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Experimental evidence for apparent competition in a tropical forest food web

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

[1]*NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*
[2]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*

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The herbivorous insects of tropical forests constitute some of the most diverse communities of living organisms[1]**. For this reason it has been difficult to discover the degree to which these communities are structured, and by what processes. Interspecific competition for resources does occur, but its contemporary importance is limited because most pairs of potentially competing insects feed on different host plants**[2]**. An alternative way in which species can interact is through shared natural enemies, a process called apparent competition**[3]**. Despite extensive theoretical discussion there are few field demonstrations of apparent competition, and none in hyper-diverse tropical communities. Here, we experimentally removed two species of herbivore from a community of leaf-mining insects in a tropical forest. We predicted that other species that share natural enemies with the two removed species would experience lower parasitism and have higher population densities in treatment compared with control sites. In both cases (on removal of a dipteran and a coleopteran leaf-miner species) we found significantly lower parasitism, and in one case (removal of the dipteran) we found significantly higher abundance a year after the manipulation. Our results suggest that apparent competition may be important in structuring tropical insect communities.**

Apparent competition is a type of indirect interaction[4,5] that is defined as a negative effect of one species on the population growth rate or abundance of another species, mediated through the action of shared natural enemies. It can occur whether or not the two species compete directly for resources[3]. Because it can produce patterns in communities that resemble those caused by resource competition (hence its name), apparent competition has been invoked widely as a process that might structure assemblages of species in which ordinary competition is not pervasive[6], for example for assemblages of herbivorous insects feeding on a diverse array of host plants[7]. The importance of apparent competition has been demonstrated experimentally in ecosystems such as the marine littoral[8,9] and between vertebrates mediated by pathogens[10], but the evidence from terrestrial invertebrate communities is less clear. Short-term apparent competition (responses within a generation) has been observed in temperate aphid communities[11,12], and long-term apparent competition (operating over more than one generation) has been demonstrated in laboratory systems[13] and has been invoked to explain changes in the abundance of agricultural pests[14]. However, we lack evidence that apparent competition can lead to long-term changes in natural insect communities, and in particular whether it may be important in tropical rainforests, where parasitism and predation can be particularly intense[15] and where levels of insect biodiversity are exceptionally high.

We investigated the role of apparent competition in structuring a community of leaf-mining insects in moist tropical forest in Belize, Central America. Leaf miners are a phylogenetically diverse group whose larvae feed inside the leaf lamina. They suffer severe mortality from a guild of parasitoid wasps that are restricted to leaf miners but which show differing degrees of host specificity[16]. Previously, we constructed a quantitative food web to describe the community and how it was interlinked[17], and found that 93 species of leaf miner were attacked by 84 species of parasitoid wasp (Fig. 1). Quantitative food webs provide an indication of the likely occurrence of interactions involving apparent competition, but as food webs are static, an experimental approach is necessary to confirm its presence. We used the food web to identify leaf-miner species that had the potential to interact strongly with other species through apparent competition.

Of the plants that were host to leaf miners, most were attacked by a single species. *Lepidaploa tortuosa* (Asteraceae), however, was mined by two common species: a fly, *Calycomyza* sp. 8 (Diptera: Agromyzidae), and a beetle, *Pentispa fairmairei* (Coleoptera: Chrysomelidae). We tested a series of hypotheses drawn from apparent competition theory[18]: that removal of the fly would lead to lower parasitism and higher abundance of other dipteran leaf miners with which this species shares parasitoids on different host plants, and that removal of the beetle would have the same effect on another beetle, *Pachyschelus collaris* (Coleoptera: Buprestidae), whose only recorded parasitoid more commonly attacks *P. fairmairei* (Fig. 1). As described in the Methods, in December 2001 we manipulated the abundance of the two focal leaf-miner species by removing *L. tortuosa* in six replicate sites. Each treatment site was paired with a
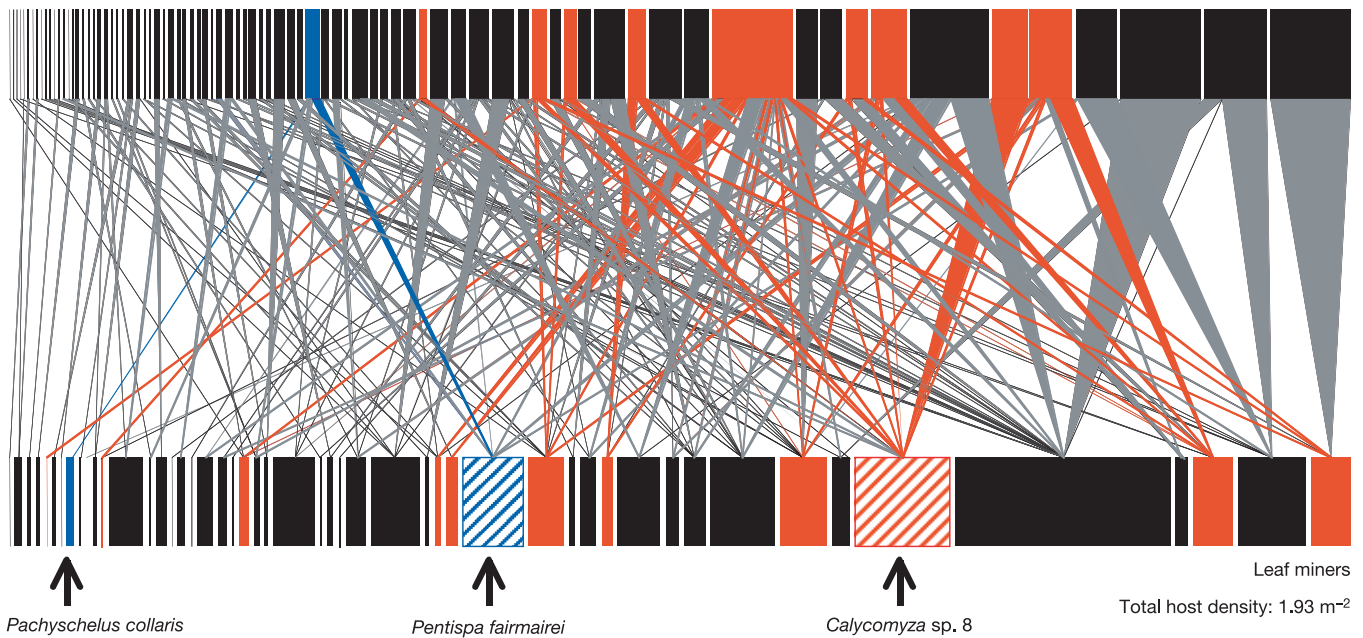
Parasitoids

Scale: hosts ×4.53

Leaf miners

Total host density: 1.93 m^{-2}

Pachyschelus collaris   Pentispa fairmairei   Calycomyza sp. 8

Figure 1 Quantitative food web[17] showing leaf-miner species (bottom bars), parasitoid species (top bars), trophic links among them, and the species predicted to be affected by the manipulation. *Calycomyza* sp. 8 and *P. fairmairei* were directly affected by host plant removal. Dipteran leaf-miner species present during the sampling period and predicted to be affected indirectly via parasitoids shared with *Calycomyza* sp. 8 are shown in red. The beetle *P. collaris* (blue) was also predicted to be affected indirectly by the manipulation through parasitoids that it shares with *P. fairmairei*. Only hosts from which parasitoids were reared are shown in the web.

control site in which a similar volume of foliage was removed, but from plants that were not attacked by leaf miners.

The abundances of the target species and the proportion parasitized were recorded approximately 5–6 leaf-miner generations after the manipulation, between October and December 2002. The dipteran leaf miners that shared parasitoids with *Calycomyza* sp. 8 together experienced 51% mortality due to parasitoid attack in control sites. As predicted, a significantly lower proportion was parasitized in treatment compared with control sites, with the manipulation reducing parasitism by a multiplicative factor of 0.6 (for details see Fig. 2a and Methods). The average density of the dipteran leaf miners was also higher in treatment compared with control sites (Fig. 2b). *Pachyschelus collaris* was at relatively low densities during the sampling period, and experienced 88% mortality due to parasitoid attack in control sites. As predicted, parasitism was lower in treatment compared with control sites, and although the estimated marginal multiplicative reduction was strong (0.1), this was associated with a large standard error (Fig. 2a). *Pachyschelus collaris* was not significantly more abundant in treatment sites, although there was a nonsignificant trend in this direction ($P = 0.14$; Fig. 2b). Thus the response of the dipteran leaf miners to the perturbation provides strong support for our predictions, whereas that of the coleopteran leaf miner is weaker but consistent.

We interpret our results as being due to indirect interactions between hosts, mediated by natural enemies. However, because the only way that we could practically manipulate leaf-miner densities was by removing the host plant, *L. tortuosa*, there is the possibility that indirect interactions between the plant and other herbivores might have influenced our results. Although we cannot formally exclude this (and such a result in itself would be interesting) we think it is unlikely. The plant constituted less than 0.01% of the biomass in the site and the manipulation caused minimal alteration to vegetation structure. We have no evidence that this plant provides important resources or is particularly attractive to parasitoids, and
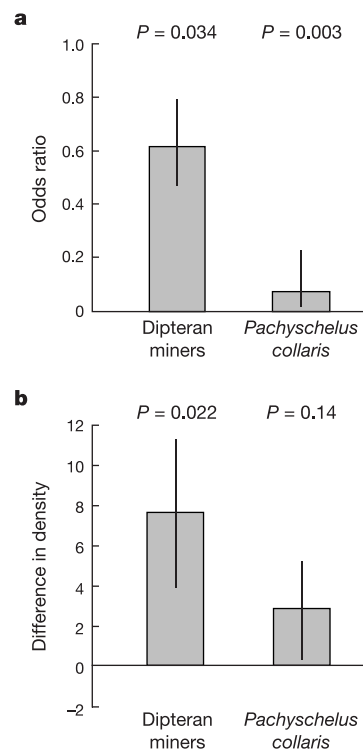

Figure 2 Effect of species removal on parasitism (**a**) and species abundances (**b**) 1 year after the manipulation. Differences in parasitism are expressed as odds ratios, the multiplicative effect of treatment, controlling for mean effects of plot and species. The null hypothesis is that the odds ratio equals one. Differences in abundance are expressed as the difference in density of leaf miners per plot caused by treatment, controlling for mean effects of plot and species. The null hypothesis is that there is no difference. Estimated effects with standard errors are shown for the two response groups. The probability associated with the test of the hypothesis that species removal will lead to lower parasitism and higher abundance is given above the histograms.

that this could explain why its absence reduces parasitism.

To our knowledge our results are the first demonstration of long-term apparent competition in natural communities of herbivorous insects, and they are also unusual in attempting to manipulate insect communities in the tropics. They support suggestions that inter-actions mediated by shared natural enemies may be a significant factor in structuring natural communities. Simple competition theory predicts that no two competitors can coexist on identical resources, and that competition can cause regularities along resource axes[19]. The equivalent apparent competition theory predicts that a shared natural enemy will drive all but one of its prey or hosts to extinction (leading to what has been called dynamic monophagy[7]), and that species can be distributed regularly over "natural-enemy space"[20]. There is a large amount of literature investigating theoretically and experimentally the biological processes that permit competitors to coexist, but the equivalent body of work on the coexistence of apparent competitors is smaller and includes few experimental tests[18,21–23]. Part of the reason for this is that, compared with competitive systems, the dynamic interactions between predators and prey, hosts and parasitoids, and so on, are much more frequently oscillatory and have a greater tendency to be unstable, making their analysis much harder[24]. Field manipulations of host–parasitoid systems are also much more difficult than those of herbivore–plant systems. If our results prove to be typical of herbivore communities, then they suggest that the development of this theory, and its associated empirical tests, will be essential to understanding the diversity and structure of insect communities, especially in the species-rich tropics.

Our results also have implications for the study of biological perturbations. It is widely appreciated that introducing or removing a strong competitor or top predator can have major effects that cascade through a community[25]. Much less attention has been paid to indirect effects mediated by natural enemies (but see refs 26, 27). For example, interventions such as selective logging may remove hosts and prey of natural enemies that also attack species feeding on other host plants. Similarly, introducing natural enemies, especially polyphagous species, may dynamically link hitherto weakly coupled parts of the community. This was highlighted recently by one study that constructed a quantitative parasitoid web based on Lepidoptera in an ostensibly pristine Hawaiian ecosystem and found the web to be dominated by polyphagous parasitoid species that had been introduced to control agricultural pests[28]. Interventions such as selective logging and biological control are normally preferable to many of their environmentally more harmful alternatives, but a better understanding of apparent competition and related phenomena is required to ensure that their environmental impact is minimized. □

Methods

Study site

The field site was in moist tropical forest near the London Natural History Museum's Las Cuevas Research Station in the 170,000-ha Chiquibul Forest Reserve, Cayo District, southwest Belize. The forest is of relatively low stature because of periodic disruption by hurricanes. In previous work[17] we characterized the quantitative structure of the community of leaf-mining insects, and their parasitoids, that attack the vegetation growing along the margins of cleared tracks at this site. Our study site was a 6-km stretch of track comprising a band of vegetation 3 m wide on each side of the 3-m wide track. It was divided into 12 plots, each 500 m in length, which were assigned alternately to treatment and control. At this site leaf miners occur at very low abundance in the forest canopy and interior understorey[17] so the plots were likely to have experienced little immigration of leaf miners and parasitoids.

Manipulation

In treatment plots all individuals of the shrubby vine *L. tortuosa* were uprooted and removed in December 2001. Some re-growth occurred (we estimate about 5% of the original biomass) and the plant removal was repeated in May 2002. In control plots the same biomass of plant material was removed from plant species, chosen at random, that were not attacked by leaf miners. We chose this control so that the distribution of host plants with leaf miners was not affected. The manipulation might have had a transient direct effect on parasitoid abundance, but this is very unlikely to have influenced

parasitism rates by the time the data were collected (to minimize any effect we removed the plant at a time of year when its associated leaf miners were at low abundance). *Lepidaploa tortuosa* is host to the monophagous *Calycomyza* sp. 8, an agromyzid leaf miner that shares a group of specialist parasitoids with a series of other dipterans, chiefly in the genus *Calycomyza*, which we predicted would be influenced by its removal. *Lepidaploa tortuosa* is also host to two species of hispine chrysomelid, *P. fairmairei* and *Basiolus lineaticollis*, whose mines cannot be distinguished and are lumped together in the food web in Fig. 1. However, rearing the adults revealed that *B. lineaticollis* was uncommon, its mines constituting 10% of the total. *Pentispa fairmairei* was reared in small numbers from other Asteraceae species in the site, but *L. tortuosa* was its most important host. We predicted that perturbation of *P. fairmairei* would affect *P. collaris*, a buprestid that feeds on the herb *Desmodium canum* and shares all its recorded parasitoids with the former.

Sampling

The abundances and proportion parasitized of the target leaf-miner species were recorded between October and December 2002. To sample the site, each plot was divided into ten subplots, and then two subplots per plot (chosen randomly) were searched for leaf miners up to a height of 2 m, every 10–14 days until the whole site had been surveyed. Leaf miners were collected and reared in the laboratory to assess current population abundances and proportion parasitized[17,29]. We checked that the manipulation had reduced the densities of *Calycomyza* sp. 8 and *P. fairmairei* by comparing the densities of all mines (both occupied and unoccupied) in control and treatment sites. For *Calycomyza* sp. 8 the effect of the manipulation was strongly significant ($F_{1,5} = 14.10$, $P = 0.0061$; log-linear generalized linear model adjusted for over-dispersion, one-tailed significance of treatment controlling for block) whereas for *P. fairmairei* the difference was more marginal ($F_{1,5} = 3.99$, $P = 0.05$; same statistical methods) because this species has alternative host plants.

Data analysis

Of the dipteran leaf-miner species that shared parasitoids with *Calycomyza* sp. 8, 12 were sufficiently common to contribute to a test of the abundance hypothesis; eight of these suffered parasitism in both treatment and control plots and thus could contribute to a test of the parasitism hypothesis. Ten of these dipteran species are highlighted in Fig. 1; a further two species were included in the analysis because additional data revealed that they also share parasitoids with *Calycomyza* sp. 8. Data were analysed using generalized linear modelling techniques implemented in the statistical package *R* (http://www.r-project.org/). For parasitism we used logistic regression, using the residual deviance to adjust standard errors if over-dispersion was present; the analysis of abundance assumed normally distributed errors. The effect of the treatment was assessed by adding it as a factor to a model already containing fixed plot effects and, in the case of the dipteran leaf miners, a fixed species factor. The test thus used a one-tailed F or χ^2 statistic depending on the type of regression and presence of over-dispersion. The effect of treatment on the proportion of leaf miners parasitized is illustrated as the estimated marginal multiplicative odds factor, and on abundance as the marginal increase in density. For the *Calycomyza* sp. 8 manipulation, the log odds effect of treatment on parasitism was -0.48 (standard error $= 0.26$, $F_{1,48} = 3.50$, $P = 0.034$) and the marginal effect on abundance was 7.56 (standard error $= 3.67$, $F_{1,48} = 4.24$, $P = 0.022$). The equivalent figures for the *P. fairmairei* manipulation are a log odds of -2.63 (standard error $= 1.19$, $\chi_1^2 = 7.37$, $P = 0.003$) and a marginal effect on abundance of 2.83 (standard error $= 2.4$, $F_{1,5} = 1.39$, $P = 0.14$).

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Ban on triazine herbicides likely to reduce but not negate relative benefits of GMHT maize cropping

J. N. Perry[1]**, L. G. Firbank**[2]**, G. T. Champion**[3]**, S. J. Clark**[1]**, M. S. Heard**[4]**, M. J. May**[3]**, C. Hawes**[5]**, G. R. Squire**[5]**, P. Rothery**[4]**, I. P. Woiwod**[1] **& J. D. Pidgeon**[3]

[1]*Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK*
[2]*NERC Centre for Ecology and Hydrology, Lancaster, Cumbria LA1 4AP, UK*
[3]*Broom's Barn Research Station, Higham, Bury St Edmunds, Suffolk IP28 6NP, UK*
[4]*NERC Centre for Ecology and Hydrology, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK*
[5]*Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK*

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The UK Farm-Scale Evaluations (FSE) compared the effects on biodiversity of management of genetically modified herbicide-tolerant (GMHT) spring-sown crops with conventional crop management[1]**. The FSE reported larger weed abundance under GMHT management for fodder maize**[2]**, one of three crops studied. Increased seed production may be important for the long-term persistence of these arable weeds and may benefit invertebrates, small mammals and seed-eating birds**[1]**. In three-quarters of FSE maize fields, growers used atrazine on the conventionally managed half, reflecting contemporary commercial practice**[3]**. Withdrawal of the triazine herbicides atrazine, simazine and cyanazine from approved lists of EU chemicals**[4] **could therefore reduce or even reverse the reported benefits of**

GMHT maize[1,2,5]**. Here we analyse effects of applications of triazine herbicides in conventional maize regimes on key indicators**[6]**, using FSE data. Weed abundances were decreased greatly relative to all other regimes whenever atrazine was applied before weeds emerged. Here, we forecast weed abundances in post-triazine herbicide regimes**[7,8]**. We predict weed abundances under future conventional herbicide management to be considerably larger than that for atrazine used before weeds emerged, but still smaller than for the four FSE sites analysed that used only non-triazine herbicides. Our overall conclusion is that the comparative benefits for arable biodiversity of GMHT maize cropping would be reduced, but not eliminated, by the withdrawal of triazines from conventional maize cropping.**

Herbicide usage for FSE fodder maize[9] is shown in Table 1. We studied the response of five key vegetation indicators[2,5,6] for total weeds, total monocotyledonous weeds (monocots) and total dicotyledonous weeds (dicots) to combinations of herbicide use (Table 2). We found the following consistent trends, exemplified in Fig. 1. Weed abundances were decreased greatly compared to any other regime, whenever atrazine was applied before weeds emerged (pre-emergence[9], see Methods) on conventional crops. For the other conventional regimes, weed abundance for the few sites that were treated only with non-triazines was consistently slightly greater than those for the triazines. With this exception, weed abundance in fields that were treated conventionally (excluding those where atrazine was used pre-emergence) appeared similar. Weed abundance under GMHT management was usually greater than that for atrazine applied post-emergence or for the other triazines applied pre-emergence.

These trends suggested three independent contrasts, tested formally in Table 3. The first comparison is within the three conventional treatment combinations (in which atrazine was applied post-emergence, $A\bar{E}$; other triazines were applied pre-emergence, $\bar{A}E$; or non-triazines alone were applied post-emergence, $\bar{A}\bar{E}$), that is, excluding those where atrazine was used as a pre-emergence
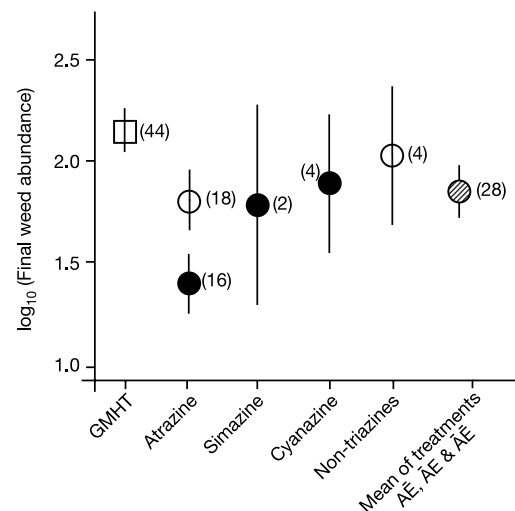

Figure 1 Mean abundance of total pre-harvest weeds and herbicide use. Consistent treatment effects from Table 2, illustrated here by mean abundance of total pre-harvest weeds in FSE fodder-maize per GMHT (square symbol) or conventional (round symbols) half-fields, and treated either with pre-emergence herbicide plus possible post-emergence application(s) (filled symbols, E) or with post-emergence herbicide only (open symbols, $\bar{E}$). Hatched symbol represents the mean of the three conventional regimes $A\bar{E}$, $\bar{A}E$ and $\bar{A}\bar{E}$: that is, all those other than atrazine applied pre-emergence. Numbers in brackets denote N, the number of half-fields. Bar represents 95% confidence interval for each mean.