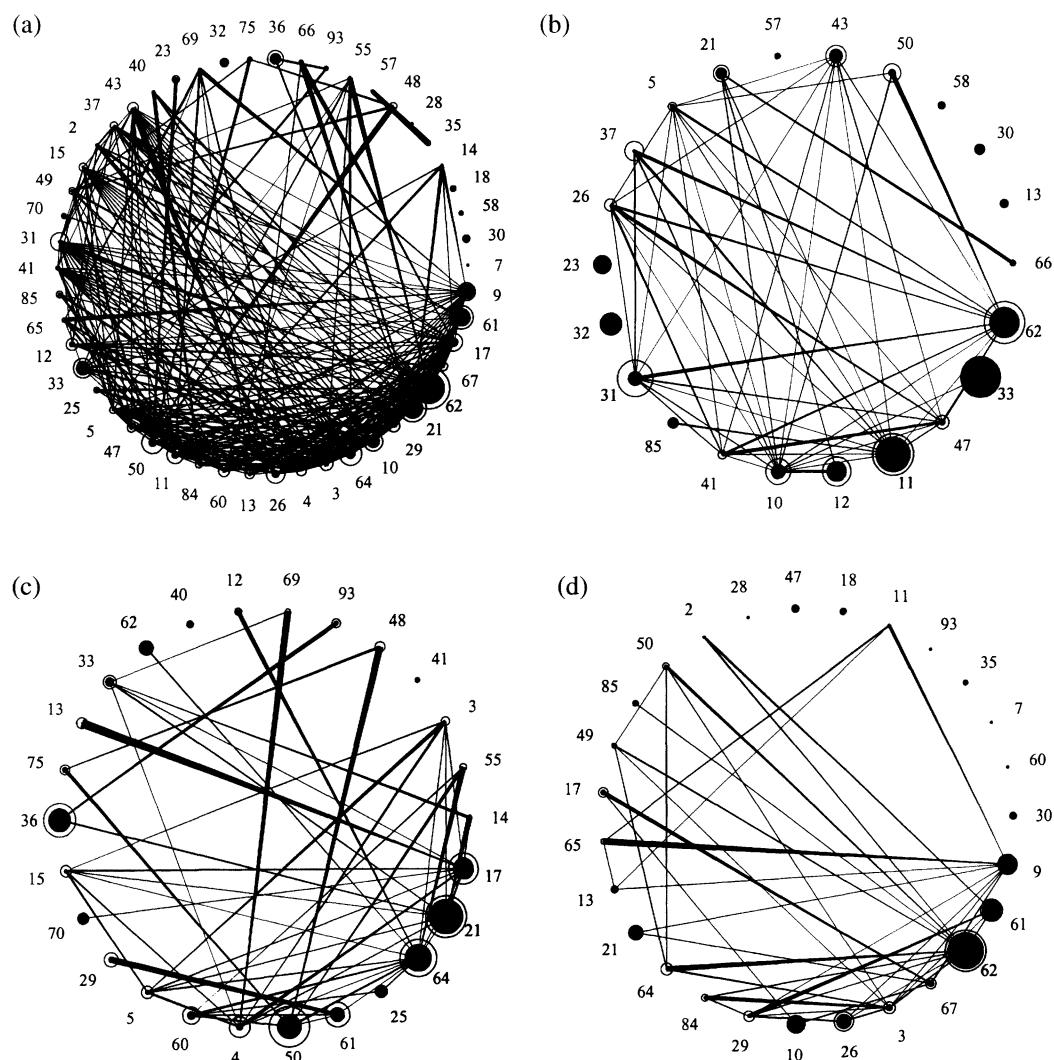
**Table 2.** Summary of food web statistics for the three seasonal webs and the summary web. The number and diversity of compartments are defined in the Methods

	Dry season	Early wet season	Late wet season	Overall
Number of host species ( $H$ )	44	48	44	93
Number of host species with parasitoids ( $H_p$ )	22	26	27	50
Number of parasitoid species ( $P$ )	38	44	57	84
Number of associations ( $L$ )	63	79	87	196
Host : parasitoid ratio ( $H/P$ )	1.16	1.09	0.77	1.11
Host : parasitoid ratio ( $H_p/P$ )	0.58	0.59	0.47	0.60
Connectance $2L/N(N - 1)$	0.019	0.019	0.017	0.013
Realised connectance $L/(H \times P)$	0.038	0.037	0.035	0.025
Realised connectance $L/(H_p \times P)$	0.075	0.069	0.057	0.047
Estimated total mines $m^{-2} month^{-1}$	0.13	0.18	0.38	0.21
Number of compartments	7	3	9	8
Diversity of compartments	2.36	1.29	2.41	1.81

relative phenology of hosts and parasitoids. The seasonal webs are rather variable in terms of compartment number, but less so in compartment diversity. In all cases the majority of species fall within a single group of linked species and hence compartmentalization is always low.

#### POTENTIAL FOR INDIRECT INTERACTIONS

The quantitative parasitoid overlap diagrams (Fig. 4) illustrate the probability ( $d_{ij}$ ) that a parasitoid currently attacking species  $i$  developed on species  $j$ . In Fig. 4 each circle is a vertex representing a host species, and the size



**Fig. 4.** Quantitative parasitoid overlap graphs. The numbered circles or vertices represent leaf-miner species, and their size is proportional to the abundance of parasitoids emerging from each host. The extent to which a vertex is shaded black indicates the importance of that host as a source of its own parasitoids. Lines between hosts indicate shared parasitism, with the width of the link at each species representing the potential influence of the other species as a source of parasitoids. The formula and assumptions used in drawing the graphs are explained in the text. (a) Summary graph, for the 9 months of sampling. (b) Dry season (February–April). (c) Early wet season (June–August). (d) Late wet season (September–November).

of each vertex is proportional to the number of parasitoids that were reared from that species of host. The extent to which each vertex is shaded black represents the magnitude of  $d_{ii}$ . If the vertex is largely black,  $d_{ii}$  is close to one, and most parasitoids are likely to have developed on the same host. If the vertex is largely white then  $d_{ii}$  is close to zero, and most parasitoids are likely to have developed on other host species. A line linking two hosts represents shared parasitism, and the width of the line at species  $i$  and  $j$  represents  $d_{ij}$  and  $d_{ji}$ , respectively: the importance of species  $j$  as a source of parasitoids attacking species  $i$  and *vice versa*. So, in Fig. 4c, the quantitative parasitoid overlap diagram for the early wet season, the majority of parasitoids attacking the fairly abundant host species 17 are likely to have developed on the same species of host, and this species is also predicted to act as a major source of parasitoids attacking host 13. Because this interaction is asymmetrical (very few of the parasitoids attacking host 17 are

likely to have developed on host 13), we predict that asymmetric apparent competition mediated by shared parasitism is likely to occur between these two species, such that increases in the abundance of host 17 lead to decreases in the abundance of host 13.

What factors determine the potential for indirect interactions? To try to answer this question we explore statistically the determinants of  $d_{ij}$  and  $d_{ji}$  treating these values as standard independent responses. In fact we do not know the sampling distribution of these quantities so the probability figures we give should be treated with caution. We omit the two ‘host complexes’ (codes 30 and 50) which contain multiple species of leaf-miner. The 2256  $d_{ij}$  terms are significantly larger than the 48  $d_{ii}$  terms (Mann–Whitney Test,  $U = 108311$ ,  $P < 0.0001$ ), reflecting host specialization by parasitoids. The distribution of  $d_{ij}$  values is non-normal, with 1764 zero values (representing pairs of hosts that do not share parasitoids) and 492 nonzero values

(representing pairs of hosts that have at least one parasitoid species in common). To further investigate the host factors that influence the presence of  $d_{ij}$  values, the data were analysed using stepwise multiple binary logistic regression. The probability that two hosts species are linked (i.e. that their  $d_{ij}$  term is nonzero) is strongly influenced by the abundance of species  $j$  ( $\chi^2_1 = 27.4, P < 0.001$ ). Thus, most indirect interactions are likely to involve the asymmetric effects of common species on rare species. Taxonomically related hosts are more likely to interact via shared parasitoids ( $\chi^2_1 = 148.0, P < 0.001$ ), and the probability of recording indirect interactions between hosts  $i$  and  $j$  increased with the number of months host  $j$  was present in the field ( $\chi^2_1 = 185.4, P < 0.001$ ). However, sharing a host plant did not influence the likelihood of two species sharing parasitoids ( $\chi^2_1 = 1.1, P = 0.29$ ).

#### STRUCTURING FACTORS

To increase the power of the statistical tests, analyses of the importance of plant, host and parasitoid factors in structuring the community include data for all species of plant, leaf-miner and parasitoid recorded during sampling (not just species included in the quantitative web).

##### (1) Leaf-miner species numbers on different plants

More abundant plants supported larger numbers of leaf-miner species than rare plants ( $\chi^2_1 = 11.4, P < 0.001$ ). After controlling for plant abundance, we found a significant effect of plant growth form ( $\chi^2_5 = 35.8, P < 0.001$ ) with leaf-miner species numbers highest on monocotyledonous herbs and lowest on palms. One of the measures of taxonomic isolation, the number of plant species in the same family present in Belize, had a highly significant effect on leaf-miner species numbers ( $\chi^2_1 = 30.6, P < 0.001$ ), but this effect was due largely to the Asteraceae, which is species-rich in Belize (Balick *et al.* 2001) and whose members tended to support many miner species in our site. No significant effect was found if the Asteraceae were omitted from the analysis, or if the number of plant species in Belize in the same genus was used as the measure of taxonomic isolation ( $\chi^2_1 = 1.59, P = 0.21$ ). We found no significant effect of leaf size ( $\chi^2_1 = 2.45, P = 0.12$ ) or host plant geographical range ( $\chi^2_1 = 0.02, P = 0.89$ ) on leaf-miner species numbers.

##### (2) Parasitoid species numbers and mortality on different hosts

We explored the correlates of the number of species of parasitoids attacking different host species, omitting the two host complexes that could not be resolved to species level in the field. The number of species recorded from a host was positively influenced by the

number of rearings ( $\chi^2_1 = 25.8, P < 0.001$ ), and by the number of months during which a host was present in the field ( $\chi^2_1 = 141.4, P < 0.001$ ). There were no significant effects of host order ( $\chi^2_1 = 0.32, P = 0.57$ ), or the presence and abundance of alternative hosts on the same host plant (presence:  $\chi^2_1 = 0.01, P = 0.92$ ; abundance:  $\chi^2_1 = 2.0, P = 0.16$ ).

We also explored the factors influencing the percentage mortality of different host species caused by parasitoids. There was a marginally significant effect of host order ( $F_{2,142} = 3.08, P = 0.05$ ) caused by greater rates of parasitism on hosts from the Diptera compared with those in the Lepidoptera or Coleoptera. There was also a significant effect of the abundance of other host species on the same host plant ( $F_{1,142} = 4.48, P = 0.04$ ). Hosts that share host plants with other abundant miners suffer greater rates of parasitism.

#### (3) Parasitoid host range

The number of hosts from which a parasitoid is reared (host range) depends strongly on sample size, the total number of individuals reared of that species ( $\chi^2_1 = 69.4, P < 0.001$ ). The mean number of hosts from which a parasitoid species was reared was 2.77 (SE = 0.31) and there was no significant difference between the host range of endoparasitoids and ectoparasitoids ( $\chi^2_1 = 1.14, P = 0.29$ ). However, there was a significant interaction between mode of parasitism and sample size, with the host range of ectoparasitoid species increasing more rapidly than the host range of endoparasitoid species as sample size increases ( $\chi^2_1 = 5.52, P = 0.02$ ).

#### MINER ABUNDANCE IN THE FOREST CANOPY AND UNDERSTOREY

Leaf-miner abundance in the forest canopy and understorey was very low, even though sampling in these habitats took place during the early and late wet season when leaf-miner abundance in our plot was high. Table 1 shows the leaf-miner abundance in the forest canopy: only two living mines were recorded during this sampling. If the 10 tree and palm species surveyed are typical of canopy plants in the Las Cuevas area, the density of miners recorded is approximately 0.0054 mines  $m^{-2}$  of ground area. This is just 2.3% of the mean value (0.235 mines  $m^{-2}$ ) in our main study site. A greater number of unoccupied mines were found, especially of single species of insect on *Coccoloba belizensis* Standl. and *Pouteria reticulata* (Engl.) Eyma. This may indicate species that are active at a different time of year, or the cumulative mining activity visible on long-lived leaves. Similarly, leaf-miner abundance in the understorey was low: only 15 occupied mines were recorded in the five understorey sections, equivalent to a leaf-miner density of 0.012 mines  $m^{-2}$ . This is approximately 5% of the mean value for sections within the plot.

## Discussion

We believe our study of a community of leaf-miners and their parasitoids in a tropical forest in Belize is the largest fully quantitative web so far constructed, and reveals some of the complexity of tropical communities. We discuss our findings in four sections. First, we consider possible sources of error in the food web, and other limitations of our methods. Secondly, we discuss our measures of community structure and their sensitivity to sampling error. Thirdly, we consider the importance of plant, host and parasitoid factors in structuring the community. Finally, we assess the role of quantitative food webs in indicating the potential for indirect interactions between hosts, mediated by shared parasitism.

### LIMITATIONS OF OUR METHODS

Quantitative parasitoid webs suffer from a number of potential sources of error, which have been discussed in detail by Memmott *et al.* (1994) and Müller *et al.* (1999). Here we concentrate on those that are particularly likely to affect our study.

The web summarizes data on the abundance of hosts, parasitoids and the links between them. Quantitative sampling of the host is relatively straightforward because of the semipermanent record the mine leaves on the host plant. Some mines can be cryptic but the vast majority will be located in the field and, with the few exceptions discussed in the Methods, can be identified to species based on a combination of host plant and mine morphology. Host densities are estimated from the abundance of tenanted mines, so differences in the length of the larval stage across species might introduce a bias. However, in the absence of diapause or other prolonged tenancy we estimate this bias to be small. There are more uncertainties in the estimation of the number and abundance of links and parasitoid species. We do this by rearing tenanted mines collected in the field, and there are two main sources of error. First, we may have differential success in rearing species of parasitoid or host. Secondly, we may prevent some parasitoid attack by bringing mines into the laboratory for rearing. Because most parasitoids attack relatively young mines we expect this source of error to be small, but not zero.

One limitation on the type of quantitative web we have constructed is that it does not distinguish hyperparasitism from primary parasitism. Obligate hyperparasitoids (species that can only develop at the expense of primary parasitoids) are rarely associated with leaf-miners and the species involved can normally be recognized as they belong to particular taxa (e.g. Perilampidae); we believe they are absent from our web. Facultative hyperparasitism, where a parasitoid will feed on the host or equally on any parasitoid already present in the mine, is widespread among leaf-miner parasitoids (Askew & Shaw 1974) and almost certainly occurs in the community we have studied.

Without laborious and detailed dissections, rates of facultative hyperparasitism cannot be determined and thus our web describes the net outcome of parasitism and not the detailed interactions within the parasitoid community. It is thus misleading to view our webs as evidence for a rigid trophic structure as there are likely to be rich interactions within the parasitoid assemblage (cf. Polis & Strong 1996).

The webs display the species of host and parasitoid, determined by morphological criteria, as uniform entities. Several factors may interfere with this. First, cryptic species (species that cannot be distinguished morphologically) may be present, particularly among the parasitoids. If the cryptic species are more specialized than the morphospecies, connectance and other web properties may be overestimated. While we cannot exclude the possibility that such species are present among the poorly known insects we encountered, we know that the morphological criteria perform very well in much more thoroughly studied temperate leaf-miner communities (Askew & Shaw 1974; Askew 1980; Rott & Godfray 2000) and we think it unlikely that this is a major source of error. A related issue is the potential presence of host preferences among parasitoids of the same species. Such host preferences might be genetic but are more likely to be cultural. It is known that several parasitoid species learn chemical cues associated with their host as they emerge from the pupa, and subsequently use these cues in host location. Similarly, female parasitoids may learn cues associated with a particular host and host plant combination during initial oviposition, and may be differentially attracted to that combination during subsequent host location (Turlings *et al.* 1992). Although such preferences are unlikely to be absolute, they may result in overestimation of the potential for indirect effects because they weaken the association between attack rates by a particular parasitoid on one host, and the abundance of alternative hosts for that parasitoid. A similar outcome would result if parasitoids did not move freely through the study area but tended to remain in localized areas or microhabitats attacking a subset of possible hosts.

Are there hosts and parasitoids that interact with the species in our web, but that we failed to sample? Our data, showing low leaf-miner abundance in the forest canopy and in the understorey, suggest that immigration of parasitoids from nearby habitats or microhabitats is unlikely to have a major influence on our measures of community structure. This and the fact that parasitoids of leaf-miners very rarely develop on other host guilds suggest that our food web describes a discrete host-parasitoid assemblage.

Finally, we have constructed a single food web (and a set of statistically nonindependent seasonal webs), and thus are unable to obtain explicit estimates of sampling error. In our case and in most other similar studies, collecting multiple food webs on this scale is logically unfeasible. A major advantage of quantitative webs over binary webs is that the relative importance of

different species and links can be assessed and the dependence of food web statistics on sampling effort can be explored by robustness analysis. In the next section, we describe some of the food web statistics and discuss their sensitivity to sampling effort.

#### FOOD WEB STATISTICS AND ROBUSTNESS

Robustness analysis has considerable potential for quantifying the extent to which sampling effort is likely to bias measures of community structure (Winemiller 1990; Goldwasser & Roughgarden 1993; Martinez *et al.* 1999). It should be useful in planning efficient strategies for sampling, and in determining when it is reasonable to compare web statistics between webs or subwebs. Depending on its purpose, a variety of procedures could be used for this type of analysis, for example dropping individual host samples at random from the data set, progressively omitting the rarest hosts, or omitting data for selected weeks or months. Here, we investigated the effects of omitting the least frequent linkages (those least likely to be detected) from the data set. This is a general approach, applicable to all varieties of food web, and not just to host-parasitoid webs.

The analysis shows that web statistics differ considerably in their sensitivity to sampling effort. For example, as found by Martinez *et al.* (1999), estimates of numbers of host and parasitoid species are quite robust to sampling intensity compared to estimates of the number of links. Parasitoids of leaf-miners typically have large host ranges, compared with other guilds of insect herbivore (Hawkins 1994), so it is not surprising that not all trophic interactions were detected during sampling. Salvo & Valladares (1999), working in Argentina, found little indication that parasitoid species assemblage sizes reached an asymptote for individual agromyzid leaf-miner species, even after over 10 000 rearings. These results suggest that documenting a definitive, comprehensive food web that includes all feasible trophic links may be an unrealistic goal. Similarly, while the absolute number of compartments in the web is sensitive to sampling intensity, our measure of compartment diversity is not. The rarity of 'true' compartmentalization in this community, and in other host-parasitoid food webs (Memmott *et al.* 1994; Müller *et al.* 1999; Rott & Godfray 2000) has implications for host-parasitoid population dynamic studies. Most host-parasitoid models and empirical studies consider only pairs or small sets of interacting species (Hassell 2000), but in our community almost all hosts and parasitoids are imbedded in a web of interactions with links to all other species in the community. Studies of pairs or small groups of interacting species may need to take this community context into account.

#### STRUCTURING FACTORS

Leaf-miners in our community were highly host plant specific: most species were confined to a single host plant

species, while a few were reared from a variety of plants in the same family. This is consistent with previous studies of leaf-miner host plant range, both in the tropics and in temperate ecosystems (Opler 1974; Spencer 1990; Hespenheide 1991; Memmott *et al.* 1994).

Studies of the insect herbivore composition on different plants – usually at a larger geographical scale – have often found that herbivore species load can be explained by plant geographical range, plant architecture and taxonomic isolation (Southwood 1961; Claridge & Wilson 1982; Godfray 1984; Strong *et al.* 1984). In an analogy to island biogeography, plants which are widespread, and which are closely related to other potential host plants, are most likely to be colonized by herbivores over evolutionary time. At the scale of our study, we found no indication that plants with relatively large geographical ranges supported more herbivores. There was some indication that taxonomically isolated plants were less likely to be colonized by herbivores, but this result may be a consequence of the large species loads on members of a single plant family, the Asteraceae. Most Asteraceae in our plot were colonized by at least one leaf-miner (several of them oligophagous within this family), and one Asteraceae species (*Lasianthaea fruticosa* (L.) K.M. Becker) was attacked by 13 leaf-miner species, the highest number recorded for any plant in our study.

Plant growth form significantly affected herbivore load, with grasses (Poaceae) supporting particularly large herbivore faunas. This was not a consequence of the colonization and subsequent radiation of a single taxon on this plant family, as herbivores on Poaceae included five Lepidoptera (from at least three different families), four Coleoptera (from two families) and three Diptera (from at least two genera). Because our plot was in a relatively open habitat, much of the vegetation searched consisted of herbs, grasses and low shrubs. This may have led to an underestimate of leaf-miner abundance and species richness on trees, although the survey of canopy leaf-miner abundance (Table 1) suggests that this is unlikely. Finally, as also reported by Memmott *et al.* (1994), abundant plants supported larger numbers of species. This may be because rare plants are more difficult for herbivores to colonize in both evolutionary and ecological time, although it is difficult to entirely exclude sampling effects: fewer miners may be found on rare plants because the total area of foliage searched will be smaller for these species.

In contrast to the host-specific herbivores, most parasitoids were highly generalist; conversely, individual leaf-miner species supported many parasitoid species. The low host-specificity of parasitoids is typical of those attacking leaf-miners (Hawkins 1994), but contrasts with the results for another tropical host-parasitoid system involving large moth larvae and their ichneumonid parasitoids in Costa Rican dry forest, where parasitoids were often strictly monophagous (Janzen & Gauld 1997). In our data, after accounting

for sample size one host factor did significantly affect the number of parasitoid species reared from a host: the number of months a host is present in the field. This is to be expected if there is a seasonal component to parasitoid diversity: hosts that are present for only a short period during the year will only be attacked by parasitoids that are also present in the field at that time.

The fraction of hosts attacked by parasitoids was higher in Diptera than in Lepidoptera or Coleoptera, a pattern also found by Memmott *et al.* (1994). But as Memmott *et al.* (1994) point out, if related parasitoids with similar biologies attack taxonomically related hosts (as is the case for the guild of opiine braconids attacking Diptera in our food web), figures for the percentage parasitism of related hosts may not be statistically independent and hence it is difficult to assess this result. The fraction of hosts attacked by parasitoids was also greater in hosts that share host plants with other abundant miners. Memmott *et al.* (1994) obtained a similar result, and suggested two possible explanations. First, some plant species may be particularly 'apparent' to both herbivores and parasitoids. Alternatively, the presence of one species may lead to local increases in parasitoid numbers which attack other potential hosts on the same plant – an aspect of apparent competition (Holt 1977; Holt & Lawton 1993). In our case, we suggest that the first explanation is more likely, since analysis of  $d_{ij}$  terms indicated that pairs of hosts that shared the same host plant were no more likely to enter into indirect interactions than pairs of hosts using different host plants.

#### INDIRECT INTERACTIONS

We believe that quantitative webs have a particular role to play in identifying the potential for indirect interactions. In our system, because individual leaf-miner species tend to be specialized, and the numbers of species and individuals attacking particular host plant species are quite low, the opportunities for direct competitive interactions among host species in the community are limited. However, the parasitoids of these herbivores are largely generalist, and it seems likely that species may influence the abundance of other species indirectly through apparent competition, mediated by shared parasitism.

Apparent competition occurs when two species have adverse effects on each other's population growth rates via a shared natural enemy (Holt 1977). An increase in the abundance of one species results in greater numbers of the shared natural enemy, in turn leading to a decrease in the abundance of a second species. Theory suggests that insect-parasitoid assemblages should be particularly prone to apparent competition, because parasitoids have generation times similar to their hosts, show pronounced responses to changes in host abundance, and frequently limit host population sizes below carrying capacity (Holt & Lawton 1993). It has been claimed that apparent competition may be as important, or more important, than resource competition in struct-

uring insect communities (Jeffries & Lawton 1984; Lawton 1986; Holt & Lawton 1993, 1994; Bonsall & Hassell 1997).

Quantitative parasitoid overlap diagrams (Godfray & Müller 1998; Müller *et al.* 1999; Rott & Godfray 2000; Fig. 4) are based on a set of measures,  $d_{ij}$ , that represent the likely influence of species  $j$  on species  $i$  via shared parasitoids: a measure of the potential for apparent competition. The most important determinant of  $d_{ij}$  was the abundance of species  $j$ . This occurs because, all else being equal, abundant hosts are more likely to be the source of many parasitoids; and since most parasitoids are generalists, the parasitoids attacking less common hosts are likely to have developed on other, more abundant hosts. Non-zero values of  $d_{ij}$  were also more frequent when hosts  $i$  and  $j$  were in the same taxonomic order. This pattern probably arises because, although most parasitoids were generalists, there are definite associations between particular parasitoids and particular host orders. For example, parasitoids in the Figitidae and Opiinae were often oligophagous within the Diptera, but were never recorded from Coleoptera and Lepidoptera. There was no evidence that leaf-miners sharing a host plant had a greater potential for indirect interactions than those on different host plants. This is in contrast to the results for temperate leaf-mining moth – parasitoid assemblages (Askew & Shaw 1974; Rott & Godfray 2000) where parasitoid complexes associated with different hosts were strongly influenced by the leaf-miners' host plants. At least two factors may account for this difference. First, parasitoids in our community may not be using host plant cues to locate their hosts. Secondly, the greater taxonomic diversity and species richness of both hosts and host plants in the Belize community may mask any host plant effects.

We stress that care must be used in interpreting dynamic community processes from static food web patterns. For example, Paine (1988, 1992) and others have pointed out that 'strong' interactions are not necessarily the most important ones, since (for example) high per capita attack rates of predators on prey can lead to predators reducing prey to such an extent that both predators and prey are rare at equilibrium. Furthermore, weakly interacting species may play an important stabilizing roles in the community (Berlow *et al.* 1999). Only experimental community manipulations can reveal such effects (Chaneton & Bonsall 2000). We are unaware of any such experiments on tropical insect-parasitoid systems, but food webs provide the 'road maps' necessary to identify potentially interacting species, and to plan manipulative experiments in the field to test these hypotheses.

#### Acknowledgements

The Leverhulme Trust and The Natural History Museum, London supported this work. We thank Chapal and Celia Bol, Ian Gauld, Laurie Henneman, John Lawton, Thomas Lewinsohn, Anna Pike and

Meg Yeadon for help and discussion. We are extremely grateful to the following for assistance in identifying specimens – Hymenoptera: Matthew Buffington, Bob Kula, Donald Quicke, Alejandro Valerio, Bob Wharton, Jim Whitfield; Lepidoptera: Don Davies, Arunas Diskus, Carlos Lopez Vaamonde, Rimantas Puplesis, Gaden Robinson; Coleoptera: Henry Hespenheide, Sharon Shute, Charles Staines; Diptera: Rob Belshaw, Graciella Valladares. Plants: colleagues in the Department of Botany at The Natural History Museum.

## References

- Askew, R.R. (1980) The diversity of insect communities in leaf-mines and plant galls. *Journal of Animal Ecology*, **49**, 817–829.
- Askew, R.R. (1994) Parasitoids of leaf-mining Lepidoptera: what determines their host ranges? *Parasitoid Community Ecology* (eds B.A. Hawkins & W. Sheehan), pp. 177–202. Oxford University Press, Oxford.
- Askew, R.R. & Shaw, M.R. (1974) An account of the Chalcidoidea (Hymenoptera) parasitising leafmining insects of deciduous trees in Britain. *Biological Journal of the Linnean Society*, **6**, 289–335.
- Askew, R.R. & Shaw, M.R. (1979) Mortality factors affecting the leaf-mining stages of *Phyllonorycter* (Lepidoptera: Gracillariidae) on oak and birch: (I) Analysis of the mortality factors. *Zoological Journal of the Linnean Society*, **67**, 31–49.
- Balick, M.J., Nee, M.H. & Atha, D.E. (2001) *Checklist of the Vascular Plants of Belize: with common names and uses*. New York Botanical Garden, New York.
- Berlow, E.L., Navarette, S.A., Briggs, C.J., Power, M.E. & Menge, B.A. (1999) Quantifying variation in the strengths of species interactions. *Ecology*, **80**, 2206–2224.
- Bird, N.M. (1998) *Sustaining the Yield. Improving timber harvesting practices in Belize 1991–98*. Natural Resources Institute, Chatham, UK.
- Bonsall, M.B. & Hassell, M.P. (1997) Apparent competition structures ecological assemblages. *Nature*, **338**, 371–373.
- Chaneton, E.J. & Bonsall, M.B. (2000) Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos*, **88**, 380–394.
- Claridge, M.F. & Wilson, M.R. (1982) Insect herbivore guilds and species-area relationships: leaf miners on British trees. *Ecological Entomology*, **7**, 19–30.
- Cohen, J.E., Beaver, R.A., Cousins, S.H., Deangelis, D.L., Goldwasser, L., Heong, K.L., Holt, R.D., Kohn, A.J., Lawton, J.H., Martinez, N., Omalley, R., Page, L.M., Patten, B.C., Pimm, S.L., Polis, G.A., Rejmanek, M., Schoener, T.W., Schoenly, K., Sprules, W.G., Teal, J.M., Ulanowicz, R.E., Warren, P.H., Wilbur, H.M. & Yodzis, P. (1993) Improving food webs. *Ecology*, **74**, 252–258.
- Cohen, J.E., Briand, F. & Newman, C.M. (1990) *Community Food Webs: data and theory*. Springer-Verlag, Berlin, London.
- Croat, T. (1978) *Flora of Barro Colorado Island*. Stanford University Press, USA.
- Delvare, G. & LaSalle, J. (2000) *Trisecodes* gen. n. (Hymenoptera: Eulophidae: Entedoninae), the first eulophid with three tarsal segments. *Journal of Hymenoptera Research*, **92**, 305–312.
- Godfray, H.C.J. (1984) Patterns in the distribution of leaf-miners on British trees. *Ecological Entomology*, **9**, 163–168.
- Godfray, H.C.J., Lewis, O.T. & Memmott, J. (1999) Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society of London, Series B – Biological Sciences*, **354**, 1811–1824.
- Godfray, H.C.J. & Müller, C.B. (1998) Host-parasitoid dynamics. *Insect Population Dynamics* (eds J.P. Dempster & I. Maclean). Academic Press, London.
- Goldwasser, L. & Roughgarden, J. (1993) Construction and analysis of a large Caribbean food web. *Ecology*, **74**, 1216–1233.
- Hassell, M.P. (2000) *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions*. Oxford University Press, Oxford.
- Hawkins, B.A. (1994) *Pattern and Process in Host-Parasitoid Interactions*. Cambridge: Cambridge University Press.
- Hawkins, B.A., Thomas, M.B. & Hochberg, M.E. (1993) Refuge theory and biological control. *Science*, **262**, 1429–1432.
- Henneman, M.L. & Memmott, J. (2001) Infiltration of a Hawaiian community by introduced biological control agents. *Science*, **293**, 1314–1316.
- Hespenheide, H.A. (1991) Bionomics of leaf-mining insects. *Annual Review of Entomology*, **36**, 535–560.
- Holt, R.D. (1977) Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.
- Holt, R.D., Grover, J. & Tilman, D. (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*, **144**, 741–771.
- Holt, R.D. & Lawton, J.H. (1993) Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist*, **142**, 623–645.
- Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.
- Janzen, D.H. & Gauld, I.D. (1997) Patterns of use of large moth caterpillars (Lepidoptera: Saturniidae and Sphingidae) by ichneumonid parasitoids (Hymenoptera) in Costa Rican dry forest. *Forests and Insects* (eds A.D. Watt, N.E. Stork & M.D. Hunter), pp. 251–271. Chapman & Hall, London.
- Jeffries, M.J. & Lawton, J.H. (1984) Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.
- Johnson, M.S. & Chaffey, D.R. (1973) *An Inventory of the Chiquibul Forest Reserve, Belize*. Land Resources Division, Surbiton, UK.
- LaSalle, J. & Gauld, I.D. (1991) Parasitic Hymenoptera and the biodiversity crisis. *Redia*, **74**, 315–334.
- Lawton, J.H. (1986) The effects of parasitoids on phytophagous insect communities. *Insect Parasitoids* (eds J.K. Waage & D. Greathead), pp. 265–287. Academic Press, London.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Croom-Helm, London.
- Martinez, N.D., Hawkins, B.A., Dawah, H.A. & Feifarek, B.P. (1999) Effects of sampling effort on characterization of food-web structure. *Ecology*, **80**, 1044–1055.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, London.
- Memmott, J. & Godfray, H.C.J. (1992) Parasitoid webs. *Hymenoptera and Biodiversity* (eds J. LaSalle & I.D. Gauld), pp. 217–234. CAB International, Wallingford, England.
- Memmott, J. & Godfray, H.C.J. (1994) The use and construction of parasitoid webs. *Parasitoid Community Ecology* (eds B.A. Hawkins & W. Sheehan), pp. 300–318. Oxford University Press, Oxford.
- Memmott, J., Godfray, H.C.J. & Gauld, I.D. (1994) The structure of a tropical host-parasitoid community. *Journal of Animal Ecology*, **63**, 521–540.
- Müller, C.B., Adriaanse, I.C.T., Belshaw, R. & Godfray, H.C.J. (1999) The structure of an aphid-parasitoid community. *Journal of Animal Ecology*, **68**, 346–370.
- Opler, P.A. (1974) Oaks as evolutionary islands for leaf-mining insects. *American Scientist*, **62**, 67–73.

- Paine, R.T. (1988) Some general problems for ecology illustrated by food web theory. *Ecology*, **69**, 1673–1676.
- Paine, R.T. (1992) Food web analysis through field measurement of per capita interaction strength. *Nature, London*, **355**, 73–75.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Rott, A.S. & Godfray, H.C.J. (2000) The structure of a leaf-miner-parasitoid community. *Journal of Animal Ecology*, **69**, 274–289.
- Salvo, A. & Valladares, G. (1999) Parasitoid assemblage size and host ranges in a parasitoid (Hymenoptera)–agromyzid (Diptera) system from central Argentina. *Bulletin of Entomological Research*, **89**, 193–197.
- Schönrogge, K. & Crawley, M.J. (2000) Quantitative webs as a means of assessing the impact of alien insects. *Journal of Animal Ecology*, **69**, 841–868.
- Southwood, T.R.E. (1961) The number of species associated with various trees. *Journal of Animal Ecology*, **30**, 1–8.
- Spencer, K.A. (1990) *Host Specialization in the World Agromyzidae (Diptera)*. Kluwer Academic Publishers, Dordrecht.
- Standley, P.C. & Steyermark, J.A. (1946–83) *Flora of Guatemala*. Chicago Natural History Museum, Chicago.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants: community patterns and mechanisms*. Blackwell Science, Oxford, UK.
- Turlings, T.C.J., Wackers, F.L., Vet, L.E.M., Lewis, W.J. & Tumlinson, J.H. (1992) Learning of host-location cues by hymenopterous parasitoids. *Insect Learning: Ecological and Evolutionary Perspectives* (eds A.C. Lewis & D.R. Papaj), pp. 51–78. Chapman & Hall, New York.
- Valladares, G.R., Salvo, A. & Godfray, H.C.J. (2001) Quantitative food webs of dipteran leafminers and their parasitoids in Argentina. *Ecological Research*, **16**, 925–939.
- Winemiller, K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, **60**, 331–367.
- Wright, A.C.S., Romney, D.H., Arbuckle, R.H. & Vial, V.E. (1959) *Land in British Honduras*. HM Stationery Office, London.

Received 31 August 2001; revision received 27 May 2002

## Appendix 1

(a) Leaf-miner species, and (b) parasitoid species included in the quantitative food webs. The codes correspond to the labels in Figs 1, 2 and 4. All parasitoids are Hymenoptera, except code 90 (Diptera)

- (a) Leaf-miners
- 1 ?*Glyptipterigidae* sp.1 (Lepidoptera: ?Glyptipterigidae); 2 ?*Heliozelidae* sp.1 (Lepidoptera: ?Heliozelidae); 3 ?*Heliozelidae* sp.3 (Lepidoptera: ?Heliozelidae); 4 ?*Nesomyza* sp. (Diptera: Agromyzidae); 5 ?*Oecophoridae* sp. (Lepidoptera: ?Oecophoridae); 6 *Anisostena championi* (Baly) (Coleoptera: Chrysomelidae); 7 *Brachys kleinii* Obenberger (Coleoptera: Buprestidae); 8 *Bucculatrigidae* sp.1 (Lepidoptera: Bucculatrigidae); 9 *Calycomyza cf. cassiae* (Frost) (Diptera: Agromyzidae); 10 *Calycomyza hyptidis* Spencer (Diptera: Agromyzidae); 11 *Calycomyza sidae* Spencer (Diptera: Agromyzidae); 12 *Calycomyza* sp.10 (Diptera: Agromyzidae); 13 *Calycomyza* sp.13 (Diptera: Agromyzidae); 14 *Calycomyza* sp.14 (Diptera: Agromyzidae); 15 *Calycomyza* sp.16 (Diptera: Agromyzidae); 16 *Calycomyza* sp.17 (Diptera: Agromyzidae); 17 *Calycomyza* sp.2 (Diptera: Agromyzidae); 18 *Calycomyza* sp.3 (Diptera: Agromyzidae); 19 *Calycomyza* sp.5 (Diptera: Agromyzidae); 20 *Calycomyza* sp.7 (Diptera: Agromyzidae); 21 *Calycomyza* sp.8 (Diptera: Agromyzidae); 22 *Chalepus horni* Baly (Coleoptera: Chrysomelidae); 23 *Chalepus* sp. (Coleoptera: Chrysomelidae); 24 *Dialectica* sp. (Lepidoptera: Gracillariidae); 25 *Gelechiidae* sp.1 (Lepidoptera: Gelechiidae); 26? *Metrochroa* sp. (Lepidoptera: Gracillariidae); 27 *Chrysaster* sp. (Lepidoptera: Gracillariidae); 28 *Gracillariinae* sp.10 (Lepidoptera: Gracillariidae); 29 *Marmara* sp.1 (Lepidoptera: Gracillariidae); 30 *Gracillariinae* sp.4 or Lepidoptera sp.1 (Lepidoptera: Family Unknown); 31 *Eucosmaphora pithecellobiae* (Davis & Wagner) (Lepidoptera: Gracillariidae); 32? *Telamoptilia* sp. (Lepidoptera: Gracillariidae); 33 *Haplopeodes* sp.1 (Diptera: Agromyzidae); 34 *Lyonetiidae* sp. (Lepidoptera: Lyonetiidae); 35 *Heliozelidae* sp.6 (Lepidoptera: Heliozelidae); 36 *Heterispa vinula* (Erichson) (Coleoptera: Chrysomelidae); 37 *Japanagromyza* sp. (Diptera: Agromyzidae); 38 *Lemurimyza* sp. (Diptera: Agromyzidae); 39 *Lepidoptera* sp.3 (Lepidoptera: Family Unknown); 40 *Lepidoptera* sp.4 (Lepidoptera: Family Unknown); 41 *Lepidoptera* sp.6 (Lepidoptera: Family Unknown); 42 *Lithocolletinae* sp. (Lepidoptera: Gracillariidae); 43 *Phylloconistis* sp. (Lepidoptera: Gracillariidae); 44 *Lithocolletinae* sp.6 (Lepidoptera: Gracillariidae); 45 *Odontopus* sp.1 (Coleoptera: Curculionidae); 46 *Odontopus* sp.2 (Coleoptera: Curculionidae); 47 *Ophiomyia* sp.1 (Diptera: Agromyzidae); 48 *Pachyschelus collaris robustus* Wat. (Coleoptera: Buprestidae); 49 *Pachyschelus purpureus bicolor* Kerr. (Coleoptera: Buprestidae); 50 *Pentispafairmairei* (Chapuis) or *Baliosus lineaticollis* Baly (Coleoptera: Chrysomelidae); 51 *Pentispamelanura* (Chapuis) (Coleoptera: Chrysomelidae); 52 *Phyllocnistinae* sp.1 (Lepidoptera: Gracillariidae); 53 *Probaenia armigeria* (Baly) (Coleoptera: Chrysomelidae); 54 *Scrobipalpula* sp.2 (Lepidoptera: Gelechiidae); 55 *Sumitrosis distinctus* (Baly) (Coleoptera: Chrysomelidae); 56 *Tischereavulverea* Walsingham (Lepidoptera: Tischeridae); 57 *Tischeria* sp.1 (Lepidoptera: Tischeridae); 58 *Tischeria* sp.12 (Lepidoptera: Tischeridae); 59 *Tischeria* sp.4 (Lepidoptera: Tischeridae); 60 *Tischeria* sp.5 (Lepidoptera: Tischeridae); 61 *Tischeria* sp.6 (Lepidoptera: Tischeridae); 62 *Tischeria* sp.7 (Lepidoptera: Tischeridae); 63 *Tischeria* sp.8 (Lepidoptera: Tischeridae); 64 *Tischeria* sp.9 (Lepidoptera: Tischeridae); 65 Unreared agromyzid sp.13 (Diptera: Agromyzidae); 66 Unidentified agromyzid sp.19 (Diptera: Agromyzidae); 67 Unreared agromyzid sp.21 (Diptera: Agromyzidae); 68 Unreared agromyzid sp.23 (Diptera: Agromyzidae); 69 Unidentified agromyzid sp.24 (Diptera: Agromyzidae); 70 Unreared agromyzid sp.26 (Diptera: Agromyzidae); 71 Unreared agromyzid sp.3 (Diptera: Agromyzidae); 72 Unreared agromyzid sp.8 (Diptera: Agromyzidae); 73 Unidentified agromyzid sp.9 (Diptera: Agromyzidae); 74 Unreared hispine sp.4 (Coleoptera: Chrysomelidae); 75 Unreared hispine sp.6 (Coleoptera: Chrysomelidae); 76 Unreared hispine sp.7 (Coleoptera: Chrysomelidae); 77 Unreared hispine sp.8 (Coleoptera: Chrysomelidae); 78 Unreared hispine sp.9 (Coleoptera: Chrysomelidae); 79 Unreared Lepidoptera sp.1 (Lepidoptera: Family Unknown); 80 Unreared Lepidoptera sp.11 (Lepidoptera: Family Unknown); 81 Unidentified Lepidoptera sp.12 (Lepidoptera: Family Unknown); 82 Unreared Lepidoptera sp.14 (Lepidoptera: Family Unknown); 83 Unidentified Lepidoptera sp.16 (Lepidoptera: Family Unknown); 84 Unidentified Lepidoptera sp.20 (Lepidoptera: Family Unknown); 85 Unreared Lepidoptera sp.22 (Lepidoptera: Family Unknown); 86 Unreared Lepidoptera sp.25 (Lepidoptera: Family Unknown); 87 Unreared Lepidoptera sp.27 (Lepidoptera: Family Unknown); 88 Unreared Lepidoptera sp.28 (Lepidoptera: Family Unknown); 89 Unreared Lepidoptera sp.32 (Lepidoptera: Family Unknown); 90 Unreared Lepidoptera sp.34 (Lepidoptera: Family Unknown); 91 Unreared Lepidoptera sp.5 (Lepidoptera: Family Unknown); 92 Unreared Lepidoptera sp.6 (Lepidoptera: Family Unknown); 93 *Uroplata fusca* Chapuis (Coleoptera: Chrysomelidae).

## (b) Parasitoid species

- 1 *Allobracon* sp. (Braconidae); 2 *Apleurotropis* sp.A (Eulophidae); 3 *Apleurotropis* sp.B (Eulophidae); 4 *Apleurotropis* sp.C (Eulophidae); 5 *Aprostocetus* sp.A (Eulophidae); 6 *Aprostocetus* sp.B (Eulophidae); 7 *Asecodes* sp.A (Eulophidae); 8 *Bracon* sp.1 (Braconidae); 9 *Bracon* sp.10 (Braconidae); 10 *Bracon* sp.11 (Braconidae); 11 *Bracon* sp.12 (Braconidae); 12 *Bracon* sp.13 (Braconidae); 13 *Bracon* sp.2 (Braconidae); 14 *Bracon* sp.3 (Braconidae); 15 *Bracon* sp.4 (Braconidae); 16 *Bracon* sp.5 (Braconidae); 17 *Bracon* sp.6 (Braconidae); 18 *Bracon* sp.7 (Braconidae); 19 *Bracon* sp.8 (Braconidae); 20 *Bracon* sp.9 (Braconidae); 21 Chalcidid sp.1 (Chalcididae); 22 Chalcidid sp.2 (Chalcididae); 23 *Chrysocharis* sp.A (Eulophidae); 24 *Chrysocharis tristis* Hansson (Eulophidae); 25 *Cirrospilus* sp.A (Eulophidae); 26 *Closterocerus cinctipennis* Ashmead (Eulophidae); 27 *Closterocerus* sp.A (Eulophidae); 28 *Closterocerus* sp.B (Eulophidae); 29 *Closterocerus* sp.C (Eulophidae); 30 *Elachertus* sp.A (Eulophidae); 31 *Elachertus* sp.B (Eulophidae); 32 *Elachertus* sp.C (Eulophidae); 33 *Elachertus* sp.D (Eulophidae); 34 *Elachertus* sp.E (Eulophidae); 35 *Elasmus* sp.A (Eulophidae); 36 *Emersonella* sp.A (Eulophidae); 37 *Euopius* sp. (Braconidae); 38 genus near *Zaeucoila* sp.1 (Figitidae); 39 genus near *Zaeucoila* sp.2 (Figitidae); 40 *Horismenus* sp.A (Eulophidae); 41 *Horismenus* sp.B (Eulophidae); 42 *Horismenus* sp.C (Eulophidae); 43 *Horismenus* sp.D (Eulophidae); 44 *Horismenus* sp.E (Eulophidae); 45 *Horismenus* sp.F (Eulophidae); 46 *Lispixys* sp. (Braconidae); 47 Microgastrinae sp.1 (Braconidae); 48 Microgastrinae sp.2 (Braconidae); 49 Microgastrinae sp.3 (Braconidae); 50 Microgastrinae sp.4 (Braconidae); 51 Microgastrinae sp.5 (Braconidae); 52 Microgastrinae sp.6 (Braconidae); 53 *Mirax lithocolletidis* Ashmead (Braconidae); 54 *Mirax* n. sp.1 (Braconidae); 55 *Mirax* n. sp.2 (Braconidae); 56 *Mirax* n. sp.3 (Braconidae); 57 *Neochrysocharis arizonensis* (Eulophidae); 58 *Neochrysocharis* sp.?? (Eulophidae); 59 *Neochrysocharis* sp.A (Eulophidae); 60 *Trisecodes agromyzae* Delvare & LaSalle (Eulophidae); 61 *Opius* sp.1 (Braconidae); 62 *Opius* sp.10 (Braconidae); 63 *Opius* sp.11 (Braconidae); 64 *Opius* sp.12 (Braconidae); 65 *Opius* sp.12a (Braconidae); 66 *Opius* sp.14 (Braconidae); 67 *Opius* sp.15 (Braconidae); 68 *Opius* sp.16 (Braconidae); 69 *Opius* sp.17 (Braconidae); 70 *Opius* sp.18 (Braconidae); 71 *Opius* sp.2 (Braconidae); 72 *Opius* sp.20 (Braconidae); 73 *Opius* sp.3 (Braconidae); 74 *Opius* sp.4 (Braconidae); 75 *Opius* sp.5 (Braconidae); 76 *Opius* sp.6 (Braconidae); 77 *Opius* sp.7 (Braconidae); 78 *Opius* sp.8 (Braconidae); 79 *Opius* sp.9 (Braconidae); 80 *Pnigalio coffeeae* Hering (Eulophidae); 81 *Pnigalio* sp.B (Eulophidae); 82 *Proacrias* sp.A (Eulophidae); 83 *Proacrias* sp.B (Eulophidae); 84 *Proacrias* sp.C (Eulophidae); 85 Pteromalidae 1 (Pteromalidae); 86 Pteromalidae 2 (Pteromalidae); 87 Pteromalidae 3 (Pteromalidae); 88 *Quadrastichus* sp.A (Eulophidae); 89 *Stiropius* sp. (Braconidae); 90 Tachinid sp. (Tachinidae); 91 *Tropideucoila* sp.1 (Figitidae); 92 *Tropideucoila* sp.2 (Figitidae); 93 *Zaeucoila* cf. *unicarinata* (Figitidae); 94 *Zaeucoila* sp.1 (Figitidae); 95 *Zaommomyia* sp.A (Eulophidae); 96 *Zaommomyia* sp.B (Eulophidae); 97 *Zaommomyia* sp.C (Eulophidae); 98 *Zaommomyia* sp.D (Eulophidae); 99 *Zaommomyia* sp.E (Eulophidae).