Apparent competition and insect community structure: towards a spatial perspective

Rebecca J. Morris[1], Owen T. Lewis[1] & H. Charles J. Godfray[2]*

[1] *Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK*
[2] *NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berks, SL5 7PY, UK (*corresponding author's e-mail: c.godfray@imperial.ac.uk)*

Morris, R. J., & Lewis, O. T. & Godfray, H. C. J. 2005: Apparent competition and insect community structure: towards a spatial perspective. — *Ann. Zool. Fennici* 42: In press.

Competition has been widely discussed as a process that may structure communities of plants and animals. Its role in insect communities is less clear, especially as many insect species do not appear to compete for resources. However, such communities could still be structured by "apparent competition" where the species interact through shared natural enemies. We explore recent attempts to assess whether apparent competition may structure herbivorous insect communities. Communities can be described by quantitative food webs from which the potential for apparent competition can be inferred. We illustrate both the construction of a diverse quantitative food web and a field experimental test of apparent competition using our work on leaf-miner communities in Belize. We consider how a spatial perspective may be incorporated into our leaf-miner community research, and speculate about the shape of apparent competition kernels and their relevance for the structure of herbivorous insect communities.

Introduction

Are ecological communities haphazard collections of species with a composition moulded by historical accident and contingency, or are they shaped by biological interactions such as competition, predation and parasitism? This question has been at the heart of community ecology since the 1960s when MacArthur and others identified resource competition as the key process structuring animal communities (MacArthur 1958, Connell 1961a). Since then the relative popularity of contingency and competition have fluctuated. The early 1980s saw the introduction of null models with more prominence being given to non-equilibrial and stochastic factors (Connor & Simberloff 1979, Wiens 1984, Chesson & Case 1986). A much more critical attitude to evidence of competition structuring communities developed, which spurred a series of careful studies, particularly in plants, that quantitatively documented competition using experimental manipulation (e.g. Gurevitch 1986). Today the prevalent view may be changing again with the development of neutral models of biodiversity that argue that many macroecological patterns shown by plant communities can be generated by models incorporating no biological interactions (Hubbell 2001). However, most ecologists now accept that competition has the potential to affect the structure of certain ecological communities some of the time.

But can competition ever be important in structuring communities of species that seldom come near to exhausting their resources? Specifically, our concern in this paper is whether competition can structure communities of herbivorous insects. This is not a side show: herbivorous insects and the natural-enemy food chains based on them may include more than 50% of all described species, a large proportion of the world's biodiversity.

Early attempts to address this question were influenced by two schools of thought. First, Hairston *et al.* (1960) proposed that "the earth is green". What they meant by this is that competition could not be the dominant force structuring herbivore communities because there was so much uneaten green food in the environment. Natural enemies must regulate herbivores below their carrying capacity. These ideas were further developed into a general theory in which the productivity of the environment determines whether the natural enemies of herbivores are abundant enough to prevent them from competing for resources (Fretwell 1977, 1987, Oksanen *et al.* 1981). A factor that complicates the application of these ideas is the poorly defined trophic structure of arthropods that feed on insect herbivores, and the prevalence of intraguild predation (Polis *et al.* 1989).

The second school was initiated by Murdoch (1966) who challenged the idea that "the earth is green" because of herbivore control by natural enemies and instead emphasised that plants are protected by physical and chemical defences. Janzen pithily encapsulated this view when he said the earth isn't green, but coloured "quinones, tannins and anthocyanins" (Janzen 1979). Like the Ancient Mariner surrounded by undrinkable water, herbivores are surrounded by poisonous or indigestible food. The little that can be eaten, perhaps young foliage or certain plant tissues, is competed for, but such competition has no effect on the bulk of unavailable food that colours the earth green. This view is supported by the clear specialisation of many insect herbivores on the most nutritious tissue, and the prevalence of "bottom-up" effects, when herbivore population densities are strongly influenced by plant quality and nutritional status (Price *et al.* 1980).

While there is no doubt that some insects are specialised on the most nutritious tissue, very many have more catholic tastes (Novotny 2005). Moreover, it is rare to find plant tissue that attracts no herbivorous insects. The demonstration of a bottom-up effect of plant quality on herbivores does not exclude the possibility of top-down forces (through natural enemies) also occurring (Haukioja 2005). In fact most ecologists now agree that bottom-up and top-down forces interact to affect herbivorous insect populations (Hunter & Price 1992, Denno *et al.* 2005). So "the earth is green" may be a little simplistic, but we believe it still encapsulates an important truth: that competition is unlikely to be significant for many contemporary herbivorous insect communities.

A further factor limits the extent to which competition may structure herbivore communities. The plant trophic level is diverse and frequently made up of a large number of species. Most herbivores only feed on a subset of these, quite often only a single species and those that do feed on the same resources often exhibit highly diverse feeding modes and specialisation for different plant parts. Inter-specific competition cannot occur if species lack shared resources. Of course, the fact that herbivores have non-overlapping resources may itself be a result of competition — the ghost of competition past (Connell 1980). Such structuring could be identified by defining an appropriate null model and looking for non-random patterns of host use. We are not aware of convincing demonstrations of past competition in herbivorous insects that exclude the alternative hypotheses we discuss below, but acknowledge that defining sensible null models is very difficult.

Apparent competition

If competition is not a major factor structuring the bulk of herbivorous insect communities, is there an alternative? If two species are consumed by a shared natural enemy then they can interact in an indirect manner (Williamson 1957). Holt (1977) formalised this theory, calling the process "apparent competition" on the grounds that the patterns it generated could appear to be caused by competition. Apparent competition is defined

as a reduction in the population density of one species when the population density of a second species increases, with the interaction mediated by a numerical increase of a third species at a higher trophic level (Holt 1977). Short-term and long-term apparent competition can be distinguished by whether it involves an aggregative behavioural response or a reproductive numerical response of the natural enemy (Holt & Kotler 1987). Holt (1977) argued convincingly that shared natural enemies could structure a community in the same way as competition for shared resources. In exactly the manner that two species cannot co-exist on a single shared resource, two species cannot co-exist if they share a natural enemy that treats them identically. With competition, the species that wins out is the one that can persist on the lower level of resource (the R^* rule; Tilman 1982); with apparent competition, the persistent species is the one that can support, in the absence of the other species, the highest density of natural enemies at equilibrium (the P^* rule; Holt *et al*. 1994). Thus a natural enemy may at a particular locality have only one prey or host, but this may not be a result of any physical or physiological constraint, but a consequence of apparent competition. This has been termed dynamic monophagy (Holt & Lawton 1993), or by analogy to resource competition could be referred to as "the ghost of apparent competition past". In competition theory, species can co-exist if they have sufficiently non-overlapping resources, and will evolve to fill vacant niches. Similarly, differences in predator or parasite profiles will allow co-existence in the face of apparent competition, and it is predicted that species will evolve to colonise enemy-free space (Jeffries & Lawton 1984).

There are thus marked symmetries between competition and apparent competition, but there are also differences. In competition theory, resources are often, but not always, assumed to have very simple dynamics, and intra- and inter-specific competition tend to lead to the stable co-existence of the persistent set of species. This is particularly true for plant communities where resources are abiotic, or sessile animal communities where the limiting resource is space (Connell 1961b, Dayton 1971). For herbivorous insects attacked by predators, parasitoids and

pathogens, the dynamics tend to be oscillatory. The two paradigmatic models of natural enemy dynamics, the Lotka-Volterra predator–prey and the Nicholson-Bailey host–parasitoid, show neutral and divergent oscillations respectively (Hassell 2000). Much research over the last thirty years has been directed at trying to understand how predator–prey and related interactions persist in the face of this inherent tendency for unstable oscillations. Theory and experiments have shown many different processes may be involved, and that it is unlikely that any one is predominant (Hassell 2000). As a result, theoretical studies of apparent competition are necessarily complicated because of the assumptions that are made about how individual interactions are stabilised, and how these processes operate in a multi-species setting.

Apparent competition can also be viewed in the context of a broader class of theories of indirect interactions. If the population density of the focal species increases rather than decreases in concert with the second species then the resulting interaction can be called apparent mutualism (Abrams 1987, Abrams & Matsuda 1996). An obvious example of this is when a top predator attacks the intermediate predator of a herbivore. This is a trophic cascade from the top predator to the herbivore (possibly also affecting the intermediate predator and the food plant or plants) (Polis *et al*. 2000). More subtle apparent mutualisms occur. Consider two herbivores with a shared natural enemy. If one increases in density and in consequence the shared predator switches to feeding on it, then the other herbivore experiences apparent mutualism. Indirect interaction theory also distinguishes between two ways in which the indirect effect occurs: by a density-mediated or a trait-mediated change (Abrams *et al*. 1996, Krivan & Schmitz 2004). The trophic cascade discussed above is an example of an effect mediated by changes in density of the intermediate species. The example of switching just given could be a case of a trait-mediated interaction where natural enemies interact with prey by inducing changes in prey phenotype. Other trait-mediated effects may involve modifying traits as diverse as behaviour, morphology, and life history (Werner & Peacor 2003). Short-term and long-term apparent competition men-

tioned above normally involve trait-mediated and density-mediated interactions respectively (Holt & Kotler 1987).

The role of apparent competition in structuring communities

How can we assess the possible structuring force of apparent competition in herbivore communities? As with "real" competition we can take a macro-ecological approach and try to distinguish patterns in actual communities that differ from a suitably constructed null model. This has proved difficult, particularly because when we move beyond herbivores to include their natural enemies, we still have relatively little information about herbivore-based insect community structure. However, while strict quantitative tests have remained elusive there is considerable circumstantial evidence pointing to its significance (Jeffries & Lawton 1984, Holt & Lawton 1994).

The second way to demonstrate apparent competition is through direct experimentation on components of the community. There are still relatively few studies that have sought to do this with insect herbivores (Chaneton & Bonsall 2000). The first was not a designed experiment but made use of a natural invasion. A species of leafhopper feeding on grapevine invaded California and this led to a reduction in density of a resident congeneric species, which also fed on grapevine. Of course this decline may have been due to direct competition, but Settle and Wilson (1990) make a persuasive case that the invader precipitated an increase in density of a shared egg parasitoid that preferentially targeted the resident leafhopper. Working with aphids, our group has shown on several occasions that aphids feeding on different plant species may show short-term apparent competition mediated by insect predators (Müller & Godfray 1997, Rott *et al.* 1998), and also that some species are unable to invade a community, even though a suitable host plant is present, because of the actions of the resident predator assemblage (Müller & Godfray 1999). In the aphid communities we study, predators seem to have a far more important impact on aphid densities than parasitoids, probably because the latter are heavily attacked by

secondary parasitoids (which thus have a positive effect on the aphids). Secondary parasitoids however, do have an impact on primary parasitoids, mediating apparent competition between species (Morris *et al.* 2001). There are also some examples of apparent competition between herbivorous mites mediated by predatory mites (Karban *et al.* 1994, Hanna *et al.* 1997, Van Rijn *et al.* 2002).

A spatial perspective on apparent competition

The majority of both theoretical and experimental studies of apparent competition have lacked a spatial component (but *see* Bonsall & Hassell 2000, Holt & Barfield 2003). How might a consideration of space help us to understand herbivore communities structured by natural enemies? Classical competition theory provides several examples of spatial mechanisms and patterns for which there are likely to be apparent competition counterparts. Character displacement occurs when two species occupy similar niches in allopatry but divergent niches in sympatry (Fenchel 1975). It has been argued that species that shared natural enemies might evolve to occupy different regions of enemy-free space in sympatry (Jeffries & Lawton 1984). Species that cannot co-exist locally may co-exist regionally as a mosaic with different species exploiting the resource at different sites (Shurin *et al.* 2004). Similarly where dynamic monophagy occurs, a natural enemy might coexist with a different prey or host at different sites (Holt 1984). Such a pattern might occur if there was a colonisation/competition trade-off with one prey or host being able to tolerate higher levels of attack (the equivalent of a superior competitor), and the other being a superior colonist (this assumes a ubiquitous predator). The outcome might be a metacommunity, a set of local communities linked by dispersal of multiple potentially interacting species, which can show very different dynamics to a local community (Leibold *et al.* 2004). Central to all these examples is the dispersal ability of the natural enemies that mediate the indirect interactions. At present our knowledge of the mobility of these natural enemies is very limited,

not only as a result of logistical difficulties in measuring insect movement, but also because of variation amongst species and the difficulties of generalisation (Roland & Taylor 1997, van Nouhuys & Hanski 2002, van Nouhuys 2005).

In the remainder of this chapter we describe first how we have attempted to explore the role of apparent competition using a largely non-spatial approach and then return to discuss how we might include a spatial perspective, and what this might tell us. We begin with ways of describing herbivore/natural enemy communities, and assessing the potential for indirect effects, through the construction of quantitative food webs. We then describe how the webs can be used to generate hypotheses about indirect interactions that can be tested by manipulation experiments in the field, and illustrate this with our field experimental test of apparent competition in a leaf-miner–parasitoid community. We then discuss how we might incorporate a spatial perspective into this research and what this might tell us, reanalysing our experimental data as an example. We finish by introducing the concept of apparent competition kernels, and discussing their significance for the dynamics and structure of herbivorous insect communities.

Quantitative food webs

In order to understand the potential for indirect effects to structure communities of herbivorous insects and their natural enemies, it is necessary to have some means of describing the community, ideally in a manner that allows comparison across systems. Food webs are an obvious means of doing this, although classical food webs are a rather blunt tool for this purpose. Classical food webs normally only incorporate presence/absence data about interactions and often agglomerate sets of similar species into functional groups or even trophospecies (Polis & Winemiller 1996). The lack of quantitative information and resolution to species level makes it particularly difficult to look for the type of patterns that apparent competition or other indirect interactions might generate.

Quantitative food webs, with all species and trophic links expressed in the same units of den-

sity, overcome these problems, though at the cost of considerably greater labour in their construction. Indeed, it is probably not possible to construct a quantitative food web resolved at species level for a complete ecosystem (the mere attempt to collect the data would probably perturb it beyond its natural state). But if one is interested in the structuring of a guild or module then one can argue that at least provisionally it is justifiable to restrict the food web to that assemblage.

Over the last ten years, our group and collaborators have built quantitative food webs of aphids and their natural enemies (Müller *et al.* 1999), and of leaf mining insects and their parasitoids (Memmott *et al.* 1994, Rott & Godfray 2000, Valladares *et al.* 2001, Lewis *et al.* 2002). Other groups have collected equivalent data for lepidopteran folivores (Henneman & Memmott 2001) and for gall-forming insects (Schonrogge & Crawley 2000). To describe the approach in more detail we concentrate on our study of leaf mining insects in tropical Central America.

How to create a leaf-miner–parasitoid quantitative food web

Leaf miners are a taxonomically heterogeneous group of insects that all share the same larval feeding habit — they feed inside the leaf lamina, making a characteristic mine which normally appears white or a lighter shade of green than the leaf because the chlorophyll bearing tissue has been wholly or partly consumed. The leaf mining habit is widespread and has evolved a number of times in the Lepidoptera, and is also common though more taxonomically restricted in the Diptera. Leaf mining beetles (Coleoptera) are also common, especially in the tropics, and there are a few temperate, leaf mining sawflies (Hymenoptera: Symphyta) (Hespenheide 1991). Virtually all leaf miners are attacked by parasitoids that lay their eggs on or in their hosts inside the mine. Mortality frequently exceeds 50%, and more species of parasitoid are found attacking individual leaf miner species than hosts in any other feeding guild (Hawkins 1994). Taxonomically, leaf miner parasitoids are almost exclusively Hymenoptera, in particular from the families Eulophidae and Braconidae. Facultative

secondary parasitism is common, that is a parasitoid female will often lay an egg on whatever already occupies the mine, a host larva or a fully or partially fed parasitoid larva. Obligate secondary parasitism, where certain species specialise as parasitoids of parasitoids, is rare in this feeding guild (unlike, for example, aphid-parasitoid assemblages).

Leaf miners have many advantages and a few disadvantages as model systems for studying herbivore community structure. First, if their communities are structured by natural enemies then the overwhelmingly most likely group to be responsible is parasitoids, and hence efforts can be focused on just one group. Leaf miners do suffer from predation, by birds and ants for example, but these tend to be relatively minor sources of mortality (though *see* Memmott *et al.* 1993, for an exception). Second, the mine forms a semi-permanent record of the presence of its creator, facilitating quantitative sampling even after the insect itself has died or become an adult. Mine morphology is also normally sufficient for species identification (in combination with knowledge of the host plant). Third, rearing leaf miners and their parasitoids is relatively simple and their small size makes this easier to do in bulk in the laboratory. Fourth, the parasitoids of leaf miners are almost exclusively restricted to hosts within this feeding niche. There are few if any links between this host–parasitoid compartment and other herbivores and their natural enemies. The two main disadvantages are that being small insects their taxonomy can be challenging, especially that of their parasitoids where in the tropics very few have been described and even morpho-typing is far from straightforward. It is also seldom possible to disentangle quantitatively the intraguild predation among the parasitoids without extensive dissection and, ideally, molecular studies.

Obtaining the data to build a quantitative food web is conceptually straightforward and can be done in a variety of ways. Typically we (1) estimate the density of leaves of different host plants at the study site, (2) estimate the proportion of leaves of each host plant mined by the species that attack it, and (3) rear samples of mines to obtain the frequency with which different parasitoid species attack each host. There are,
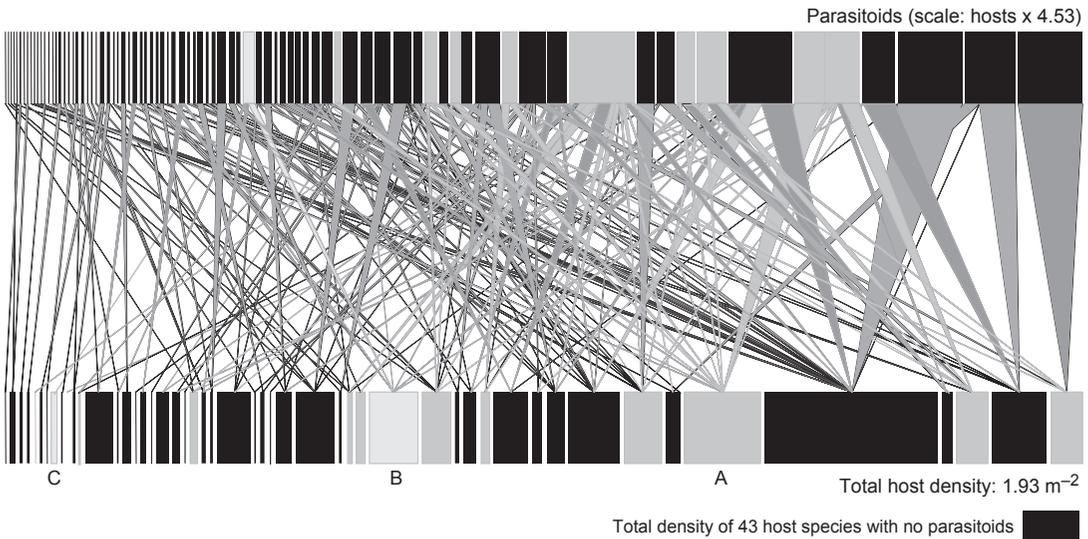
however, a number of possible sources of bias. Estimates of leaf miner densities should be based only on tenanted mines, or should be corrected for the length of time vacated mines are present. For leaf miners with one generation a year on a deciduous host plant, sampling for leaf miner density may be done most easily immediately the last mine is vacated. In estimating rates of parasitism, collections for rearing should not be made too early to preclude parasitoid attack, but even late collections may to some degree underestimate parasitism. More specific sampling issues are discussed by Memmott *et al.* (1994), Rott and Godfray (2000), Valladares *et al.* (2001) and Lewis *et al.* (2002).

The Belize leaf-miner–parasitoid quantitative food web

An example of a quantitative food web is shown in Fig. 1. The data were collected in hurricane-affected moist tropical forest in the Chiquibul Forest Reserve in south-west Belize. The web includes all leaf miners found at the 8500 m^2 study site, 93 species of moth, beetle and fly, which were attacked by 84 species of parasitoid. 272 species of plant were found in the study site, of which 71 were attacked by leaf miners. For clarity, the plants are not included in the food web; the majority of leaf miners are monophagous and the majority of host plants are attacked by only one leaf miner species.

The two trophic levels, hosts and parasitoids, are represented by a series of bars in a lower and an upper register, respectively. Each bar within a register represents a host or parasitoid species, the width of the bar representing that species' abundance. Hosts and parasitoids could be drawn at the same scale, but because parasitoids are always less abundant than hosts we depict them on a magnified scale so that their relative abundance can be discerned more easily. Parasitoids are linked with their hosts by "wedges", their relative widths at the parasitoid end denoting the fraction of the parasitoid population developing on that host.

The web tells us a number of things. First it reveals the complexity of the community, the extent to which it is interlinked. Let the numbers

Parasitoids (scale: hosts x 4.53)

C   B   A   Total host density: 1.93 m^{-2}

Total density of 43 host species with no parasitoids

Fig. 1. Quantitative leaf-miner–parasitoid food web. The two series of bars represent the abundance of leaf miners (bottom) and parasitoids (top), and the width of the links between the two trophic levels represent the relative frequency of each host-parasitoid association. The letters A and B refer to the two species removed in the manipulation experiment (*Calycomyza* sp. 8 and *Pentispa fairmairei* respectively), and the bars and links in the two shades of grey represent the species predicted to be affected by the manipulation. Letter C refers to *Pachychelus collaris*, the species affected by removal of species B.

of host in the web be H and the number of parasitoids P. As all parasitoids must develop on at least one species of host, the minimum number of links in the web is P and the maximum is $H \times P$. So if we define the number of observed links as L then the statistic $C = (L - P)/P(H - 1)$, which must be in the range $0 \leq C \leq 1$ gives a measure of the connectivity. For our web, $C = 0.027$, indicating a relatively sparsely connected community. How can we assess the robustness of this statistic? If we sampled more intensively we might discover new species and new links. We cannot know this of course, but we can use the quantitative information in the web to explore what we would have concluded had we sampled less thoroughly. In Fig. 2 we plot the value of C for a series of webs in which we have started by omitting the weakest link and then progressively excluded more and more links in order of increasing strength (with link strength defined as natural logarithms of the number of links per m^2). The x-axis denotes the threshold link strength below which a link is excluded, and we allow a parasitoid to "disappear" when all its constitutive links are omitted. Removing links does lead to a decrease in our connectance sta-
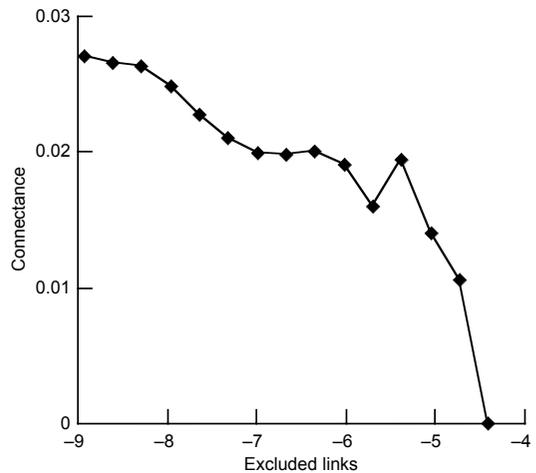
Fig. 2. Connectance of the leaf-miner–parasitoid food web when links are excluded in order of increasing strength. The x-axis denotes the threshold link strength (as natural logarithm) below which a link is excluded. A parasitoid "disappears" when all its constitutive links are omitted.

tistic, slowly at first and then more rapidly until all remaining parasitoids attack just a single host (and hence $C = 0$). Because C declines slowly at first we conclude that sampling more intensely
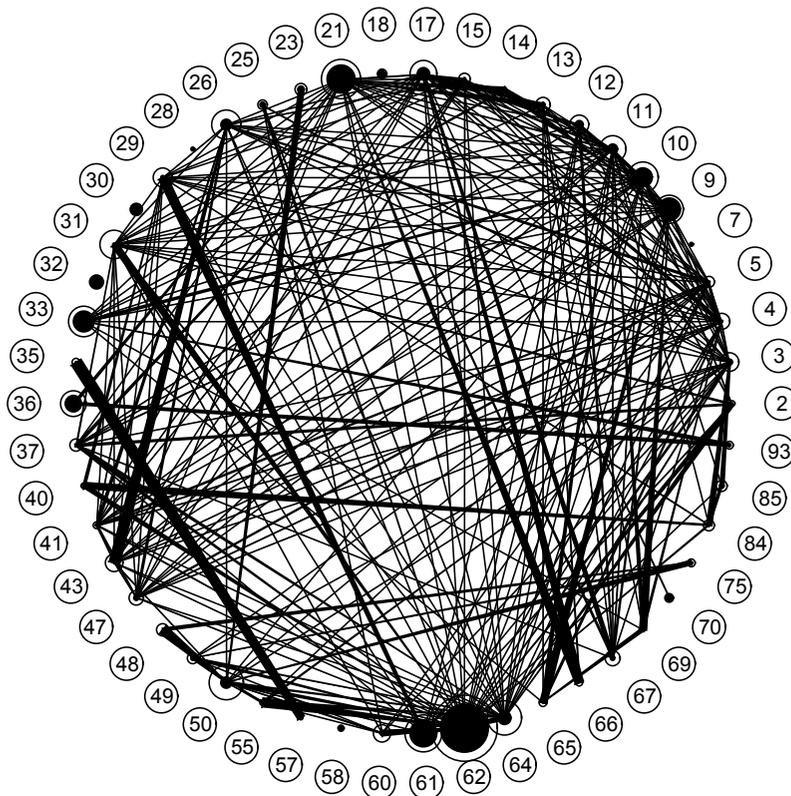
Fig. 3. Quantitative parasitoid overlap graph for the leaf-miner–parasitoid community. The numbered vertices represent leaf miner species, and their size is proportional to the abundance of parasitoids emerging from each host. The extent to which a vertex is shaded in black indicates the importance of the host as a source of its own parasitoids. Lines between hosts indicate shared parasitoids, with the width of the link at each species representing the potential influence of the other species as a source of parasitoids.

would lead to the discovery of further links, but not to a substantial increase that would alter our conclusion that this is a relatively poorly connected community.

Second we can explore the potential for indirect effects. This increases with connectivity, C, but is also influenced by the precise architecture of the food web. The web in Fig. 1 consists of eight disconnected subwebs, though of the 134 species of hosts and parasitoids fully 118 are in one subweb, the other subwebs consist either of single pairs of hosts and parasitoids (five examples) or of groups of three species (two examples). Consider all pairs of hosts in the web, of which there are $H(H-1)/2 = 1225$. Now ask if a connection can be traced between each member of a pair through intermediate hosts and parasitoids. Then classify the pair by the number of intermediate parasitoids in the shortest link. Let A_i be the fraction of pairs whose shortest connecting path contains i parasitoids, and define $A_\emptyset$ as the fraction of pairs that have no connections at all because they are in separate compartments

(unconnected subwebs). For the Belize web: $A_1 = 0.21$; $A_2 = 0.34$; $A_3 = 0.13$; $A_4 = 0.006$ and $A_\emptyset = 0.30$. Thus despite the relatively low connectance, the vast majority of the hosts in the main subweb are linked through either one (30%) or two (48%) intermediate parasitoids. This suggests a considerable potential for indirect effects to propagate through the web.

There are other statistics and tests for structuring that can be carried out on the web, but its other main function is to generate hypotheses about indirect effects that can then be tested in the field, and it is to this we turn in the next section.

Testing for apparent competition in a quantitative food web

In order to look more closely at the potential for apparent competition occurring in a quantitative food web, quantitative parasitoid overlap graphs can be constructed (Müller *et al.* 1999). These
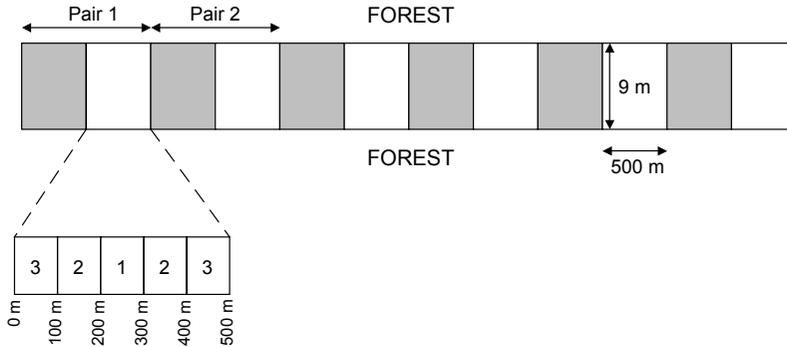
Fig. 4. Spatial arrangement of the six pairs of treatment and control plots for the manipulative experiment testing for apparent competition in a quantitative food web. Treatment plots are shaded and control plots unshaded. The plots were situated along a track, surrounded on either side by forest. For sampling purposes each plot was subdivided into five sections each 100 m in length, which were classified as (1) central, (2) near-central and (3) marginal.

show the extent to which hosts are likely to be dynamically linked by shared parasitoids. Define d_{ij} as the probability that a parasitoid attacking species i developed on species j (where j may be the same species as i). We calculate d_{ij} as

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

where α_{ik} is the strength of the link between host i and parasitoid k. Implicit in this calculation is the assumption that parasitoids of one species show no host races or spatial segregation within the study site. The quantitative parasitoid overlap graph for the Belize leaf-miner–parasitoid community is shown in Fig. 3 which reveals that most leaf miners share parasitoids with at least one other leaf miner species. The probability that two leaf miner species share parasitoids, in other words that their d_{ij} is non-zero, is strongly influenced by the abundance of species j. Therefore most indirect interactions are likely to be asymmetric with the common species having a greater effect on the rare species than vice versa.

Quantitative food webs and quantitative overlap graphs only reveal a snapshot in time of a community or assemblage. In order to test whether dynamic interactions like apparent competition are occurring we have to carry out manipulation experiments. Using the quantitative overlap graph for the Belize leaf-miner community, we identified two common leaf

miner species, a fly and a beetle, that had the potential to interact with several other species through apparent competition. These two species, a monophagous dipteran, *Calycomyza* sp. 8 (Diptera: Agromyzidae), and an oligophagous coleopteran, *Pentispa fairmairei* (Coleoptera: Chrysomelidae), both attacked the same host plant, the vine *Lepidaploa tortuosa* (Asteraceae). We eliminated both focal species from the community by removing *L. tortuosa* in six replicate treatment plots in a 54 000 m^2 study site along the length of a track through the forest (for details *see* Morris *et al.* 2004). The treatment plots were paired with six control plots (Fig. 4), in which we removed a similar amount of vegetation from plants that were not attacked by leaf miners. The manipulation was repeated 6 months later to prevent re-growth of the host plant in the treatment plots, which might have allowed the manipulated herbivores to re-invade the experimental plots, and the consequences of the manipulation assessed after 10–12 months (approximately 5–6 leaf miner generations later).

Based on apparent competition theory, we predicted that the removal of these species would lead to a reduction in the numbers of the parasitoid species that attacked them, and that this would in its turn increase the abundance of those hosts in the web dynamically linked to the removal species. Both *Calycomyza* sp. 8 and *Pentispa fairmairei* share parasitoids with many leaf miner hosts. We focus on twelve common dipteran miners (all Agromyzidae) that
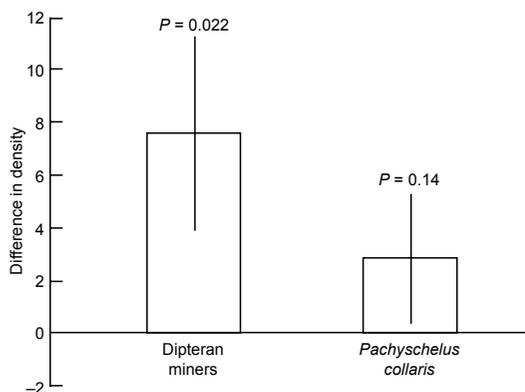
Fig. 5. Effect of species removal on leaf miner abundances one year after the manipulation. Estimated effects with standard errors are shown for the two response groups expressed as difference in density of leaf miners per plot caused by treatment, controlling for mean effects of plot and species. The null hypothesis is no change.

are dynamically linked to *Calycomyza* sp. 8, and one beetle miner, *Pachyschelus collaris* (Coleoptera: Buprestidae) that is dynamically linked to *Pentispa fairmairei*. Detailed results and analysis can be found in Morris *et al*. 2004. Here we show the results for the comparison of the abundance of the two classes of host in treatment and control sites.

In both cases the abundance of miners was higher in treatment compared with control sites (Fig. 5). For the dipteran miners the result was significant ($F_{1,48} = 4.24$, $P = 0.022$) while for the beetle the trend was not significant ($F_{1,5} = 1.39$, $P = 0.14$). Parasitism of the leaf miners was high over this period, averaging 51% for the flies and 88% for the beetle.

The response of the dipteran leaf miners to the manipulation provides strong support for our predictions from apparent competition theory, while that of the coleopteran is weaker but consistent (alternative explanations are discussed but considered unlikely by Morris *et al*. 2004). We believe these results are the first experimental demonstration of long-term apparent competition in a natural community of herbivorous insects and they support suggestions that interactions mediated by shared natural enemies may be a significant factor in structuring natural communities.

Incorporating spatial scale into quantitative food webs

All food webs inevitably summarise information collected over a particular spatial scale and a particular time scale, and although ecologists have been encouraged to document the spatial and temporal scales at which they have made their observations (Cohen *et al*. 1993), this is not always done. For direct interactions (herbivory or predation) we can observe whether two species interact. For indirect interactions, things are less straightforward: species that appear from food webs to be linked indirectly may in reality be isolated in time or in space. For example, if two hosts share a common parasitoid, but occur on spatially isolated host plants that rarely grow in close proximity (taking into account the mobility of the parasitoid), the opportunities for apparent competition between these herbivores may be greatly overestimated if the food web data are used uncritically. The extent to which food webs accurately reflect dynamic interactions structuring communities will thus depend on the appropriateness of the scale over which trophic interactions have been recorded.

So far, the scale at which our quantitative food web data have been collected has been determined as much by practical considerations as by consideration of the spatial scale over which indirect effects are likely to propagate. These considerations suggest some straightforward modifications of the methods used for gathering quantitative food web data to allow the webs to be interpreted in a spatial context. This might be achieved simply by recording the spatial location of individuals and interactions, and arranging the sampling protocol in such a way that spatial heterogeneity within plots is not confounded with temporal changes in the community (as is the case if, for example, a quantitative sample is taken along a single transect or within a single quadrat at each sampling interval). We believe that such a modification could be easily incorporated into sampling regimes, and whilst this would inevitably increase the necessary work, the resulting data would open the way for a wide range of spatially explicit analyses of direct and indirect interactions.

The Belize apparent competition experiment: a spatial analysis

Experiments to test hypotheses about apparent competition and other indirect interactions must be carried out at an appropriate spatial scale. Experimental plots should be large enough to ensure that the local populations of species in adjacent plots are not mixing completely, whilst allowing a certain amount of immigration and emigration to play a realistic role in within-plot interactions. In reality there is always likely to be a trade-off here between maximising treatment effects, and employing an experimental design that is logistically feasible. Although the initial analysis of our apparent competition experiment was not spatially explicit, we can say something about spatial effects because each control and treatment site was a 500 m linear stretch of "gap vegetation" growing along a track, which we divided into 100 m sections for sampling.

We used these data to investigate whether there is an edge effect for each plot, predicting that individuals nearer to the margins of treatment plots will be less affected by the manipulation than those in the centre. To do this we classified the 100 m sections as (1) central, (2) near-central — the two 100 m sections either side of the central section, and (3) marginal — the two 100 m sections at the edges of the plot (Fig. 4). Six species of dipteran that shared parasitoids with *Calycomyza* sp. 8 were common enough for us to use in this analysis.

There were significantly more leaf miners in the near-central parts of treatment plots compared with the controls (average increase of miners per plot: 7.58 ± 4.57, $p = 0.05$), and there was a trend for the same response in the central areas (2.48 ± 2.18, $p = 0.13$ — note that the central area is smaller than the other two and hence the statistical power to detect differences is reduced). In the marginal areas there was a non-significant decrease in leaf-miner density (-1.84 ± 2.23, $p = 0.20$). These results, admittedly rather crude, suggest that manipulations at spatial scales of more than 100 m will be required to study apparent competition at least in this system. This is consistent with the results of our manipulative field experiment that provided evidence of apparent competition using plots of 500 m in length.

We hypothesise that this scale may reflect the typical movement patterns of the parasitoids that we believe mediate the indirect effects.

Apparent competition kernels

For sessile organisms like plants, competition is expected to be most intense when individuals are close together, and to decline with distance. Competition kernels describe how the strength of competition experienced by an individual depends on its number of neighbours and their distance, and possibly on other factors such as species identity and relative size (Law *et al.* 2001, Purves & Law 2002). An understanding of competition kernels is extremely valuable allowing, for example, the prediction of ecological succession and the final make up and spatial structuring of the community (Bolker *et al.* 2003). What is the equivalent for phytophagous insects? The majority of phytophagous insects are relatively monophagous and thus can only be influenced by competitors on the same host plant species. The competition kernel will thus be strongly influenced by plant distribution. In a highly diverse environment such as a tropical rainforest, where individuals of the same species may be widely separated, the resulting competition kernel may be very narrow.

Extending the notion of a competition kernel to include apparent competition changes the picture. Insect herbivores that previously had no effect on the kernel because they fed on different host plants (or perhaps were in some other way spatially separated, for example in different forest strata) can now influence its shape. If apparent competition is genuinely an important structuring force in insect communities, then their dynamics and structure are likely to depend critically on the neighbourhood over which apparent competition occurs (Morris & Lewis 2002). This in turn will largely be a function of food web structure and natural enemy mobility. As mentioned earlier in this chapter, at present we have very little information on the mobility of parasitoids and other categories of natural enemy. Quantifying this, and measuring the scale over which indirect interactions can propagate, should be a priority for future work.

Concluding remarks

We have discussed the structuring role of apparent competition in herbivorous insect communities, and explored how a spatial perspective may be introduced. We argue that apparent competition is as likely as traditional competition to produce spatial patterns, and believe that searching for patterns such as mosaic distributions and character displacement caused by shared natural enemies is very worthwhile. Our work up to now on the role of apparent competition in tropical leaf-miner communities has involved the construction of quantitative food webs and a large-scale manipulative experiment, though with a largely non-spatial approach. In this chapter we have considered the importance of spatial scale on the outcome of this experiment and our preliminary analyses indicates the value of explicitly taking this into account.

Ecologists naturally start off investigating simple trophic interactions at single sites in the field. To make their studies more realistic, both spatial processes and great community complexity can be introduced. For obvious logistic reasons, these two dimensions of added realism have tended to be explored independently, at least by experimental ecologists. Studying and especially manipulating spatially extensive communities will be challenging, but the rewards of greater insight into how natural communities are structured are likely to be great.

References

Abrams, P. A. 1987: On classifying interactions between populations. — *Oecologia* 73: 272–281.

Abrams, P. A. & Matsuda, H. 1996: Positive indirect effects between prey species that share predators. — *Ecology* 77: 610–616.

Abrams, P. A., Menge, B. A., Mittelbach, G. G., Spiller, D. A. & Yodzis, P. 1996: The role of indirect effects in food webs. — In: Polis, G. A. & Winemiller, K. O. (eds.), *Foodwebs: integration of patterns and dynamics*: 371–395. Chapman & Hall, New York.

Bolker, B. M., Pacala, S. W. & Neuhauser, C. 2003: Spatial dynamics in model plant communities: what do we really know? — *Am. Nat.* 162: 135–148.

Bonsall, M. B. & Hassell, M. P. 2000: The effects of metapopulation structure on indirect interactions in host-parasitoid assemblages. — *Proc. Roy. Soc. Lond. B* 267: 2207–2212.

Chaneton, E. J. & Bonsall, M. B. 2000: Enemy-mediated apparent competition: empirical patterns and the evidence. — *Oikos* 88: 380–394.

Chesson, P. L. & Case, T J. 1986: Overview: nonequilibrium community theories: chance, variability, history, and coexistence. — In: Diamond, J. & Case, T. J. (eds.), *Community ecology*: 229–239. Harper & Row, New York.

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.

Connell, J. H. 1961a: Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle — *Balanus balanoides*. — *Ecol. Monog.* 31:61–104.

Connell, J. H. 1961b: The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. — *Ecology* 42: 710–723.

Connell, J. H. 1980: Diversity and the coevolution of competitors, or the ghost of competition past. — *Oikos* 35: 131–138.

Connor, E. F. & Simberloff, D. 1979: The assembly of species communities: chance or competition? — *Ecology* 60: 1132–1140.

Dayton, P. K. 1971: Competition, disturbance and community organisation: the provision and subsequent utilization of space in a rocky intertidal community. — *Ecol. Monog.* 41: 137–389.

Denno, R. F., Lewis, D. & Gratton, C. 2005: Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. — *Ann. Zool. Fennici* 42: **00–00. this issue**

Fenchel, T. 1975: Character displacement and coexistence in mud snails (Hydrobiidae). — *Oecologia* 20: 19–32.

Fretwell, S. D. 1977: The regulation of plant communities by food chains exploiting them. — *Persp. Biol. Med.* 20: 169–185.

Fretwell, S. D. 1987: Food-chain dynamics — the central theory of ecology. — *Oikos* 50: 291–301.

Gurevitch, J. 1986: Competition and the local distribution of the grass *Stipa neomexicana*. — *Ecology* 67: 46–57.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960: Community structure, population control, and competition. — *Am. Nat.* 44: 421–425.

Hanna, R., Wilson, L. T., Zalom, F. G. & Flaherty, D. L. 1997: Effects of predation and competition on the population dynamics of *Tetranychus pacificus* on grapevines. — *J. Appl. Ecol.* 34: 878–888.

Hassell, M. P. 2000: *The spatial and temporal dynamics of host–parasitoid interactions*. — Oxford University Press, Oxford.

Haukioja, E. 2005: The role of plant chemistry in regulating phytophagous insect populations. — *Ann. Zool. Fennici* 42: **00–00. this issue**

Hawkins, B. A. 1994: *Pattern and process in host–parasi-*

toid interactions. — Cambridge, Cambridge University Press.

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. — *Annu. Rev. Entomol.* 36: 535–560.

Holt, R. D. 1977: Predation, apparent competition and the structure of prey communities. — *Theor. Pop. Biol.* 12: 197–229.

Holt, R. D. 1984: Spatial heterogeneity, indirect interactions and the coexistence of prey species. — *Am. Nat.* 142: 377–406.

Holt, R. D. & Barfield, M. 2003: Impacts of temporal variation on apparent competition and coexistence in open ecosystems. — *Oikos* 101: 49–58.

Holt, R. D. & Kotler, B. P. 1987: Short-term apparent competition. — *Am. Nat.* 130: 412–430.

Holt, R. D. & Lawton, J. H. 1993: Apparent competition and enemy-free space in insect host–parasitoid communities. — *Am. Nat.* 142: 623–645.

Holt, R. D. & Lawton, J. H. 1994: The ecological consequences of shared natural enemies. — *Annu. Rev. Ecol. Syst.* 25: 495–520.

Holt, R. D., Grover, J. P. & Tilman, D. 1994: Simple rules for interspecific dominance in systems with exploitative and apparent competition. — *Am. Nat.* 144: 741–777.

Hubbell, S. P. 2001: *A unified neutral theory of biogeography*. — Princeton University Press, Princeton, N.J.

Hunter, M. D. & Price, P. W. 1992: Playing chutes and ladders — heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. — *Ecology* 73: 724–732.

Janzen, D. H. 1979: New horizons in the biology of plant defences. — In: Rosenthal, G. A. & Janzen, D. H. (eds.), *Herbivores: their interactions with secondary metabolites*: 331–350. Academic Press New York.

Jeffries, M. J. & Lawton, J. H. 1984: Enemy free space and the structure of ecological communities. — *Biol. J. Linn. Soc.* 23: 269–286.

Karban, R., Hougen-Eitzmann, D. & English-Loeb, G. M. 1994: Predator-mediated apparent competition between two herbivores that feed on grapevines. — *Oecologia* 97: 508–511.

Krivan, V. & Schmitz, O. J. 2004: Trait and density mediated indirect interactions in simple food webs. — *Oikos* 107: 239–250.

Law, R., Purves, D. W., Murrell, D. J. & Dieckman, U. 2001: Causes and effects of small-scale spatial structure in plant populations. — In: Silvertown, J. & Antonovics, J. (eds.), *Integrating ecology and evolution in a spatial context*: 21–44. Blackwell Science, Oxford.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. 2004: The metacommunity concept: a framework for multi-scale community ecology. — *Ecol. Lett.* 7: 601–613.

Lewis, O. T., Memmott, J., LaSalle, J., Lyal, C. H. C., Whitefoord, C. & Godfray, H. C. J. 2002: Structure of a diverse tropical forest insect-parasitoid community. — *J.*

Anim. Ecol. 71: 855–873.

MacArthur, R. H. 1958: Population ecology of some warblers of northeastern coniferous forests. — *Ecology* 39: 599–619.

Memmott, J., Godfray, H. C. J. & Bolton, B. 1993: Predation and parasitism in a tropical herbivore community. — *Ecol. Ent.* 18: 348–352.

Memmott, J., Godfray, H. C. J. & Gauld, I. D. 1994: The structure of a tropical host–parasitoid community. — *J. Anim. Ecol.* 63: 521–540.

Morris, R. J. & Lewis, O. T. 2002: The role of indirect interactions in structuring tropical insect communities. — *Oikos* 97: 308–311.

Morris, R. J., Lewis, O. T. & Godfray, H. C. J. 2004: Experimental evidence for apparent competition in a tropical forest food web. — *Nature* 428: 310–313.

Morris, R. J., Müller, C. B. & Godfray, H. C. J. 2001: Field experiments testing for apparent competition between primary parasitoids mediated by secondary parasitoids. — *J. Anim. Ecol.* 70: 301–309.

Müller, C. B., Adriaanse, I. C. T., Belshaw, R. & Godfray, H. C. J. 1999: The structure of an aphid-parasitoid community. — *J. Anim. Ecol.* 68: 346–370.

Müller, C. B. & Godfray, H. C. J. 1997: Apparent competition between two aphid species. — *J. Anim. Ecol.* 66: 57–64.

Müller, C. B. & Godfray, H. C. J. 1999: Predators and mutualists influence the exclusion of aphid species from natural communities. — *Oecologia* 11: 120–125.

Murdoch, W. W. 1966: Community structure, population control, and competition — a critique. — *Am. Nat.* 100: 219–226.

Novotny, V. 2005: Host specificity and spatial distribution of tropical insect herbivores. — *Ann. Zool. Fennici* 42: **00–00. this issue**

Oksanen, L., Fretwell, S. D., Arruda, J. & Niemelä, P. 1981: Exploitation ecosystems in gradients of primary productivity. — *Am. Nat.* 118: 240–261.

Polis, G. A., Myers, C. A. & Holt, R. D. 1989: The ecology and evolution of intraguild predation — potential competitors that eat each other. — *Annu. Rev. Ecol. Syst.* 20: 297–330.

Polis, G. A. & Winemiller, K. O. 1996: *Food webs: integration of patterns and dynamics*. — Chapman & Hall, New York.

Polis, G. A., Sears, A. L. W., Huxel, G. R., Strong, D. R. & Maron, J. 2000: When is a trophic cascade a trophic cascade? — *TREE* 15: 473–475.

Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N. & Weis, A. E. 1980: Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. — *Annu. Rev. Ecol. Syst.* 11: 41–65.

Purves, D. W. & Law, R. 2002: Experimental derivation of functions relating growth of *Arabidopsis thaliana* to neighbour size and distance. — *J. Anim. Ecol.* 90: 882–894.

Roland, J. & Taylor, P. D. 1997: Insect parasitoid species respond to forest structure at different spatial scales. — *Nature* 386: 710–713.

Rott, A. S. & Godfray, H. C. J. 2000: The structure of a leafminer-parasitoid community. — *J. Anim. Ecol.* 69: 274–289.

Rott, A. S., Müller, C. B. & Godfray, H. C. J. 1998: Indirect population interactions between two aphid species. — *Ecol. Lett.* 1: 99–103.

Schonrogge, K. & Crawley, M. J. 2000: Quantitative webs as a means of assessing the impact of alien insects. — *J. Anim. Ecol.* 69: 841–868.

Settle, W. H. & Wilson, L. T. 1990: Invasion by the variegated leafhopper and biotic interactions: parasitism, competition and apparent competition. — *Ecology* 71: 1461–1470.

Shurin, J. B., Amarasekare, P., Chase, J. M., Holt, R. D., Hoopes, M. F. & Leibold, M. A. 2004: Alternative stable states and regional community structure. — *J. Theor. Biol.* 227: 359–368.

Tilman, D. 1982: *Resource competition and community structure*. — Princeton University Press.

Valladares, G. R., Salvo, A. & Godfray, H. C. J. 2001: Quantitative food webs of dipteran leafminers and their parasitoids in Argentina. — *Ecol. Res.* 16: 925–939.

van Nouhuys, S. 2005: Habitat fragmentation at different trophic levels in insect communities. — *Ann. Zool. Fennici* 42: **00–00. this issue**

van Nouhuys, S. & Hanski. I. 2002: Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. — *J. Anim. Ecol.* 71: 639–650.

Van Rijn, P. C. J., Van Houten, Y. M. & Sabelis, M. W. 2002: How plants benefit from providing food to predators even when it is also edible to herbivores. — *Ecology* 83: 2664–2679.

Werner, E. E. & Peacor, S. D. 2003: A review of trait-mediated indirect interactions in ecological communities. — *Ecology* 84: 1083–1100.

Wiens, J. 1984: On understanding a non-equilibrium world: Myth and reality in community patterns and processes. — In: Strong, D. R., Simberloff, D., Abele, L. G. & Thistle, A. B. (eds.). *Ecological communities: conceptual issues and the evidence*: 439–457. Princeton University Press, Princeton.

Williamson, M. H. 1957: An elementary theory of interspecific competition. — *Nature* 180: 442–425.