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Studying insect diversity in the tropics

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Understanding the extent and causes of insect diversity in the humid tropics is one of the major challenges in modern ecology. We review some of the current approaches to this problem, and discuss how future progress may be made. Recent calculations that there may be more than 30 million species of insect on earth have focused attention on the magnitude of this problem and stimulated several new lines of research (although the true figure is now widely thought to be between five and ten million species). We discuss work based on insecticidal fogging surveys; studies of herbivore and parasitoid specificity; macroecological approaches; and the construction of food webs. It is argued that progress in estimating insect diversity and in understanding insect community dynamics will be enhanced by building local inventories of species diversity, and in descriptive and experimental studies of the trophic structure of communities. As an illustration of work aimed at the last goal, we discuss the construction and analysis of quantitative host–parasitoid food webs, drawing on our work on leaf miner communities in Central America.

Keywords: biodiversity; community ecology; invertebrates; parasitoid webs; quantitative food webs; tropical forests

1. INTRODUCTION

The diversity of insects in the humid tropics has amazed biologists since the days of Bates, Wallace and the other 19th-century explorer–naturalists. As can be seen from their diaries and notebooks, contemplation of how such wonderful abundance and variety might arise was instrumental in pointing Darwin and especially Wallace to the theory of natural selection. Yet, as bemoaned by May (1988, 1990) and others, a century and a half later we have only a rough idea of the actual dimensions of insect species diversity, and an even poorer understanding of the processes through which it is generated and maintained. Only a small fraction (certainly fewer than 20%) of tropical insects have even been described by entomologists. And all the while habitats are contracting and being destroyed at an historically unprecedented rate.

Insect community ecologists working in the tropics believe they have special problems compared with their colleagues studying plants or vertebrates. The sheer weight of the number of species oppresses the whole subject; and with the exception of a few taxonomic groups, of which the butterflies are the most prominent, field identification is impossible or very difficult. Even the determination of morphospecies usually requires special experience in the systematics of the insects concerned. But a hundred years ago the situation was not that different for botanists confronted with forests, which might contain several hundred tree species per square kilometre; while 20 years ago textbook discussion of tropical plant community ecology consisted largely of data-free lists of speculative processes. Today, botanists still face great taxonomic challenges in the tropics, but community ecologists can choose to work in sites where essentially all plants are described and where, in some cases, field guides are available to allow identification by non-specialists. What is more, plant community ecologists have made spectacular strides at understanding how large numbers of species may coexist at a single site. Again, the problem is very far from being solved, but there are competing ideas and active research programmes designed to distinguish among them (e.g. Hubbell & Foster 1986; Terborgh *et al.* 1996; Pacala 1997; Wills *et al.* 1997; Zhang & Lin 1997; Hubbell 1997; Yu *et al.* 1998; Hubbell *et al.* 1999; Kobe 1999).

Our thesis here is that insect ecologists can learn from the success plant ecologists have had in understanding tropical diversity. We suggest this is based on two main foundations: the availability of complete or near-complete floral inventories for a number of different areas, and the intensive study of plant demography and interspecific interactions at particular ecological research sites. The floral inventories are more than just species lists, but include estimates of relative abundance and some basic ecology as well: for example, whether the plants are trees, herbs, epiphytes or lianas, and their basic soil and moisture requirements. They provide a baseline that allows other more poorly known sites to be assessed for richness, structure and endemism. The intensively studied sites are those such as at Barro Colorado Island in Panama, where all plants above a certain size are measured and mapped, and their population dynamics followed over a number of years. We argue that entomologists need to develop their equivalents of these programmes.

The paper is organized as follows. We first examine the question of exactly how many species of insects there are

in the tropics. This question has focused much recent research in tropical insect diversity and has stimulated several new approaches to the subject. It has been discussed quite often recently, and our aim is not to provide another review but to argue that work in this area also suggests that entomologists should follow the example of plant community ecologists. We ask what are the entomological equivalents of floral inventories and what basic ecological information should they include, and then turn to the harder problem of the type of intensive population or community study that is required to reveal the mechanisms underlying insect diversity. Throughout the paper we tend to concentrate on herbivorous insects and their natural enemies, the groups with which we are most familiar. We also largely adopt a population perspective, and do not consider the important questions of how insects and other invertebrates influence ecosystem functions (see Eggleton *et al.*, this issue).

2. HOW MANY INSECT SPECIES?

J. Ray, working in the 17th century and knowing only the British fauna well, estimated there might be 10 000 to 20 000 species of insects on earth. The age of the explorer–naturalists led to a radical upward revision of this estimate, so that by 1980 the most frequently quoted figure was between three and five million (e.g. Southwood 1978). This figure was challenged by Erwin in a short but extraordinarily influential paper published in 1982 in the *Coleopterist's Bulletin*. Erwin used the relatively new technique of insecticide fogging to sample insects in the canopies of 19 individual trees of *Luehea seemannii* Triana & Planch (Tiliaceae) in Panama. Fogging involves pumping a cloud of a fast-acting insecticide (usually a pyrethroid) into the canopy and collecting the insects that fall from the foliage. Erwin collected approximately 1200 species of Coleoptera, which he divided into herbivores, predators, fungivores and scavengers. For each category he estimated the fraction that were host plant specialists; for example, he assumed that 20% of herbivores were host-plant-specific and that in total 163 (13.5%) of the species were specialized (or effectively specialized) on *L. seemannii*. If beetles make up 40% of all insects; if two-thirds of all insects inhabit the canopy; and if there are 50 000 species of tree on earth, then the estimated number of insect species is about 30 million (i.e. $163 \times (100/40) \times (3/2) \times 50\,000$).

In his original paper and in later commentaries, Erwin stressed the very rough nature of this calculation, and it has since been subject to a variety of critiques (Stork 1988, 1993; May 1990; Thomas 1990; Hodkinson & Casson 1991; Hammond 1994). The figure of 50 000 tree species is generally regarded as secure, but a number of authors have suggested that Erwin overestimated the fraction of insects in the canopy and the fraction of insects that are beetles. Errors in these two figures will increase and decrease the estimate of total diversity respectively. But the hardest figure to assess is the estimate of host specificity, which nearly all subsequent authors think is too high (see § 2(b)). If the most extreme value that has been suggested for each separate component is substituted into the calculation, then figures ranging from three to about 80 million species of insect on earth can be obtained.

Most workers in the field today believe Erwin's estimate was too high and current estimates of insect biodiversity tend to be in the range of five to ten million species, not very different from the 1980 consensus. But Erwin did the subject an immense service in stimulating new fieldwork, and in drawing into the field theoretical and macroecologists who had not previously worked in this area. The new work roughly falls into four categories: further studies using insecticide fogging; examination of tropical insect host range; arguments based on macroecology; and food web studies.

(a) *Fogging*

As Erwin stressed both in his original article and subsequently (Erwin 1982, 1991), extrapolation from data collected on a single tree species is uncomfortable and further fogging studies were urgently needed. This challenge was taken up in tropical America by Erwin himself (Erwin 1983) and others (e.g. Adis *et al.* 1984; Davies *et al.* 1997); in Africa (e.g. Basset *et al.* 1992; Wagner 1997); in Asia (e.g. Morse *et al.* 1988; Stork 1988, 1991; Hammond *et al.* 1997); and in Australia (e.g. Basset & Kitching 1991). The studies show an inordinate fondness for beetles, although other groups have also been examined and a few studies have surveyed the full spectrum of insects (e.g. Basset & Kitching 1991; Guilbert 1997; Kitching *et al.* 1997). Most of the authors listed here contributed to the book, *Canopy arthropods* (Stork *et al.* 1997), which provides an excellent summary of the current state of the field.

The different studies have confirmed the enormous number of insects that inhabit tropical forest canopies, although the exact ratio of canopy to forest floor insects is still uncertain (Hammond *et al.* 1997), and the widely held view that the canopy of tropical forests represents the 'heart of biotic diversity' has been challenged (Hammond 1994). The data suggest that both the taxonomic composition and the feeding guild structure of samples are fairly similar on different continents (Stork 1993; Davies *et al.* 1997). Sufficient data also exist to point to global patterns in insect diversity: more species tend to be found in the canopies of tropical American trees than those in Africa or Asia, for example. More data are required, but this does seem to suggest a correlation between plant and insect diversity.

Fogging studies have been less successful in resolving the issues raised by Erwin's calculation. The most tricky problem is the extent of host specificity. As will be discussed in § 2(b), host specificity can be addressed directly by studying what different species eat. However, for Erwin's purposes, the actual biological basis of host specificity is irrelevant: what is needed is a statistical scaling factor that allows one to estimate total insect diversity from host-plant-based subsamples. Host specificity itself is too simple, but a more sophisticated measure was provided by May (1990): $p_k(i)$ the fraction of insects collected from a focal species of tree (species k) that would also be collected in similar samples of i other tree species. In principle $p_k(i)$ can be measured in the field by fogging studies; in practice this is probably impossible. To estimate the components of $p_k(i)$ with any degree of certainty (i.e. with standard errors) is likely to require studies that include an order of magnitude more tree

individuals and species than any conducted so far. (Some tropical studies have compensated for the few trees fogged by using subsamples within a tree as statistical replicates, but we fear this is pseudoreplication.) As a single tree can produce many thousands of individuals of hundreds of species, processing such data would create huge logistical difficulties. A further problem is that tree species themselves are unlikely to be uniform statistical replicates: $p_k(i)$ depends on k. Southwood (1961) first showed that different temperate tree species are fed on by different numbers of insects, and this and subsequent work found that the differences are influenced by plant geographic range, taxonomic isolation, plant structure and biochemistry, and possibly historical factors (Strong *et al.* 1984). Similar processes must certainly operate in the tropics. In addition, many of the insects fogged from a particular tree are likely to be what Moran & Southwood (1982) called 'tourists' (Stork 1988), i.e. species that use the tree for purposes other than food. Thus, differences in tree structure that influence the retention of tourists will also influence $p_k(i)$.

(b) *Herbivore and parasitoid specificity*

Studies of host-plant specificity and their obverse, the number of species of herbivore per tree, are interesting in their own right (e.g. Strong *et al.* 1984; Futuyma & Moreno 1988), and have been studied for many years in the tropics, although this area has also been stimulated by Erwin's arguments (Gaston 1992, 1993; Basset 1992). A number of reasons have been put forward for both higher and lower host specificity of herbivores in the tropics (Janzen 1973; Price 1991). For example, the resource fragmentation hypothesis states that higher diversity leads to lower population densities for individual species and hence less host specificity, as the most specialized species are unable to maintain themselves on the most fragmented resources. Alternatively, it has been suggested that the intense biotic interactions characteristic of the humid tropics will select for greater levels and diversity of chemical defences by plants, and this will tend to lead to greater specialization. Related to the last hypothesis is the idea that high predator pressures in the tropics, especially from ants, may select for specialized defence strategies that may involve the evolution of a restricted host range (Bernays & Graham 1988).

Most studies of herbivore host-plant specificity in the tropics have focused on groups of insects that are already known to have an intimate relationship with particular plant taxa or plant structures. Some of the best work concerns butterflies, beginning with classic studies of South American Ithomiinae and Heliconiinae (Nymphalidae), which have specialized on Solanaceae and Passifloraceae, respectively (Gilbert & Smiley 1978). In some sites, the biology of most species is known, and the majority of species are monophagous, with a few feeding on a restricted range of species. However, the host plant of a butterfly may not be the same throughout its range. Thomas (1990) used data on heliconiine butterflies in one of the first criticisms of the assumptions underlying Erwin's calculations. Not all butterflies are as host-specific. Gilbert & Smiley (1978) also discuss work on a genus of tropical Satyrinae (Nymphalidae), *Euptychia*, which feeds largely on grasses. Approximately 80% of

species had a wide host range within the Poaceae (grass family).

Sufficient data on butterfly host range has accumulated that meaningful comparisons between temperate and tropical faunas can be made. Marquis & Braker (1994) compared host specificity data for Costa Rican butterflies with data for four geographically limited areas in the USA, and for Great Britain. They found that Costa Rican butterflies showed significantly higher host specificity than temperate butterflies. On a larger geographical scale, Fiedler (1998) has compared the host range of west Palaearctic and South-East Asian (Malaya + Borneo) butterflies (excluding Hesperiidae). As Fiedler carefully notes, the databases are far from perfect, yet it is very impressive that information on host-plant family for over 50% of Malayo-Bornean butterflies is now available. Fiedler found no difference in host-plant range (measured by the number of families used) between tropical and temperate species, with even a suggestion in some groups of higher polyphagy in the tropics. Interestingly, the diversity of host-plant families used by butterfly families (as opposed to individual species) is much higher in the tropics than in the temperate regions. Perhaps host-plant switches are more common in the tropics (in turn influenced by the greater number of tropical plant families), or perhaps the temperate pattern reflects post-glacial colonization by a relatively restricted number of butterfly and plant clades.

No other group of insects matches the butterflies in the host-plant data available for a complete fauna, but more restricted data are available for some groups. Janzen (1977) studied the diversity of seed-feeding beetles (chiefly Bruchidae) in Costa Rican dry forests. Ninety-five beetle species were reared from 83 species of tree, the vast majority from only a single host-plant species. The high level of species specificity was significant considering Janzen's argument that host-specific seed-feeders might prevent seedling recruitment in a shadow surrounding the parent tree, a process that could be very important in maintaining tree diversity. Strong (1977) also studied a relatively specialized group of insects, hispine beetles (Chrysomelidae), which live in the rolled leaves of *Heliconia* (Heliconiaceae). Interestingly, more widespread host plants had more insect herbivore species, the pattern found in temperate tree-feeding herbivores (Southwood 1961).

Butterflies, which tend to feed on herbs and vines, and internally feeding herbivores may not be representative of the mass of externally feeding species that make up a large proportion of the herbivores in tropical tree canopies. Studying free-living species in the higher strata of the rainforest is much more difficult. In a series of groundbreaking studies, Basset and colleagues (Basset 1992, 1994; Basset *et al.* 1996, 1997) have attempted to estimate host ranges directly by collecting herbivores from particular tropical tree species. Originally they concentrated on one dominant tree species (*Argyrodendron actinophyllum*) in the semi-tropical rainforests of Queensland (Basset & Kitching 1991; Basset 1992), but subsequently they have studied a number of tree species, especially of the genus *Ficus* (figs) in highland and lowland New Guinea (Basset *et al.* 1996, 1997). They use a variety of sampling techniques, including fogging and interception traps, and assess host range by feeding tests in the laboratory. The results of their work are

complex and not easy to summarize. Briefly, for the leaf-chewing guild they normally find levels of host specialization substantially below those guessed at by Erwin. Were their estimates to be substituted into Erwin's calculations, values of six to eight million for insect species diversity would be obtained. But Basset *et al.* (1996) explicitly counsel against making this substitution, and the major value of their work is to reveal some of the geographical and biological idiosyncrasies underlying differences in the herbivore species attacking tropical trees. For example, they argue convincingly that the extensive resinous gum of *Ficus* and the high fibre, low nitrogen, alkaloid and water content of the locally abundant *Argyrodendron* all exert a strong influence on herbivore specificity.

Many of the arguments about herbivore specificity are paralleled in discussions of the host specificity of tropical parasitoids. This debate was kindled by Owen & Owen (1974) and Janzen & Pond (1975), who found ichneumonid wasps to be comparatively rare in the tropics. This was surprising, as the Ichneumonidae are a large (perhaps the largest) family of insects, and most are parasitoids of Lepidoptera and Coleoptera, which are disproportionately abundant in the tropics. Janzen & Pond (1975) and Janzen (1981) suggested that resource fragmentation may restrict the number of specialized parasitoids that occur in the tropics, while Rathcke & Price (1976) argued that higher predation pressures may restrict parasitoid number, a type of interguild competition. Gauld *et al.* (1992) and Gauld & Gaston (1994) hypothesized that because of higher predation pressures, tropical hosts are likely to have sequestered more plant chemicals for defence, hence making them harder to colonize by parasitoids. Consistent with the last idea is the observation that egg parasitoids do not have reduced diversity in the tropics (Hespenheide 1979; Noyes 1989), and neither do certain ichneumonid subfamilies that attack pupae and internal wood-borers. Eggs, pupae and wood-borers are thought not to have high levels of chemical defence, although there are many exceptions (Brower 1989). A further possibility is that while ichneumonids are rare, their place is taken by other types of parasitoids, such as the egg and pupal parasitoids just mentioned (Hespenheide 1979; Godfray 1994).

Sime & Brower (1998) have recently made an important contribution to this debate. They emphasize that the low diversity of tropical ichneumonids is not a unitary phenomenon; it is no surprise that the two subfamilies of ichneumonid specialized on sawflies are rare in the tropics because so are their hosts (Gauld 1986). The interesting phenomenon to explain is the parallel drop in species numbers in the several clades specialized on beetles and lepidopterans. They also point out that rigorous tests of the different hypotheses require both a phylogenetic framework and extensive ecological data, neither of which is available so far. In the absence of the latter, they review data on the number of parasitoid species attacking palatable and unpalatable butterflies, concluding that unpalatable species have fewer parasitoids than palatable taxa, and that there are more unpalatable species in the tropics. They thus tentatively support the Gauld *et al.* (1992) chemical defence hypothesis.

Another group that declines in species richness towards the tropics is the aphids. Aphids are weak flyers, and rely on wind and passive dispersal to arrive at the correct host plant. Dixon *et al.* (1987) suggested that the lower density of individual plant species in the tropics might make it impossible for herbivores with such hit-and-miss host location strategies to survive. However, aphids are also uncommon in southern hemisphere temperate regions (Heie 1994) and it is possible that the southerly decline in aphid density reflects the slow dispersal of a group that has evolved in northern temperate regions. Sessile aphid colonies are also highly susceptible to predation, which many species avoid by having unpredictable distributions in time and space; such a strategy may not be possible in tropical regions where predation rates are frequently much higher.

(c) *Macroecological arguments*

By this we mean arguments based on large-scale patterns of species abundances, sizes, host ranges, etc., although we are aware of overlap between this and previous sections.

There are few large animals and plants left to be discovered in the world. Our ignorance about the number of insect species on earth (and, more generally, the total number of all species on earth) is largely due to the small species. If on a double-log plot the number of species is plotted against their characteristic length, a unimodal distribution is obtained, but with a linear decline in species numbers for animals larger than about 1 cm. May (1988, 1990) suggested that were we to understand the processes generating this pattern, it would be possible to estimate global insect and animal diversity, especially as we can be fairly certain that the right-hand section of the graph is correct. We now know from well-studied groups that the reduced number of species at small body sizes is a real phenomenon and not a result of insufficient sampling of the smallest species (Dial & Marzluff 1988). The most reasonable null model for the shape of the species-number–body-size distribution is a log-normal distribution, but most empirical data sets show positive skew; that is, the mode of the distribution is shifted towards small body sizes, and there is a longer-than-expected tail of large-bodied species.

Unfortunately, the factors determining the species-number–size distribution are poorly understood, although there are a variety of interesting suggestions which have spawned a large literature. It has been suggested that the fractal nature of the world may lead to a greater number of niches at smaller spatial scales (Lawton 1984; Morse *et al.* 1985), although Fenchel (1993) has pointed out that if the environment is truly fractal then heterogeneity of resources will be similar at all spatial scales. Energetic models based on metabolic costs and optimal body sizes for different taxa have also been the subject of much debate (Brown *et al.* 1993; Blackburn & Gaston 1996; Chown & Gaston 1997). A problem with most models is that they fail to explain the positive skew (but see Kozlowski & Weiner 1997). Ultimately, any departure from the null hypothesis of a log-normal distribution must be generated by size-dependent speciation and extinction (Dial & Marzluff 1988; Maurer *et al.* 1992).

In the absence of a theoretical understanding of the size–abundance relationship, it might still be possible to use this technique if we had empirically derived patterns.
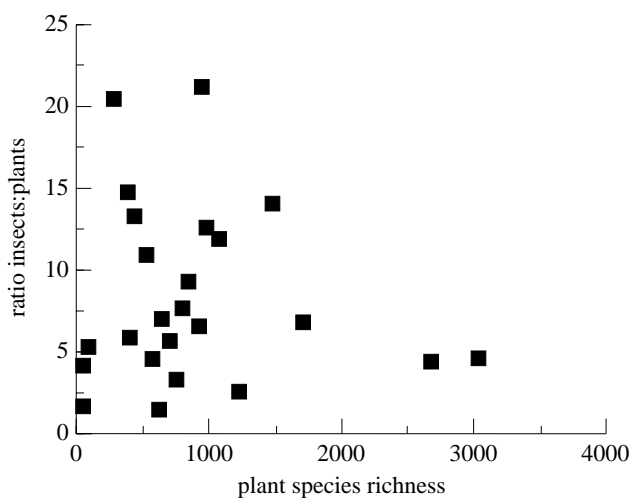
Figure 1. The ratio of insect species to plant species as a function of total plant species richness for a variety of countries of different size and latitude. Data from Gaston (1992), who provides a detailed discussion of the shortcomings and approximations of this analysis.

A number of these have now been studied for tropical insects (Morse *et al.* 1988; Basset & Kitching 1991) but their interpretation is difficult. The problem is to distinguish between those parts of the pattern that are due to statistical sampling effects and those that reflect underlying biological patterns. May's (1988) solution to these problems was intensive study of a restricted number of sites, something we return to in §3(a).

Other macroecological approaches may provide insights into total insect numbers. It has long been known that insect species richness correlates with plant species richness, both at local (e.g. Southwood *et al.* 1979; Siemann *et al.* 1998) and regional levels (Prendergast *et al.* 1993). There are exceptions, for example Vane-Wright (1978) found that some floristically diverse islands had small butterfly faunas. Dixon *et al.* (1987) found that the ratio of aphids to plant species declined precipitately with increasing plant diversity (i.e. towards the tropics), while for butterflies the ratio remained roughly constant. Gaston (1992) extended this approach to all insects and again found no relationship between insect-to-plant ratio and plant species richness (figure 1), although he stressed the problems with the available data and the preliminary nature of his analysis. If anything, there was a tendency for the ratio to be lower in the tropics. Equally interesting was the huge variation in the ratio, especially for regions of low plant diversity. Of course, if the ratio is approximately constant, then the total number of insect species on earth follows directly from the number of plant species. Employing this logic gives estimates in the range three to eight million (Gaston 1992). This is similar to pre-Erwin estimates, which in fact were calculated, explicitly or implicitly, using the same logic (i.e. that the ratio of insects to other organisms in the tropics was similar to that in temperate areas).

Extrapolation from local inventories to broader geographical areas may provide a way of accurately estimating global species richness (May 1988; Colwell & Coddington 1994). Such an extrapolation requires data on species turnover or beta diversity: the extent to which species

composition changes between samples or habitats. A variety of measures of beta diversity have been devised (Wilson & Schmida 1984; Magurran 1988), but for the purpose of extrapolation, a simple measure of complementarity such as the Marczewski–Steinhaus distance may be most useful (Colwell & Coddington 1994).

Although there appear to be rather few data on beta diversity of tropical insects, beta diversity in general is often thought to be greater in the tropics (Hammond 1994; Hespenheide 1994). This would be expected if tropical species have, on average, smaller geographic ranges ('Rapoport's rule': Stevens 1989), since moving a given distance between sampling sites would be more likely to take the observer across the margin of a species' range. However, the evidence for the existence of a Rapoport effect is ambiguous (Gaston *et al.* 1998). Furthermore, Colwell & Hurtt (1994) have shown that a spurious Rapoport effect can be generated by sampling bias alone, given equal sampling effort and a latitudinal gradient in species richness. Where species richness is greatest, the presence of individual species is more likely to be missed at a given level of sampling effort, leading to underestimates of range sizes in the species-rich tropics. The effect will be amplified if tropical habitats contain a higher frequency of rare species (e.g. Morse *et al.* 1988; Basset & Kitching 1991; Lawton 1991). Carefully planned inventories should be able to resolve the difficulties introduced by such sampling biases.

Although not strictly a macroecological approach, we mention here also the question of whether the fraction of undescribed species in a sample can be used to estimate the total diversity of that taxon, or indeed of all insects (Gaston 1991). This is what Hodkinson & Casson (1991) tried to do based on a sample of 1690 species of Hemiptera (true bugs) collected during extensive surveys of tropical rainforest in Sulawesi. Of these species, 37.5% were described. If there are a little under one million described insect species, and if the fraction of undescribed species is constant across all orders, then a total of 2.5 million species is obtained. In fact, other orders are almost certainly more poorly known than the Hemiptera, and hence 2.5 million is likely to be an underestimate. The estimate of 189 000 for total Hemiptera obtained in the same way (there are 71 000 described species) may be more accurate. Gauld & Gaston (1995) used a similar calculation based on a thorough survey of Costa Rican Hymenoptera (20 000 to 40 000 species) to estimate global Hymenoptera species richness at 0.3 to 2.0 million.

(d) *Food web studies*

May (1990) also suggested that the study of food webs might help understand total insect richness. At the time he wrote, Cohen *et al.* (1990) had just published their survey of food web patterns based on ECOWeB, a compilation of over 200 binary food webs from a variety of different habitats and taxa. Some of the patterns that emerged involved the ratios of the number of species in different trophic levels, and the ratio between trophic links and species. Clearly, food web invariants could be extremely valuable in estimating total diversity, but also in giving an insight into how diversity is maintained.

Since May's 1990 paper, analysis of a series of new, large and purpose-built webs has in the main not

supported these patterns, while reanalysis of the original data has also cast doubt on the ubiquity of the invariant properties (Warren 1989, 1990; Hall & Raffaelli 1991; Martinez 1991, 1992, 1993a,b, 1994; Martinez & Lawton 1995; Pimm et al. 1991; Polis 1991; Bengtsson 1994; Goldwasser & Roughgarden 1993, 1997). The majority of the new webs describe aquatic systems, with exceptions being work on an area of desert (Polis 1991) and a Caribbean island (Goldwasser & Roughgarden 1993, 1997). We describe below our attempts to build food webs involving tropical herbivores and their parasitoids, but apart from this the only large-scale food web is that collected in Puerto Rico (Reagan & Waide 1996). This study has documented a very large number of trophic links, although its main emphasis has not been on interactions involving insects.

3. INVENTORIES AND FOOD WEBS

In this section we argue that progress in understanding tropical insect diversity is most likely to result from two approaches. The first is from intensive surveys of the diversity of insects (and other organisms) at particular sites: the creation of taxon inventories. The second is from building quantitative food webs that show the patterns of trophic interactions between species, and suggest testable hypotheses about how they interact.

(a) *Creating inventories*

Efficient and well-targeted collecting techniques—including both modern developments like canopy fogging (Lowman & Wittman 1996; Stork et al. 1997) and more widely available, 'low-tech' alternatives (Gadagkar et al. 1990)—are likely to lead to increasingly comprehensive species catalogues in tropical forests over the next few decades. However, we are still a very long way from an inventory of all the world's insects. Only a small fraction of all insect species have even been named—perhaps a million species worldwide—and rates of species description are low in the tropics compared with temperate countries (Gaston 1994).

Faced with the daunting task of establishing a global inventory, we join with a number of authors who have advocated the creation of local inventories of the biodiversity of specific sites of varying size (May 1988; Solbrig 1991; di Castri et al. 1992; Vernhes & Younès 1993; Yoon 1993). Ultimately, extrapolation from local inventories may provide a way of accurately estimating global species richness (May 1988; Hammond 1992; Colwell & Coddington 1994), while many of the macroecological issues discussed above also require the sorts of data that only inventories can supply. Furthermore, inventories are potentially of great value for informing conservation decisions, since land-use decisions are usually made at local scales, where insects and other arthropods can provide a rich source of data on environmental change (Kremen et al. 1993).

How should we set about constructing local insect inventories? The inventories that have proved so valuable to tropical botanists have involved plots where all individuals can be labelled and identified. Clearly this is not possible for insects, but a more systematic and quantitative approach to cataloguing insect diversity will increase greatly the usefulness of the data collected. In the past,

data on insect species richness of particular sites has typically been collected in two contrasting manners (Coddington et al. 1991; Longino 1994). Systematists often collect samples in ways that maximize the number of species collected (the 'get them all' approach; Longino 1994), but the unsystematic nature of the sampling means that ecological generalizations and extrapolations are difficult to make from the resulting inventories. On the other hand, samples collected to answer ecological questions may be more amenable to analysis and extrapolation (the 'sample a few, estimate the rest' approach; Longino 1994), but are often poor representations of the total fauna present at a site. The challenge lies in achieving an optimal compromise between these complementary approaches (Coddington et al. 1991). It is increasingly accepted that the best way forward is to use a sampling protocol that combines intensive inventories at a handful of reference sites with less intensive but carefully directed sampling at a larger number of geographically and ecologically varied sites (Hammond 1992; Colwell & Coddington 1994). A number of schemes with the goal of making this sort of structured inventory are now either up and running or in an advanced stage of development (Gamez 1991; di Castri et al. 1992; di Castri & Younès 1994; Longino 1994; Longino & Colwell 1997; but see Kaiser 1997).

To maximize their value, sampling protocols for these inventories must be carefully planned (Coddington et al. 1991; Hammond 1992; Colwell & Coddington 1994). At intensively studied sites, sampling schemes should be designed to estimate local species richness as accurately as possible, for as wide a range of taxa as possible. May (1988) suggests 1 ha of tropical forest as an appropriate area for such an inventory, with additional sites used to investigate the distinctiveness or complementarity of inventories (Colwell & Coddington 1994). Intensively studied sites could then be used to identify and calibrate methods to investigate diversity at more extensive sites in different parts of the world, perhaps by using selected indicator taxa or assemblages (Hammond 1992; Kremen et al. 1993). Measuring turnover or complementarity is as important as measuring local (alpha) diversity, if results are to be generalized over geographical scales (Colwell & Coddington 1994; Bartlett et al. 1999).

A number of other issues must also be addressed in the design of sampling protocols for species inventories. First, the seasonal component of diversity must be measured, since many tropical insects vary in abundance or may not be represented in samples taken at certain times of year (e.g. Wolda 1987; DeVries et al. 1997; Richardson et al. 1997). Second, sampling effort should be apportioned in relation to species diversity, since under certain circumstances constant sampling effort can generate misleading patterns (Colwell & Coddington 1994; Colwell & Hurtt 1994). Although it may be difficult to estimate species richness before the start of the inventory, increasingly accurate estimates of total species richness can be obtained as sampling proceeds using a variety of extrapolation techniques (reviewed by Colwell & Coddington 1994). For practical reasons, it will also be important to develop methods that can be used by non-specialists and which maximize the efficiency of data collection (e.g. Gamez 1991; Oliver & Beattie 1996; Longino & Colwell 1997).

Finally, to maximize the value of tropical insect inventories, comparable studies in temperate countries will be needed. Although temperate faunas are much better known in terms of their species composition, and despite the longer history of research in temperate countries, systematically collected data on abundance, distribution and species turnover are not available. Given the better resolution of temperate faunas, compiling similar data for temperate habitats should be relatively simple.

(b) *The value of food webs*

Inventories are valuable in determining the magnitude, distribution and taxonomic composition of biodiversity, but say little about its maintenance and dynamics. To address these questions, we need not only information about the numbers and identities of species, but also about how they interact. Of course, as has been stressed by Paine (1988), food webs themselves are just static snapshots of community structure and tell us a limited amount about community dynamics. However, to use Paine's metaphor they provide roadmaps of community structure and are invaluable in generating testable hypotheses about how species interact. For hyperdiverse groups such as insects, complete food webs of whole tropical communities are almost certainly impossible. However, a number of research groups have tackled more limited goals.

Food-plant surveys are now available for a few groups of herbivorous insects, and these occupy an intermediate position between inventories and food webs. As is to be expected, butterflies lead the way and there are now some excellent summaries of the food plants used by large butterfly faunas, for example South-East Asia (Eliot 1992; Igarashi & Fukudu 1997) and Costa Rica (DeVries 1987, 1997). For some large butterfly groups, food plants are recorded for 50% or more species. More is known about the biology of some smaller taxa. As mentioned above, heliconiine butterflies which are Passifloraceae specialists have been intensively studied in the New World tropics, and patterns of geographical variation in host-plant use have been established (Gilbert & Smiley 1978; Thomas 1990). Apart from butterflies, the only major project we are aware of involves the stakhanovite labours of Janzen and colleagues who are systematically rearing macrolepidoptera and their parasitoids from all species of host plants in tropical dry forest in Costa Rica. Only preliminary results have been published so far (Janzen & Gauld 1997), but this work promises unique insights into herbivore and parasitoid diet breadth and biology.

Community studies of groups other than herbivorous insects include the communities feeding in subtropical treeholes in Australia (e.g. Kitching 1987), those inhabiting the water-filled pitchers of tropical *Nepenthes* (pitcher plants; Beaver 1985), dung beetle communities (Hanski & Cambefort 1991) and the *Drosophila*-dominated communties in rotting fruit (Sevenster & van Alphen 1996). For herbivorous insects, the pollinators, parasitoids and inquilines of fig fruit have been studied by a number of groups (Janzen 1979; Compton & Hawkins 1992; Basset et al. 1997), though as yet seldom from a community ecology perspective (cf. Compton et al. 1994). Fig wasps are a particularly attractive model system for community

studies as the widespread distribution of *Ficus* means that they are effectively replicated across the earth's tropics. Finally, there have been a number of studies that have surveyed and sampled all or a large proportion of the herbivores attacking one particular plant species or group, for example, the herbivores attacking *Passiflora* (Benson et al. 1976; Benson 1978; Gilbert & Smiley 1978) and the chrysomelids feeding on *Heliconia* (Strong 1977, 1982a,b). However, few of these studies include trophic levels higher than herbivores.

The problem with building food webs anywhere, and in the tropics in particular, is that it is very difficult to establish the presence and strength of trophic links. Predation is a rare event and hard to observe, and the employment of techniques such as radioactive or heavy metal tracers is logistically and technically demanding. However, host–parasitoid interactions are much easier to document, primarily because parasitism is less evanescent than predation, and trophic links can be established through rearing or dissection. Hawkins and colleagues have built up a huge global database of the number of parasitoids attacking different species of host (reviewed in Hawkins 1994). They have established consistent differences in the number of parasitoid species attacking hosts, which feed in different manners (leaf miners, leaf rollers, gall makers, external folivores, etc.). They have also attempted to test ideas about resource fragmentation by comparing parasitoid species numbers attacking tropical and temperate hosts (Hawkins et al. 1992), although sampling biases and other problems with the database make this very difficult (Godfray 1994; Sime & Brower 1998).

Hawkins's database includes literature records of parasitoids reared from specific hosts, which in the tropics tend to be economic pests. We have taken a different approach and set out to collect systematically data on the parasitoids attacking specific guilds of host at a single study site. We choose groups of hosts that share most species of parasitoids with each other, and relatively few species with members of other guilds. The food webs obtained we call parasitoid webs to emphasize that they contain data on only one type of consumer. Three types of parasitoid web can be distinguished (Memmott & Godfray 1993, 1994): connectance webs, which contain just presence–absence data on trophic connections; semi-quantitative webs, where the relative numbers of all parasitoid species attacking each host is known; and quantitative webs, where the density of all hosts, parasitoids and trophic links can be expressed in the same units. We have concentrated on quantitative webs, which, while more onerous to collect, provide information about the strength of trophic links and are thus less sensitive to sampling bias than binary food webs.

4. TROPICAL PARASITOID WEBS

(a) *Building quantitative food webs*

In this section, we describe the construction of a quantitative parasitoid web, with reference to our own two tropical parasitoid webs. Similar methods can be used to construct most parasitoid webs. We chose leaf miners—insects whose larvae live between the upper and lower leaf epidermis—for our studies, because their

parasitoids are restricted to feeding on leaf miners and because they are relatively simple to rear. Thus, a web focusing on leaf miners will provide a relatively self-contained subsection of the whole food web from any one habitat. An additional advantage is that the permanent, species-specific marks left on leaves by leaf miners provide a normally unambiguous way of associating parasitoids with their correct hosts.

We have used two tropical field sites for web construction, one in Costa Rica and the other in Belize. In Costa Rica the field site consisted of a plot of tropical dry forest measuring 170 m × 100 m, located in the Parque Nacional de Guanacaste on the Pacific side of northern Costa Rica. The plot vegetation consisted of secondary forest, with trees growing to a height of approximately 10 m and a thick understorey of herbs, shrubs, vines and bamboos. In Belize, the field site was an area of moist tropical forest near the Las Cuevas Research Station in the Chiquibul National Park, Cayo District. This forest is regularly affected by hurricanes, and the area used as a field site consisted largely of vegetation that had grown up following Hurricane Hattie in 1961. Leaf miner abundance was low in the forest understorey, whereas miners were abundant along trail edges, which were probably artificial analogues of gaps in the forest caused by tree falls. Our field site was a trail running through the forest, 1700 m long and 5 m wide.

There are three main stages to constructing a quantitative parasitoid web: (i) quantitative sampling of the herbivores (which may be parasitized); (ii) rearing the hosts and parasitoids; and (iii) identifying the insects. In both Costa Rica and Belize, line transects were used to sample the hosts, and the abundance of parasitoids was obtained by rearing hosts collected in the field. Typically all mines infesting leaves a fixed distance from the line transect are collected and their status (tenanted or vacated) and the host plant recorded. The aim is to be able to express the density of each species and the frequency of the interactions between species in common units, for example in individuals or interactions per square metre of habitat. Different sampling methods may be required for other herbivores; for example, point transects or random quadrats may prove more suitable as sampling methods (as in the temperate parasitoid web described in Müller *et al.* (1999)). The chosen method will depend on the density and distribution of the herbivore, and the type of vegetation being sampled. Normally, insufficient tenanted mines for rearing are amassed during the quantitative sampling and additional mines are collected by stratified collecting throughout the site. In Belize, where leaf miner larvae were feeding throughout the year, sampling of miners was carried out year-round. In the more seasonal Costa Rican site, collection was carried out over two consecutive wet seasons.

The second stage of web construction is rearing the herbivores and their parasitoids. For tropical leaf miners, individual leaves containing the herbivore were placed in airtight plastic pots or bags until the larvae pupated. In some cases leaves must be kept fresh by placing their petioles in water, or the larvae may have to be transferred artificially to a new leaf. Often the larvae pupate in the mine or pot/bag, but sometimes a suitable pupation medium has to be provided. Especially in the humid tropics, constant attention is required to prevent the

growth of mould, and also to preserve adult hosts and parasitoids before they rot. Obviously, different techniques will be required for other groups of insects.

The third and final stage of web construction is insect identification. It is almost impossible for one person to be an expert in all the fields of identification required to construct a tropical web. The Costa Rican web, for example, contained species from 35 plant families, 18 herbivore families and ten parasitoid families. Fortunately, 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.

Quantitative parasitoid webs suffer from a number of potential sources of error (Memmott *et al.* 1994; Müller *et al.* 1999; Rott & Godfray 1999). First, there may be biases in the ease with which hosts are sampled (some leaf mines are almost transparent) or in the relative success rate in rearing different species of parasitoid. By collecting mines to be reared, attack by late-acting parasitoids may be underestimated. The food webs do not include an explicit estimate of sampling error, although the quantitative nature of the sampling allows an implicit estimation of the confidence that can be placed in the trophic links involving any species (unlike a binary web). Not all trophic links are resolved using the methods we have described. Facultative hyperparasitism is common among parasitoids of leaf miners, and can only be resolved by painstaking dissections of large number of mines. It may not always be possible to associate parasitoids with particular host species where several miners feed on the same species of plant (and similarly if obligate hyperparasitoids are present their primary parasitoid hosts may be difficult to identify). There may also be taxonomic uncertainties concerning component species. Finally, replication of parasitoid webs is often not possible for logistic reasons.

(b) *Patterns in the web*

Of the two tropical leaf miner parasitoid webs we have studied, that from the moist hurricane forest in Belize is still being constructed and analysed, while a full description of the tropical dry forest web from Costa Rica was presented by Memmott *et al.* (1994). Here we briefly describe the patterns reported in Memmott *et al.* (1994) and then apply a new type of analysis to these data, the quantitative overlap graph described by Müller *et al.* (1999).

The study site contained 88 species of plants in 39 families. Ninety-two species of leaf miner were recorded, belonging to the insect orders Lepidoptera, Coleoptera and Diptera. Only 36% of the plant species were mined and the maximum number of miner species per plant species was nine. Ninety-three species of parasitoid were reared, all but one in the Hymenoptera (the exception was in the Tachinidae, Diptera). In nearly all cases it was possible to identify the host species from the leaf mine morphology, but unfortunately the major exception was a very common group of four hispine beetles attacking low-growing bamboos. Obligate hyperparasitism is rare among leaf miner parasitoids and probably all but two (rare) species of parasitoids were able to develop directly on the leaf miner. Not all the hosts and parasitoids recorded from the site were common enough to appear in the quantitative sampling and the quantitative parasitoid

parasitoids (scale: miners × 5)
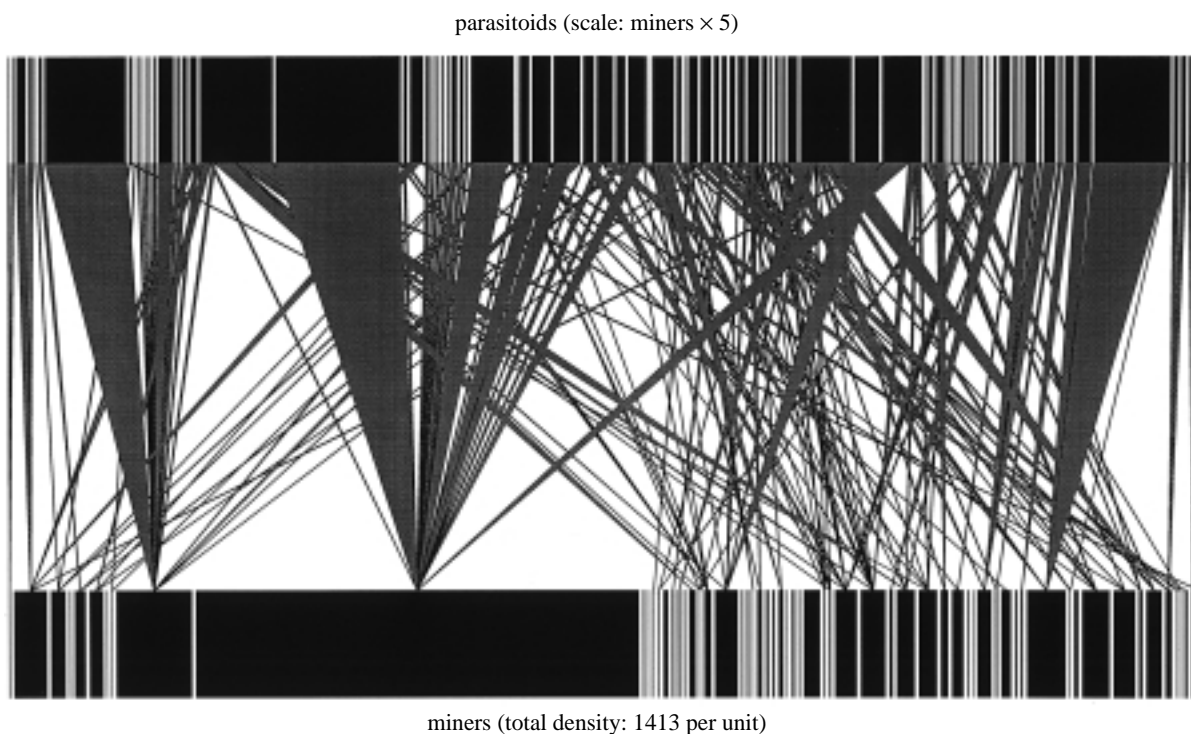

miners (total density: 1413 per unit)

Figure 2. Quantitative parasitoid web for leaf miners in a tropical dry forest in Costa Rica. The lower range of bars describes the relative density of 63 species of leaf miner sampled in the study site. In two cases, miner species that could not be distinguished in the field were lumped. The largest bar consists of four species of hispine beetle miner. Subsequent study showed this group consisted of one rare species and three of about equal abundance. The upper range of bars (drawn at five times the scale) represent the abundances of 86 species of parasitoid. The associations between parasitoids and hosts are shown by the grey wedges (redrawn from Memmott *et al*. 1994).

web contained 63 host species (67%) and 86 (92%) parasitoid species (figure 2).

The majority of leaf miners (88%) were recorded from just a single species of plant and those that were more polyphagous tended to attack related hosts; only two miners were recorded from plants in different families. Host mortality from parasitoids averaged 32%, with a tendency for miners from certain orders to be more vulnerable than others. No parasitoids were recorded from 19 hosts, but these tended to be uncommon: there was a strong relationship between sample size (number of mines collected) and the number of species of parasitoid reared (this explained 76% of the variance). Sample size and miner abundance in the site are themselves closely correlated, suggesting that rare hosts are only discovered by a fraction of the parasitoid species that could potentially attack them. One of the advantages of quantitative over-connectance webs is that it is far easier to demonstrate and allow for the pervasive effects of trophic link sampling. Just as more common hosts had more species of parasitoids recorded from them, more common parasitoids tended to be reared from more species of host. However, another factor was also important here: the mode of parasitoid attack. Endoparasitoids that delayed host development (termed koinobionts) had fewer hosts than ectoparasitoids that killed the host at oviposition (idiobionts). Parasitoids that feed internally have to withstand attack by the host's immune system and thus presumably have to be better attuned to host physiology and hence more specialized than species feeding on dead or inert hosts.

An important issue in food web ecology is the extent to which natural webs are compartmentalized: that is, divided into independent units. We chose to study leaf miners and their parasitoids because we believe their parasitoids are restricted to hosts that feed in this way; thus the whole parasitoid web can be viewed as a compartment of a large entity. However, the web was not divided into further, smaller compartments (except trivially for those hosts from which no parasitoids were reared). We lack, at the moment, a statistical test to detect whether a quantitative web is divided into weakly connected compartments, but inspection of figure 2 shows no evidence for this.

One of the main aims of building the web was to examine the degree to which hosts are dynamically linked by shared parasitoids. In food web theory, a way of showing this is through predator overlap graphs, which consist of points (vertices) representing prey linked by lines (edges) if they share a common predator (Cohen 1978; Sugihara 1984). It has been hypothesized that the resulting structures may have some non-random mathematical properties (intervality, triangulation) that reflect general patterns in the structure of natural communities. The problem, however, is that classical predator overlap graphs are binary (i.e. they show whether a predator is shared, not the strength of the linkage) and hence are susceptible to sampling artefacts. We can illustrate this with the predator (parasitoid) overlap graph for the Costa Rican data (figure 3). The 63 hosts are represented by the vertices around the edge of the circle; the hosts are linked if the same parasitoid species was reared from
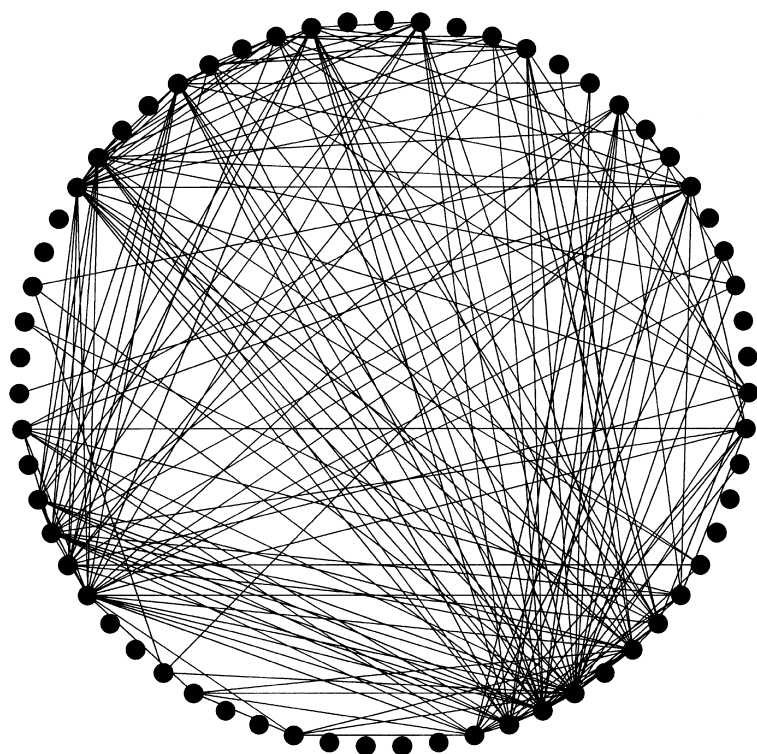
Figure 3. Parasitoid overlap graph. As described more fully in the text, the 63 vertices arranged in a circle represent different miner host species; a line connecting two species indicates that they share a parasitoid.

both. Of the 1953 possible links (i.e. $(n(n-1))/2$ where $n=63$) only 198 (10.1%) were observed. But this figure reflects sampling intensity and would rise if more mines were reared. Moreover, the distribution of links per host appears non-random, with some hosts being more extensively connected than others. Given a fixed number of hosts and links, the appropriate null model for randomly distributed links is the hypergeometric distribution (Müller *et al.* 1999), and it can be shown that the data in figure 3 differ significantly from this expectation. The reason for this is that more common hosts are attacked by larger number of parasitoids and hence are more likely to share parasitoids. We suspect that similar arguments might underlie other non-random properties such as those mentioned above. It then depends on your point of view whether these patterns are viewed as simple statistical consequences of sampling, or a manifestation of community pattern determined by the underlying species abundance distributions.

Some of these problems can be circumvented by working with quantitative parasitoid overlap diagrams. There are many ways these can be constructed and here we use the recipe described in Müller *et al.* (1999). The logic behind this is to ask what is the probability (d_{ij}) that a parasitoid currently attacking species i developed on species j (where j may be the same species: d_{ii}). These probabilities can be calculated from food web data if we assume that parasitoids of one species move randomly through the community, and there are not races or biotypes associated with different host species. Making this assumption,

$$d_{ij} = \sum_{k} \left[\frac{\alpha_{ik}}{\sum_{l} \alpha_{il}} \frac{\alpha_{jk}}{\sum_{m} \alpha_{mk}} \right],$$

where α_{ik} is the absolute density of the trophic link between host i and parasitoid k (and hence the summations in k and l are over all parasitoids and in m over all hosts). The resulting diagram is shown in figure 4. The host vertices have been drawn in different sizes to represent the number of parasitoids that were reared from each (hence hosts with no parasitoids appear missing). The extent to which each vertex is shaded black represents the magnitude of d_{ii}: if largely black, $d_{ii} \rightarrow 1$ and most parasitoids are likely to have developed on the same host, if largely white, then $d_{ii} \rightarrow 0$ and most parasitoids are likely to have developed on other species. A line linking two hosts still represents shared parasitoids, but now the width of the line at species i and j represents d_{ij} and d_{ji}; the importance of species j as a source of parasitoids attacking species i and vice versa.

The diagram suggests several patterns in the web, some but not all of which are similar to those seen in quantitative overlap diagrams of temperate parasitoid communities (Müller *et al.* 1999; Rott & Godfray 1999). First, as expected, species from which many parasitoids were recorded are linked more often to other species than those attacked by fewer parasitoids (and, although not shown here, this is correlated with host abundance). Second, there is a tendency for more common species to act as sources of their own parasitoids; hence, we would expect their population dynamics to be relatively autonomous. Third, and not observed in the other parasitoid webs, there are a number of strong symmetrical interactions where two species are mutually important as sources of each other's parasitoids. It is these species that we would predict are most likely to be dynamically linked through apparent competition. As an increasing number of quantitative webs are constructed in both tropical and temperate countries, it will become possible to see whether generalizations can be made about food
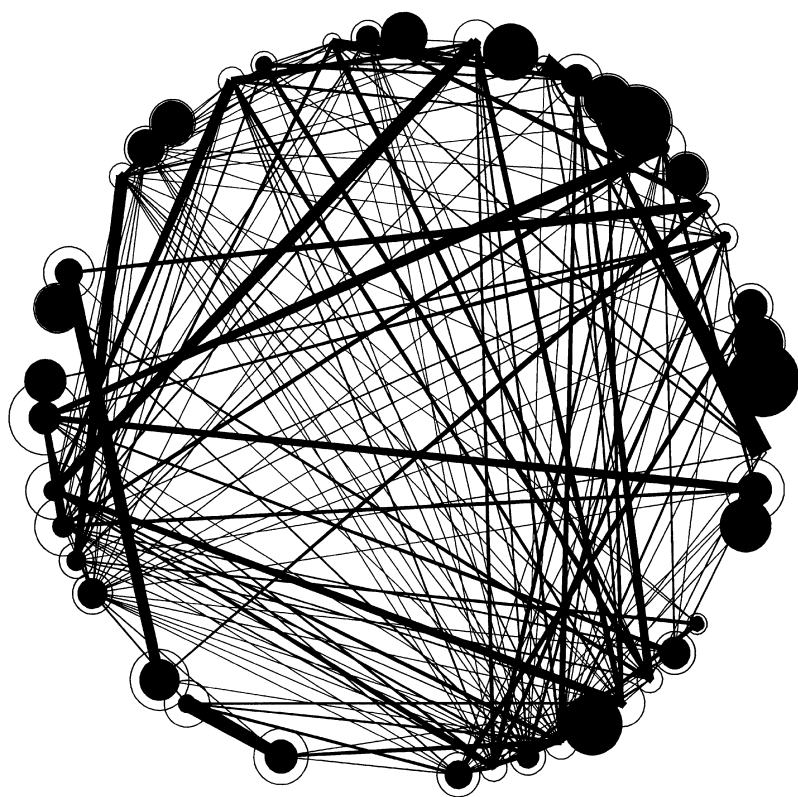
Figure 4. Quantitative parasitoid overlap graph. As figure 3, but now the size of the vertex indicates the number of parasitoids reared from that host (hence the vertex is missing if no parasitoids were reared). The extent to which a vertex is coloured black indicates the degree to which a species acts as host for its own parasitoids (see definition in text). The links show shared parasitoids, and the width of the connecting line between hosts i and j at species i indicates the importance of species j as a source of parasitoids that attack species i (note that links between two species may be asymmetrical).

web structure—for example, whether certain patterns are typical of tropical communities but not temperate ones.

5. CONCLUSIONS

Darwin (1889, recently quoted by Longino (1994)) wrote: 'The number of minute and obscurely coloured beetles is exceedingly great. The cabinets of Europe can, as yet, boast only of the larger species from tropical climates. It is enough to disturb the composure of an entomologist's mind, to look forward to the dimensions of a complete catalogue'. And how much more discomposing to think about moving beyond a mere catalogue to attempt to understand the forces shaping that diversity. Yet plant ecologists are making large strides in this direction and it is our belief that real progress can also be made in understanding insect and other invertebrate community structure in the tropics.

We believe that many of the problems concerning large-scale patterns in insect communities, the questions that Erwin so effectively brought to general attention, can best be answered through the construction of taxonomic inventories at a restricted number of sites. The construction of such inventories requires close collaboration between systematists, ecologists and also statisticians, whose critical role perhaps has been under-recognized so far (but see Colwell & Coddington 1994). To understand the dynamic processes underlying insect biodiversity, we believe a two-pronged approach is needed. The first component is descriptive and hence slightly unfashionable: the construction of food webs describing the patterns of trophic linkages between insects in a community. The second component is experimental: manipulation of tropical insect communities to test hypotheses generated by the webs. It is this that we have been

attempting in building quantitative parasitoid webs, although we stress there are many different approaches to this problem and we claim no special primacy for ours. We argue that inventories and food webs are the entomological equivalents of the tropical botanical permanent field plots that have proved so valuable in stimulating ideas about tropical plant diversity. They reveal the structure and patterning of communities, and generate hypotheses about how the component species interact that can then be studied experimentally.

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