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STABLE COEXISTENCE IN INSECT COMMUNITIES DUE TO DENSITY- AND TRAIT-MEDIATED INDIRECT EFFECTS

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Abstract. Density-mediated and trait-mediated indirect interactions between species may have important roles in structuring ecological communities. Here we dissect their contributions to community stability in a model herbivore–natural enemy interaction consisting of two aphid species (*Acyrthosiphon pisum* and *Megoura viciae*) and a specialist parasitoid (*Aphidius ervi*) that attacks only one of the aphids (*A. pisum*). In replicated cage experiments, we found that the two aphid species alone were unable to coexist, with *A. pisum* competitively excluding *M. viciae*. We also found that the simple host–parasitoid interaction between *A. pisum* and the parasitoid was unstable. However, the three-species community persisted for at least 50 weeks. We constructed a series of models to explain the stability of the full community and conclude that it is due to a combination of density-mediated and trait-mediated indirect interactions. Parasitoid attack on the susceptible host reduces the interspecific competition experienced by the non-host (a density-mediated effect), and the presence of the non-host reduces the searching efficiency of the parasitoid (a trait-mediated effect).

Key words: aphid; coexistence; community; indirect interaction; interference; microcosm; model; parasitoid; structure; trait mediated.

<div style="writing-mode: vertical">SPECIAL FEATURE</div>

INTRODUCTION

In view of the manifest complexity of ecological communities it is paradoxical that some of the simplest models of ecological interactions suggest species exclusion rather than coexistence as their typical outcome. For example, if two nonidentical species compete for the same resource, then the one that is able to persist at the lowest density excludes the other (Tilman 1977). For predator–prey interactions, the Lotka-Volterra model, which assumes a linear functional response and no developmental time lags, produces neutral cycles (Lotka 1925, Volterra 1926), and if these biologically unrealistic assumptions are relaxed, then the system is normally unstable with diverging oscillations leading to the extinction of predator or prey (Nicholson and Bailey 1935).

A significant part of population biology has been concerned with adding realism to these simple models to try to understand coexistence (Chesson 2000, Hassell 2000, Amarasekare 2003). One obvious line of research is to explore what happens when competition and predation act simultaneously, as is typical in natural systems (Gurevitch et al. 2000, Chase et al. 2002, Haag et al. 2004). Chase et al. (2002) recently reviewed this field and concluded that, depending on how the two processes interact, the effects on coexistence may be positive, negative, or absent. Coexistence is most

likely to occur when there is a trade-off between competitive ability and susceptibility to predation, and when the effects of predation are positively density-dependent and disproportionately affect the competitively superior species when it increases in density. This mechanism has been demonstrated or can be invoked to explain the coexistence of competing plants (Pacala and Crawley 1992, Proulx and Mazumder 1998), *Drosophila* species (Carton and Kitano 1981, Kraaijeveld and Godfray 1997), intertidal invertebrates (Paine 1966, Menge and Sutherland 1976), and rotifers (Lapesa et al. 2002). Coexistence is also more likely when the predator is a generalist that switches to feed on the currently most available prey, and whose dynamics are thus weakly coupled with individual prey species (Abrams and Matsuda 1996, Bonsall and Hassell 1999, van Baalen et al. 2001).

Communities of herbivorous insects are complex and their structure is influenced both by competition for resources and by the action of natural enemies (Hudson and Stiling 1997, Müller and Godfray 1999*b*, Morris et al. 2004). Parasitoids are an important class of natural enemies whose population dynamics have been intensely studied because of their importance in the biological control of pests, but also because the relatively simple relationship between attack and recruitment to the next generation makes them valuable model systems in ecology (Hassell 2000). One way in which parasitoids can influence community structure is when they attack more than one species of host, which then become dynamically linked even if they feed on completely different resources, a phenomenon called ap-

parent competition (Holt 1977). Here we are concerned with competing herbivores, only one of which is attacked by a parasitoid. This is a relatively common occurrence, as many species of parasitoids have a very narrow host range. In this system too, the dynamics of the two competitors and the parasitoid can be tightly coupled.

Such a system can also be considered in terms of the theory of indirect interactions (Kerfoot and Sih 1987, Wootton 1993, Abrams 1995, Werner and Peacor 2003). Although the two competitors may show direct interference competition, very commonly, they only influence each other indirectly through their effects on the density of the shared limiting resource. The non-host and the parasitoid also interact indirectly, in this case, mediated through the densities of both the susceptible host and the shared resource. These are examples of density-mediated indirect interactions (DMII; Abrams 1995), which are transmitted purely through trophic interactions affecting population densities. Trait-mediated indirect interactions (TMII) occur when one species affects the dynamics of another through causing a change in the behavior (or other trait) of a third species (Wootton 1993, Abrams 1995). For example, the presence of a top predator may change the behaviour of an intermediate predator to the advantage of its prey; a TMII then exists between the first and third trophic levels. In recent years, an increasing number of examples of TMIIs have been identified (Werner and Peacor 2003, Schmitz et al. 2004). They have also been hypothesized to be significant in insect herbivore communities, including communities of aphids and their natural enemies (Müller and Godfray 1999a, Vos et al. 2001, Nelson et al. 2004).

Here we report experiments designed to understand the interaction between two species of aphid that co-exist on the same food plant in an old-field community that we have been studying for the last 10 years (Müller et al. 1999). The pea aphid (*Acyrthosiphon pisum* Harris) and the vetch aphid (*Megoura viciae* Buckton) are found together feeding on *Lathyrus pratensis* L. and *Vicia* spp. *M. viciae* is only rarely attacked by parasitoids, while the braconid *Aphidius ervi* (Haliday) is a common natural enemy of *A. pisum*. In replicated laboratory cage experiments, we show that *A. pisum* can competitively exclude *M. viciae* in the absence of the parasitoid and that the two-species interaction between *A. pisum* and *A. ervi* is unstable. But if all three species are introduced together, the community is able to persist. We explore the mechanisms underlying this using a simple model that suggests that direct interactions and DMIIs alone cannot explain the persistence. However, we observed that the presence of *M. viciae* influenced the searching behavior of the parasitoid, a TMII. Incorporating this in the model allowed the system to persist, and we hypothesize that both types of indirect interaction are in operation in this community.

METHODS

Study organisms

Megoura viciae and *Acyrthosiphon pisum* are common aphids that reproduce parthenogenetically in over-lapping generations in spring and summer. At 20°C, the generation time of these aphids is ~10 days. At our study site, they both feed on *Lathyrus pratensis* and *Vicia* spp., and while *A. pisum* is found on other Fabaceae, these populations appear to be genetically distinct. *A. pisum* is attacked by a wide range of predators, parasitoids, and pathogens. In contrast, we have rarely found *M. viciae* mummified by parasitoids or fungal pathogens in the field, and it appears not to be susceptible to the aphid fungal pathogens with the broadest host range (*Pandora neoaphidis* and *Zoophthera phalloides*) when exposed to them in the laboratory (J. Ferrari, *unpublished data*). Dixon (1958) reported it to be poisonous to some generalist predators. *Aphidius ervi* (Braconidae, Aphidiinae) attacks several species of aphid, although at our study site, *A. pisum* is by far its most common host (Müller et al. 1999). It is a solitary species that lays eggs in early-instar aphids. After a period of arrested development, during which the aphid continues to feed and grow, the parasitoid larva consumes and kills its host, and then spins a cocoon inside the mummified skin of the aphid. At 20°C, the adult male parasitoids emerge 12 days and females emerge 14 days after oviposition.

Experimental design

The population dynamics of three combinations of aphids and parasitoid were compared in replicated population cages in an initial experiment lasting 19 weeks. The three communities were (1) competitors only (*M. viciae* and *A. pisum*); (2) host–parasitoid only (*A. pisum* and *A. ervi*), and (3) all three species (*M. viciae*, *A. pisum*, and *A. ervi*). Each combination was replicated 10 times, and the populations maintained in 30 × 30 × 30 cm Perspex cages, each containing eight pots with four *Vicia faba* variety "The Sutton" seedlings each, in controlled-environment rooms at 20°C and 75% humidity. To maintain the populations, twice a week, the two pots containing the oldest plants were replaced with new ones containing young, two-week old seedlings. Whenever plants were replaced, all the aphids and mummies (parasitized aphids) present on the old plants were transferred to the new ones. The experiments were initiated by the introduction of five wing-less adults of the appropriate aphid species. For both *M. viciae* and *A. pisum*, all individuals used were members of the same clones, which had originally been collected from *Lathyrus pratensis* at Silwood Park in the south of England. The parasitoid populations were established by introducing two young mated females two weeks after the introduction of the aphids, and then a further two similar females one week later (this two-stage introduction allowed for an immediate establish-
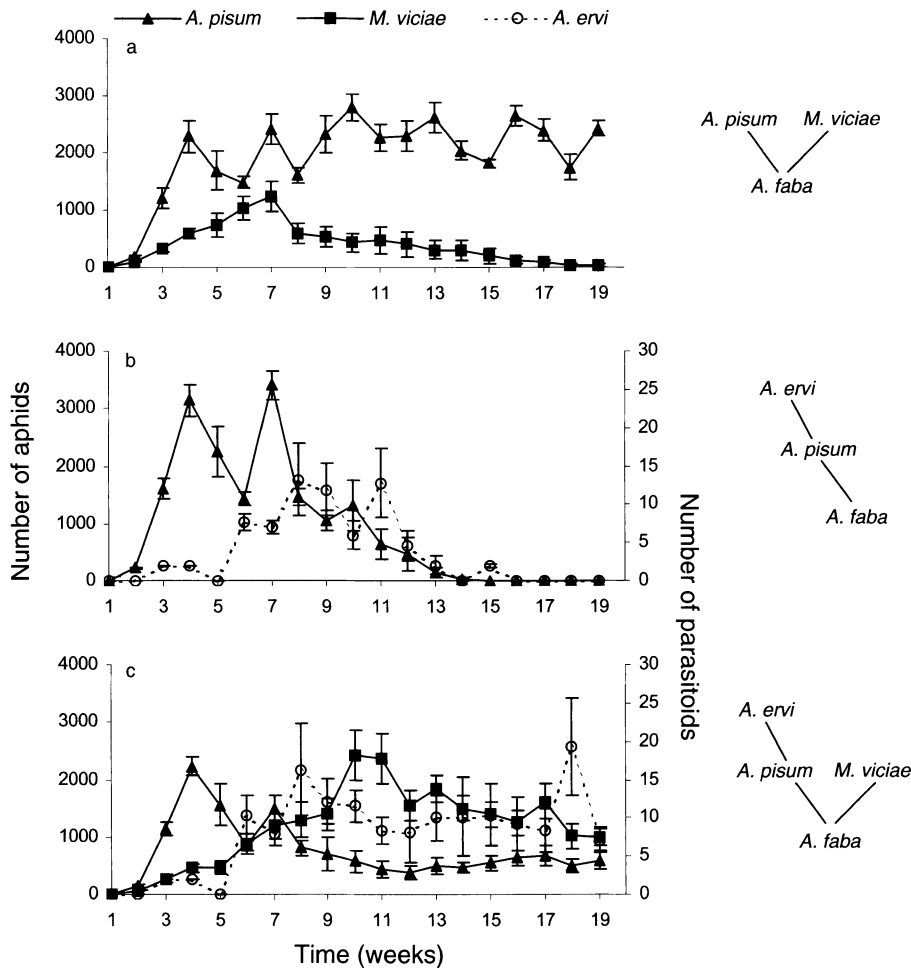
SPECIAL FEATURE

FIG. 1. Population sizes (means ± SE) in the three experimental communities, averaged over replicates, for weeks 1–19. (a) Resource competition between the aphids *Megoura viciae* and *Acyrthosiphon pisum*. Note the exclusion of *M. viciae*. (b) Unstable host–parasitoid dynamics of *A. pisum* and *Aphidius ervi* leading to the extinction of both species. (c) Persisting populations of all three species in the full community.

ment of overlapping generations). Once a week, the number of aphids of each species was counted on four pots (one from each of the four "cohorts" of plants in the cage), and, at the same time, the total number of adult parasitoids was also counted.

At the end of the main 19-week experiment, data collection was suspended, but the cages from the three-species treatment were continued under the same plant rotation regime. Aphid and parasitoid numbers were then estimated again in five of those in weeks 41–50, to obtain information about more long-term dynamics. With generation times of ~10 days for the aphid species and ~14 days for the parasitoid, the 50 weeks of the experiment represent ~35 and ~25 generations, respectively. Although it is difficult to estimate, in the field, these aphids are generally assumed to have <10 generations in the seven months between spring emergence and the production of overwintering eggs in autumn. Our experiment is therefore probably equivalent

to at least three years in the field, in terms of the number of generations.

RESULTS

The results of the three sets of competition cage experiments are shown in Fig. 1. In the first set, the two aphid species were allowed to compete in the absence of parasitoids (Fig. 1a). The densities of both species initially increase, but then, while *A. pisum* numbers remained high and fluctuated around an average of 2081 ± 77 per cage (mean ± SE), the numbers of *M. viciae* steadily declined. At the end of the 19-week experiment, the latter species was extinct in two cages, at very low numbers (<50) in seven more, and declining in the last cage, where there were still 300 individuals present. *A. pisum* thus seems to be able to competitively exclude *M. viciae*.

In the second set of cages, the interaction between *A. pisum* and its parasitoid *A. ervi* was studied (Fig.

1b). Aphid numbers initially increased, followed more slowly by the number of parasitoids (which have a longer generation time). The rise in the number of parasitoids led to a rapid decline in the density of aphids, and in all cages, first the aphid and then the parasitoid became extinct between weeks 10 and 15. Thus, at least in the simple environment of our population cages, a persistent interaction between the host and parasitoid does not seem to be possible.

The two aphid species and the parasitoid were all present together in the third set of cages (Fig. 1c). In one, the parasitoid failed to establish itself, and hence, only nine cages were included in the analyses. The initial increase in aphid numbers is similar to that in the first set of competition cages, but then the presence of the parasitoid prevented A. pisum from reaching the very high densities seen previously, and population numbers in the last 10 weeks of the experiment averaged 641 ± 58 aphids per cage, only 28% of that achieved in the absence of the parasitoid. M. viciae, in contrast, averaged 1624 ± 100 individuals per cage in the last 10 weeks, very much higher than when competing with A. pisum in the absence of A. ervi. Statistical analyses confirm these differences: When treating cumulative M. viciae densities as a derived response variable, there was a significant effect of the presence of parasitoids on this aphid's populations ($F_{1,17} = 31.5$, $P < 0.0001$), and the numbers of M. viciae in week 19 were 24 times greater in the three-species cages than in the competition cages (Wilcoxon rank sum test, $P < 0.001$). The probability that A. pisum by chance always went extinct in the second set of cages and always persisted in the third set is very small (1.9×10^{-6}).

The third set of population cages with all three species present was maintained under the same renewal regime for a further 31 weeks. In all cases, the three species persisted together. The population sizes in five of these cages were again measured between weeks 41 and 50. There was some variation in numbers, but average counts were 484 ± 67 and 1643 ± 112 individuals per cage for A. pisum and M. viciae, respectively.

In all three sets of cages, the A. pisum populations appeared to cycle with a period of three weeks (Fig. 1). This is particularly clear in the competition cages (Fig. 1a). We believe that this was caused by an interaction between aphid dynamics and the plant-renewal regime. When aphid numbers were high, rapid colonization of newly introduced seedlings resulted in reduced plant growth and survival. This, in turn, led to a decrease in the aphid population, allowing better growth and survival of subsequent seedling cohorts. Though related phenomena might occur in the field, the patterns observed here are probably due to our regular resource-renewal regime.

MODEL

To try to understand the mechanisms underlying extinction and coexistence in the population cages, we constructed a series of simple models to explore the interactions between the three species. We based these on the classical Lotka-Volterra competition and predation equations developed for populations with overlapping generations. These are clearly simplified representations of real populations, ignoring, for example, age structure, but nevertheless, we believe they provide a useful first step in analyzing the observed dynamics. The goal of this modeling exercise was not to describe the detailed interactions with a realistic model, but rather to develop heuristic models to test the plausibility of proposed mechanisms that may explain coexistence in the full community. Our strategy was to parameterize models using data from the aphid competition cages and the A. pisum–parasitoid cages, and then to see whether they were sufficient to explain the dynamics of the three-species population cages.

Competition

Consider the standard Lotka-Volterra competition model

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - \alpha_{21} N_1) \qquad (1)$$

where N_i is number of aphid species i per cage ($i = 1$, A. pisum; $i = 2$, M. viciae), and r_i is the intrinsic rate of increase of aphid species i. In this formulation, competition is represented by the α terms, with α_{ii} indicating intraspecific competition (these parameters can also be interpreted as the reciprocal of carrying capacity) and α_{ij} indicating interspecific competition.

To estimate these parameters, we fitted the model to the population trajectories from the aphid-competition cages by minimizing the sum of squares of the deviations. We found it was not possible to obtain estimates of all parameters because the amount of information in the trajectories about intraspecific competition in M. viciae was very low (their dynamics were dominated by competition with A. pisum). Because the aphids are of similar size and feeding habit, we assumed $\alpha_{11} = \alpha_{22}$, which allowed us to estimate $r_1 = 3.22$, $r_2 = 2.82$, $\alpha_{11} = \alpha_{22} = 3.82 \times 10^{-4}$ (i.e., carrying capacity $\approx$ 2600), $\alpha_{12} = 3.70 \times 10^{-4}$ and $\alpha_{21} = 3.97 \times 10^{-4}$. Note the estimates of intra- and interspecific competition are similar, but that M. viciae suffers slightly more than A. pisum. The model with the fitted parameters provides a good description of population trajectories (Fig. 2a).

Host–parasitoid interaction

To describe the interaction between A. pisum (N_1) and its parasitoid (P), we modified the basic Lotka-Volterra predator–prey model by including (1) the effects of intraspecific aphid competition, (2) a type II (saturating) functional response for the parasitoid, and (3) density-dependent parasitoid recruitment;
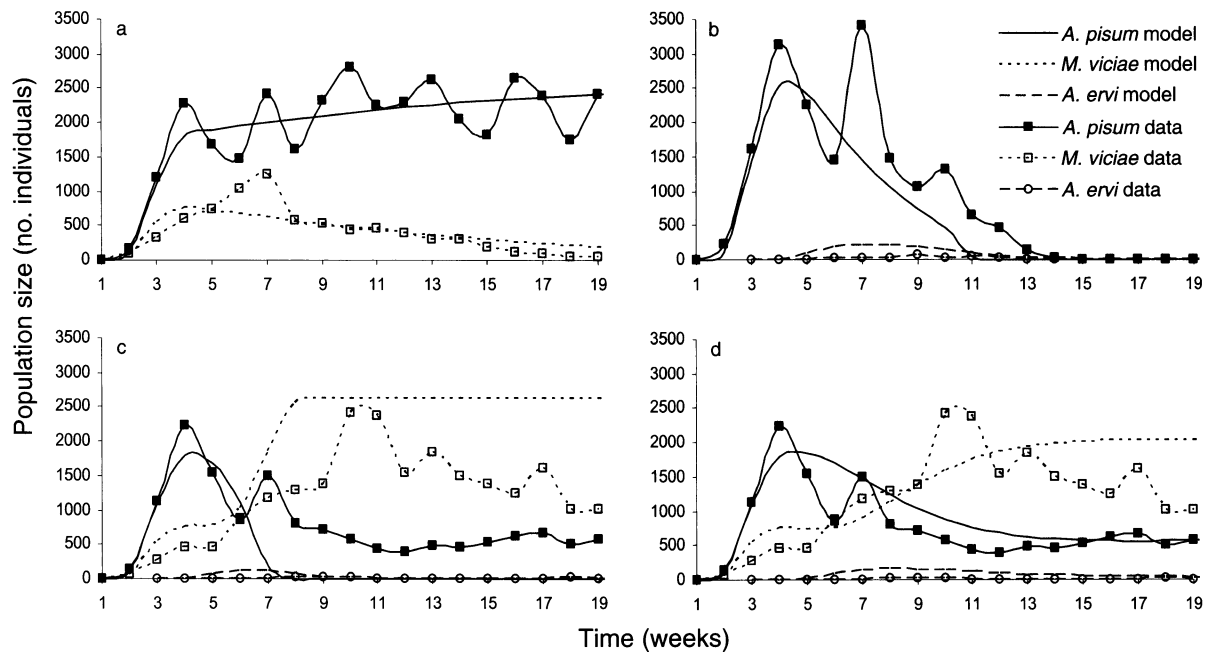
FIG. 2. Fit of models to the observed data for *Acyrthosiphon pisum*, *Megoura viciae*, and *Aphidius ervi* in the (a) competition experiment, (b) host–parasitoid experiment, (c) full-community experiment with simple population model, and (d) full-community experiment with model incorporating an interference effect between *M. viciae* and *A. ervi*.

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1) - N_1 \frac{\alpha_{1P} P}{1 + bN_1}$$

$$\frac{dP}{dt} = N_1 \frac{s\alpha_{1P} P}{1 + bN_1 + cP} - \mu P. \qquad (2)$$

The first term in the prey equation represents population growth and competition modeled in exactly the same way as Eq. 1. The second term represents parasitism with α_{1P} the per capita attack rate of the parasitoid when rare, and b the parameter controlling the reduction in attack rate with increasing host density, which may be interpreted as a handling time. The first term of the parasitoid equation is identical, except that we also include parasitoid sex ratio (s) and an effect of parasitoid density on parasitoid recruitment controlled by the parameter c (Turchin 2003). We included this latter term to represent observed density-dependent mortality of parasitized aphids prior to mummification. We suspect this is caused by parasitized aphids often leaving their feeding site immediately after attack, and then failing to settle because they keep getting disturbed by parasitoids (though while not feeding they can normally avoid superparasitism). Finally, parasitoids die at a density-independent rate of μ.

Using the values for r_1 and α_{11} from the competition cage experiments, and an observed sex ratio of $s = 0.5$, we obtained estimates of the four further parameters in Eq. 2 by again minimizing the squared deviations of the model and data. The estimates were $\alpha_{1P} = 2.81 \times 10^{-1}$, $b = 2.33 \times 10^{-2}$, $c = 1.26$, and $\mu = 6.34 \times 10^{-1}$. The relatively high value of c reflects the

observation that, at high parasitoid densities, aphid mortality due to parasitoid attack is very high, while parasitoid recruitment becomes virtually zero. The fitted model predicts unstable host–parasitoid dynamics similar to those observed in the cages, but in the model, parasitoid densities are sometimes much higher and aphid extinction is more rapid (Fig. 2b).

Three-species interaction

The competition and host–parasitoid interactions described by Eqs. 1 and 2 can be simply combined to produce a model to predict the interactions between all three species:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2) - N_1 \frac{\alpha_{1P} P}{1 + bN_1}$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - \alpha_{21} N_1)$$

$$\frac{dP}{dt} = N_1 \frac{s\alpha_{1P} P}{1 + bN_1 + cP} - \mu P. \qquad (3)$$

The model fails to replicate the observed dynamics (Fig. 2c). *A. pisum* is driven to extinction by its parasitoid, an effect that seems to be accelerated by competition with *M. viciae*. We conclude that something novel is occurring in the three-species interaction that makes it more than a simple combination of the competitive and host–parasitoid interactions.

Observations of parasitoid behavior suggested that *A. ervi* "waste time" when encountering clusters of *M. viciae*. Although *A. ervi* rarely attempts to attack *M.*

viciae, when an encounter occurs, the aphid displays a vigorous anti-predator response that often results in the parasitoid either being kicked off the plant or abandoning the search for hosts in the area. This prompted us to include an effect of *M. viciae* densities in the functional response of the parasitoid:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2) - N_1 \frac{\alpha_{1P} P}{1 + b N_1 + \omega N_2}$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - \alpha_{21} N_1)$$

$$\frac{dP}{dt} = N_1 \frac{s \alpha_{1P} P}{1 + b N_1 + \omega N_2 + cP} - \mu P \qquad (4)$$

where the parameter ω can be interpreted as the time wasted when a parasitoid encounters an unsuitable host (N_2). This is exactly equivalent to "recognition time" in classical diet models from foraging theory (Hughes 1979, Stephens and Krebs 1986), although the mechanism is quite different. Using the parameter estimates from the competition and host–parasitoid models above, we can estimate ω by minimizing the squared deviations of the model and the data for the first 19 weeks as before. The estimated value is $\omega = 4.34 \times 10^{-2}$, which indicates that an encounter with *M. viciae* wastes an amount of time equivalent to 1.8 successful attacks on *A. pisum*. The revised model is plotted with the data in Fig. 2d. All three species are now predicted to coexist, as observed, and the quantitative match to data is reasonably good. The model predicts *A. pisum* and *M. viciae* densities at weeks 41–50 to be 667 and 1915, respectively, which is ~16% more than actually observed (484 and 1643, respectively), but the ratio of the densities of the two species is more accurately predicted.

DISCUSSION

We have shown how indirect effects can combine to stabilize a three-species community, all of whose two-species-component communities are unable to persist. Our community consisted of a superior competitor, which is attacked by a natural enemy that is capable of driving it to extinction. In the three-species community, the natural enemy reduced the growth rate of the superior competitor such that the inferior competitor could persist, a density-mediated indirect interaction (DMII). The natural enemy itself was prevented from overexploiting its hosts by a trait-mediated indirect interaction (TMII): The presence and behavior of the inferior competitor reduces the searching efficiency of the parasitoid.

The particular system we studied consisted of two aphids and a parasitoid that attacked only one of them. At least in the simplified environment of our cage experiments, *A. pisum* outcompeted *M. viciae*, although in our field sites, the two species co-occurred each year. Our experiments show that preferential parasitism of

A. pisum can allow *M. vicae* to escape competitive exclusion. In terms of the simple Lotka-Volterra model, *M. viciae* increased when rare in the absence of predators only if $\alpha_{21} N_1^* < 1$, where the asterisk indicates an equilibrium density. The carrying capacity of *A. pisum* is $N_1^* = 1/\alpha_{11}$ and, hence, *M. viciae* is excluded because *A. pisum* has stronger inter- than intraspecific effects ($\alpha_{21} > \alpha_{11}$), the standard Lotka-Volterra criterion for exclusion. Suppose parasitoid attack reduces *A. pisum* densities to a fraction q of carrying capacity; *M. viciae* invasion is possible if $\alpha_{21} q N_1^* > 1$, which implies $q \alpha_{21} > \alpha_{11}$. Substituting our estimates for the competition coefficient produces $q = 0.96$. Although arguments based on a model as simple as the Lotka-Volterra must be interpreted cautiously, they do suggest that a modest decrease in *A. pisum* densities may be sufficient to promote coexistence.

To what degree do these results apply in the more complex field environment? Preliminary experiments in which the two species were introduced on the same plant in the field showed that *A. pisum* outcompeted *M. vicae*, as in the cage experiments when natural enemies were excluded (F. J. F. van Veen, *unpublished data*). *A. pisum* and *M. viciae* are frequently found feeding on the same host plant individual, but at densities considerably lower than those achieved in the cages. Part of the reason for this is that mature host plants are nutritionally poor in comparison with the rapidly growing seedlings used in the experiment, but in addition, the aphids are subject to a much wider range of natural enemies than the single-parasitoid species in our experiments. However, as mentioned in the *Methods*, *M. viciae* seems unattractive to a wide range of natural enemies, not only parasitoids, but also predators and pathogens. We would expect interference with predators to occur with a similar effect to that of the parasitoids observed in the cages. *M. viciae*'s lethal toxicity to ladybird larvae (Dixon 1958), for example, gives an obvious mechanism for interference with predators, but whether interference with the pathogens occurs is less obvious. Thus, we think it likely that *M. viciae* is protected from competition by its resistance to natural enemies, although it is possible that other mechanisms may also be involved, and *A. pisum* is likely to gain some protection from parasitoids and predators (but probably not pathogens) through the presence of *M. viciae*. In the field, the trait-mediated indirect interactions may also be more complicated because parasitoids can use aphid-induced plant volatiles for long-distance host location (Powell et al. 1998). Thus, although interfering with the searching behavior of the parasitoid once it has arrived on the plant, the presence of *M. viciae* could also have a negative effect on any *A. pisum* on the same plant by attracting parasitoids to it. Indications are, however, that the response of *A. ervi* is specific to volatiles produced through the feeding of host aphids only, although its response to *M. viciae* has not been tested (Powell et al. 1998).

SPECIAL FEATURE

Though the presence of the parasitoid can explain the persistence of the two competitors, it does not necessarily imply that the interaction is stable. Indeed, when we combined the simple competition and predation models, the host–parasitoid interaction was predicted to be unstable. The reason for this is that the parasitoid overexploits its hosts, causing a decline in its own population, followed by further rounds of recovery and overexploitation until an extinction occurs. Clearly this is not what occured in our cage experiments, and observations suggested that the presence of the non-host *M. viciae* interfered with the searching efficiency of the parasitoid. When a parasitoid approaches *M. viciae*, even though it is not a host, the aphid mounts a vigorous kicking response. Perhaps because the aphid existed in much denser aggregations than *A. pisum*, this causes the parasitoid to disperse and otherwise waste time that in *M. viciae*'s absence would be used in attack and oviposition. Individual pea aphids may also find refuges from parasitoid attack in aggregations of *M. viciae*, so reducing the risk of over-exploitation and extinction.

The model provides an indication of the strength of this effect. We can ask what density of pea aphids, $\tilde{N}_1$, will allow the parasitoid population to be able to increase when rare. This is the density that ensures a parasitoid will, on average, produce one female offspring and is equivalent to the host threshold in epidemiology, the density at which the basic epidemiological number, R_0, equals 1. Rearranging Eq. 4, we obtain $\tilde{N}_1 = \mu(1 + \omega N_2)/(a_{1P} - b\mu)$. In the absence of *M. viciae*, the threshold is very low, ~2 aphids per cage (a typical figure for parasitoids, and the reason that R_0 is little used in parasitoid population dynamics). The host threshold rises linearly with *M. viciae* density with slope $\mu\omega/(a_{1P} - b\mu) = 0.10$ so that near the *M. viciae* carrying capacity, a density of >250 aphids per cage is required for *A. ervi* populations to increase. This suggests that *M. viciae* can protect low-density populations of *A. pisum* from parasitoid attack, although, as *A. pisum* is the superior competitor, it will ultimately displace the former and reach a density at which the parasitoid can invade.

There are many other cases where a host is protected from parasitism by a third, non-host species. The best-known examples concern aphids and also other insects that have a mutualistic association with ants: The aphids provide honeydew for the ants and receive protection from at least some natural enemies in return (though specialist parasitoids are frequently ignored by ants [Mackauer and Volkl 1993]). Our study shows that protection from natural enemies can also occur when the third species is a competitor of the host, rather than a mutualist. Optimal diet models have been applied to parasitoid-searching strategies, and these predict that the presence of a non-host species that still requires recognition or handling time can influence host attack rates (Godfray 1994). However, there are no experimental data to support these predictions.

Selective parasitoid attack has been suggested to influence the outcome of competition in at least one case. Ants are attacked by minute parasitoid flies of the family Phoridae that, especially in the New World tropics, can cause significant mortality. Exclusion experiments have demonstrated that the presence or absence of host-specific parasitoids can determine the outcome of competition at bait stations (Feener 1981), and that such interactions may have a major role in structuring ant communities (LeBrun and Feener 2002).

In their recent review of trait-mediated indirect effects, Werner and Peacor (2003) distinguished between the presence of a third species influencing the interaction between (say) a host and parasitoid by (1) altering the parasitoid's behavior (phenotypic plasticity) and by (2) altering the environmental context in which the interaction occurs. They give a series of aquatic examples of the latter; for example, it has been shown that the presence of barnacles changes the background color and texture of intertidal rocks, leading to a reduction in predation of limpets by gulls (Wootton 1993). Our results may fall into this category of TMII; the presence of *M. viciae* altering the environmental conditions in which the parasitoid searches for hosts, although it is also possible that the parasitoid modulates its behavior in the presence of the non-host species. A similar situation exists between some competing plants and vertebrate herbivores (Proulx and Mazumder 1998). Here, herbivory on a palatable, superior competitor can release unpalatable plants from competition, while the presence of the unpalatable plants in an area causes a reduction in grazing to the benefit of the palatable plants.

There is much concern about how the loss of individual species from ecosystems may lead to a series of unpredicted consequent losses (e.g., Levin 1999, Koh et al. 2004). Our study provides an example of such a case. The removal of a competitor (*M. viciae*) would lead one to expect an increase in density of its competitor (and the competitor's natural enemy), but because of the trait-mediated interactions, it destabilizes the whole system.

To conclude, our laboratory experiments and model have shown how competitive and host–predator interactions, and density- and trait-mediated indirect effects, can combine together to influence the persistence of a community module in cage experiments. The challenge now is to explore how these and other effects combine in the much more complex environment in the field.

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SPECIAL FEATURE