COMMUNITY ECOLOGY - ORIGINAL PAPER

Resource competition and shared natural enemies in experimental insect communities

**Thomas S. Jones · H. Charles J. Godfray ·
F. J. Frank van Veen**

Abstract Much theory has been developed to explore how competition for shared resources (exploitation competition) or the presence of shared natural enemies (apparent competition) might structure insect and other communities. It is harder to predict what happens when both processes operate simultaneously. We describe an experiment that attempted to explore how shared natural enemies and resource competition structured a simple experimental insect community. Replicated communities were assembled in population cages consisting of the aphid species *Acyrthosiphon pisum* and *Megoura viciae* either alone or competing for a resource, their shared host plant *Vicia faba*. Each combination was set up with and without the parasitoid *Praon dorsale* which attacked both species of aphid. Population dynamic data show that interspecific resource competition was the dominant process structuring the community. Though juvenile parasitoids could develop successfully inside hosts of both species, they failed to suppress either aphid below their carrying capacities and were unable to persist on one species. We suggest that intense resource competition may reduce the value of individual aphids as hosts for parasitoids such that their population growth rate is less than zero and discuss whether this phenomenon occurs in natural and agricultural communities.

Keywords Aphid · Community structure ·
Food web · Indirect interactions · Microcosm

Communicated by Thomas Hoffmeister.

T. S. Jones · H. C. J. Godfray · F. J. F. van Veen (✉)
NERC Centre for Population Biology and Division of Biology,
Imperial College London, Silwood Park Campus,
Ascot SL5 7PY, UK
e-mail: f.vanveen@imperial.ac.uk

Present Address:
T. S. Jones
Institute of Environmental Sciences, University of Zürich,
Winterthurerstrasse 190, 8057 Zürich, Switzerland

Present Address:
H. C. J. Godfray
Department of Zoology, University of Oxford,
South Parks Road, Oxford OX1 3PS, UK

Introduction

Resource competition is one of the most important processes that determine the persistence and abundance of species in many diverse ecological communities (Gause 1934; Tilman 1977; Begon et al. 1996; Morin 1999). The significance of resource competition for communities of phytophagous insects is less clear with some authors arguing that it is too weak or too intermittent to explain patterns in their distribution and abundance (Hairston et al. 1960; Slobodkin et al. 1967; Lawton and Strong 1981; Strong et al. 1984). Supporting this view is the observation that plants are rarely defoliated by phytophagous insects which thus appear not to be resource limited (Hairston et al. 1960) and the restricted experimental evidence for resource competition between insect herbivores (Lawton and Strong 1981). Also many communities consist of species each specialised on different food plant species where resource competition is impossible. Proponents of the role of resource competition point to the experimental studies that have unequivocally demonstrated its existence in natural systems (Dempster 1963; Denno et al. 1995) and argue that competition may be more subtle than

that leading to gross resource depletion. For example, insects may compete for the least chemically defended plant parts (Janzen 1973), or interact by triggering inducible defences in the plant (Moran and Whitham 1990).

Interactions between prey species mediated by their shared natural enemies can structure ecological communities in a similar way to resource competition (Holt 1977; Sih et al. 1985) and it has been argued that this may be a more important process affecting many phytophagous insect communities (Lawton and Strong 1981; Holt and Lawton 1993; Holt and Lawton 1994; van Veen et al. 2006). When two prey species share a natural enemy they may negatively affect one another via elevated natural enemy numbers, a process that has been called apparent competition to emphasise its similarities with resource competition (Holt and Lawton 1993; Holt et al. 1994). Theory predicts that apparent competition can lead to species being excluded from communities (Holt 1977), and this has been demonstrated in population cage experiments involving simple assemblages of insect species (Bonsall and Hassell 1997; Bonsall and Hassell 1998). Just as theory predicts that in the most simple case two species cannot persist on a single resource, so theory also predicts that two prey species cannot persist when attacked by a common natural enemy. A variety of processes may act to prevent exclusion through apparent competition including the presence of alternative prey species, a preference by the natural enemy for the most common prey species, and the spatial or temporal separation of prey species (Holt and Lawton 1993; Holt et al. 1994).

Natural communities are assemblages of species connected to one another by a complex network of interactions, and the dynamics of a pair of species may be linked via several interaction pathways simultaneously. For example, where prey species share the same food resources as well as common natural enemies, resource and apparent competition may interact to influence community structure (Hanna et al. 1997; Snyder and Ives 2001; Snyder and Ives 2003; Finke and Denno 2004). Simple models predict that the winner in exploitation competition is the species that suppresses the resource to its lowest level at equilibrium—the R^* rule; (Tilman 1990)—and that the winner in the case of apparent competition is the species that sustains the greatest predator population—the P^* rule; (Holt et al. 1994). When both processes operate simultaneously the outcome depends on a variety of processes such as the productivity of the system, the relative mortality caused by predation and resource depletion, and any trade-offs between competitive ability and defence against natural enemies (Holt et al. 1994). How these processes interact can be explored using experimental manipulation in simple microcosm communities. The results can then be used to make predictions about the processes determining the structure and function of

larger communities in more natural environments (Holt et al. 1994; Wilson et al. 1996; Petchey et al. 1999; Long et al. 2007).

In this paper we describe experiments that investigate the role of resource competition and shared natural enemies in a simple insect community. *Acyrthosiphon pisum* and *Megoura vicae* are two aphids that can both feed on the same host plant, *Vicia faba* (broad bean). Previously we have shown that *A. pisum* is the dominant competitor and in laboratory microcosms can exclude *M. viciae*. However, if a specialist parasitoid of *A. pisum* is introduced then competitive exclusion is prevented and the three-insect community persists indefinitely (van Veen et al. 2005). Here we explore the dynamics of the system when the aphids not only share the same food resource but also share a natural enemy, the parasitoid wasp *Praon dorsale*. We had several a priori hypotheses about the system's dynamics. First, if the parasitoid caused significant mortality for both hosts we expected the species which could support the highest parasitoid density to exclude the other. Alternatively, if the parasitoid preferentially attacked the more common host, or if there was an interspecific trade-off in the aphids between competitive ability and natural enemy defence, we predicted coexistence to be observed. To help interpret the results we also investigated the relative performance of *P. dorsale* juveniles developing in *A. pisum* and *M. viciae* hosts.

Materials and methods

Study organisms

Megoura viciae (Buckton) and *Acyrthosiphon pisum* (Harris) are species of aphid that co-occur in natural communities feeding on *Lathyrus pratensis* and *Vicia* spp., and which may be found on the same plant individual. Populations of both species of aphid used in this experiment originated from single clones collected from *L. pratensis* at Silwood Park in the South of England. Prior to the start of the experiment they had been reared for at least 50 generations on *Vicia faba* in separate population cages.

A. pisum is attacked by a number of species of primary parasitoid and also by generalist aphid predators and pathogens (Van Veen et al. 2008). In contrast, *M. viciae* is rarely attacked by parasitoids, pathogens or predators (Van Veen et al. 2008), and there is experimental evidence that *M. viciae* is toxic to some predators (Dixon 1958), suggesting that it is a less suitable host for natural enemies than *A. pisum*.

Praon dorsale (Haliday) is a member of the Aphidiinae (Hymenoptera, Ichneumonoidea, Braconidae) and is a primary parasitoid of aphids. It is known to have a broad host

range (Starý 1966) and in a quantitative food web of an aphid-parasitoid community at Silwood Park it was recorded from eight species of aphid including *M. viciae* and *A. pisum* (Müller et al. 1999). *P. dorsale* is a sexual solitary koinobiont endoparasitoid that oviposits inside immature aphids. After parasitism the first instar larva suspends development while the aphid continues to feed and grow; when it resumes growth it consumes the host and spins a cocoon underneath the husk of the aphid (called a mummy) where it pupates. A laboratory population of *P. dorsale* was initiated from mummified nettle aphids (*Microlophium carnosum*) collected in the field at Silwood Park. Prior to the start of the experiment duplicate cultures of *P. dorsale* were maintained in population cages with *M. viciae* or *A. pisum* as hosts.

Experimental design

Population dynamics

Population cages containing six different combinations of species were set up (Fig. 1). Three contained only aphids: *M. viciae* and *A. pisum* alone and the two species together, while the remaining three had these same combinations of aphids but with the addition of *P. dorsale*. The communities containing just the single aphid species were replicated 4 times, all other communities 8 times.

Each replicate was maintained in a 30 × 30 × 30-cm clear Perspex population cage containing eight pots of *Vicia faba* (variety, The Sutton) and kept in a controlled environment room at 20°C, relative humidity 75%, with a 16:8-h light:dark cycle. Four *V. faba* seeds were planted in each pot and allowed to grow in a greenhouse for 2 weeks before being placed in the cages. The pots were replaced in a staggered renewal regime: twice a week the two oldest pots were removed and any aphids or parasitoid mummies found on them were returned to the cage along with two fresh pots of bean plants. Aphid populations were initiated by adding five 7- to 9-day-old adult apterae of the appropriate species to each cage, followed by another five apterae 1 week later to ensure overlapping generations.

P. dorsale females from both stock cultures were pooled and allowed to oviposit in 2nd instar *A. pisum*. The resulting adult offspring were collected and allowed to mate prior to introduction into the experimental cages. Ten weeks after the first aphids were introduced, two young (24–72 h old) mated female *P. dorsale* were added to the appropriate cages, followed by another two 1 week later, again to ensure overlapping parasitoid generations. In replicates where both species of aphids were present the densities of *M. viciae* were very low at this stage due to resource competition with *A. pisum*. Approximately 100 *M. viciae* apterae were added to these cages (both replicates with and
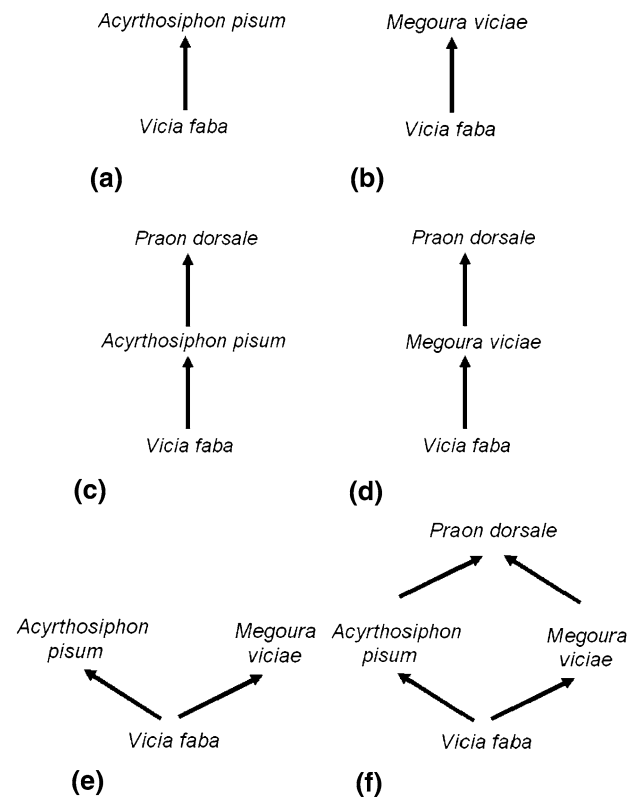

Fig. 1 The six communities used in the experiments. **a**, **b** Single-species communities consisting only of the aphid (and the host plant). **c**, **d** Aphid-parasitoid communities including one aphid species and the parasitoid. **e** Aphid competition community including both aphid species but no parasitoid. **f** Three-species community with both aphids feeding on the same host plant in the presence of the parasitoid

without *P. dorsale*) at the same time as the first parasitoids were introduced.

Once a week the number of aphids and aphid mummies of each species were counted on one of the pair of pots containing bean plants of the same age in each cage. To count the aphids plants were removed from the cage and placed on a white tray. Any aphids that fell onto the tray were returned to the cage with the plants. The numbers of adult parasitoids were also counted in each cage. Data were collected for 16 weeks from communities without parasitoids and for 27 weeks from communities with parasitoids. This represented ~11 (*M. viciae*) and ~19 (*A. pisum*) generations for the aphids and approximately eight generations for the parasitoid.

Parasitoid performance

Juvenile parasitoid performance on the two aphid species was assessed by exposing ten second instar aphids of either *A. pisum* or *M. viciae* on a *V. faba* plant to one mated female *P. dorsale* for 24 h. Twelve replicates for each species were carried out. Aphids were kept in a

controlled-environment room (20°C, relative humidity 75%, with a 16:8-h light:dark cycle), and were checked daily until mummification. Mummies were kept in individual gelatine capsules and monitored every 24 h. The following measures of parasitoid performance were recorded: (1) development time from oviposition to mummification, (2) duration of pupal period (i.e. from mummification until the emergence of the adult), and (3) successful parasitism rate. The experimental design also provided supplementary data on whether aphids that did not mummify reached adulthood or died as nymphs.

Data analysis

Population dynamics

Differences in the population dynamics of species in the various communities were compared using mixed-effects ANOVA; the response variables were the weekly density counts that had been square-root transformed to normalise the error variance. Mixed-effect techniques allow replicate short time series to be analysed within an ANOVA framework taking into account the potential non-independence of repeated measures (Pinheiro and Bates 2000). Only time series of the same length were compared and where there was minor variation the shortest time series determined the number of weeks' data that were included in the analysis. Community type (Fig. 1a–f) was treated as a fixed factor and time as a continuous variable in an analysis of covariance. Some of the comparisons included data from the initial phase of the experiment where insect numbers increased rapidly from a small number of founder individuals before reaching an asymptote. To model the non-linearity found in these population trajectories quadratic and cubic terms for the time variable were included in the initial model. Amongst-replicate variation was modelled as a random effect involving both the slope and intercept.

For each comparison we asked whether the main effect of community type or its interaction with time was significant. We interpret the first effect as an influence of community type on average density of the response species, and the second as community type affecting long-term population trends.

We also compared the cumulative numbers of different species across communities (a derived variable obtained by summing the weekly counts). These data were analysed using generalised linear modelling techniques assuming Poisson error variances, or if overdispersion was present, using a quasi-Poisson approach (McCullagh and Nelder 1989). All analyses were conducted using the statistical package R version 2.5.0 for Mac OS X (R Core Development Team 2007).

Parasitoid performance

Student's *t*-test was used to compare the mean times from oviposition until mummification and emergence of *P. dorsale* reared on either *M. vicae* or *A. pisum*. Separate χ^2-tests were used to determine whether there was an association between host species and the following: (1) the proportion of aphids mummified; (2) of the aphids that did not mummify, the proportion that survived to reach adulthood; and (3) the proportion of mummies that produced a parasitoid (pupal survival).

Results

Single-species communities

First we consider *A. pisum* and *M. viciae* populations in isolation. *A. pisum* numbers increased to an initial peak before reaching an asymptote at $\sim$3,500 $\pm$ 250 for the remainder of the experiment (Fig. 2a). *M. viciae* numbers showed a similar pattern, increasing to a peak followed by a small decline before numbers asymptoted at $\sim$2,500 $\pm$ 250 (Fig. 2b). No extinctions of either species were recorded.

Aphid-parasitoid communities

We now ask whether the presence of the parasitoid *P. dorsale* influences *A. pisum* or *M. viciae* dynamics in the two communities containing a single aphid species. In both cases, *P. dorsale* failed to establish in two cages (there was no evidence that the introduced females produced any offspring) and these were excluded from further study. The analysis included data collected in the weeks following the addition of parasitoids, which were compared with the equivalent time period from the aphid-only treatments. After *P. dorsale* addition, aphid numbers remained approximately constant for the duration of the experiment for both aphid species (Fig. 2c–d) and were not significantly different from the cages without parasitoids [*A. pisum*, community type, $F_{1,8} = 1.3$, not significant (NS); interaction with time, $F_{1,48} = 0.008$; *M. viciae,* community type, $F_{1,8} = 0.35$, NS; interaction with time, $F_{1,49} = 0.08$, NS; for analysis of cumulative numbers see Table 1]. In the *A. pisum* cages, *P. dorsale* numbers increased to an initial peak after which numbers declined steadily (Fig. 2c). At the end of the experiment, 17 weeks after *P. dorsale* were added, the parasitoid was extinct in four cages, at very low numbers in one cage (two individuals) and at relatively high numbers in the final cage (32 individuals). In contrast, in the *M. viciae* cages, *P. dorsale* numbers increased steadily for the remainder of the experiment (Fig. 2d) and at the end, 17 weeks after *P. dorsale* was introduced, it was still pres-

Fig. 2 The square root of the mean number of aphids per cage in the six experimental communities, averaged across replicates. **a** *Acyrthosiphon pisum* in isolation, **b** *Megoura viciae* in isolation. Following an initial period of growth both populations are relatively stable. **c** *Praon dorsale–A. pisum* interaction. After an initial period of population growth, *P. dorsale* declines towards extinction. **d** *P. dorsale–M. viciae* interaction. *P. dorsale* is able to invade and persist. **e** Resource competition between *M. viciae* and *A. pisum*. *M. viciae* is competitively excluded. **f** *A. pisum* and *M. viciae* competing for a shared resource and parasitised by *P. dorsale*. *M. viciae* is competitively excluded and *P. dorsale* declines as in **c**. **e**, **f** *Arrows* indicate the times at which additional *M. viciae* were added (see Materials and methods)
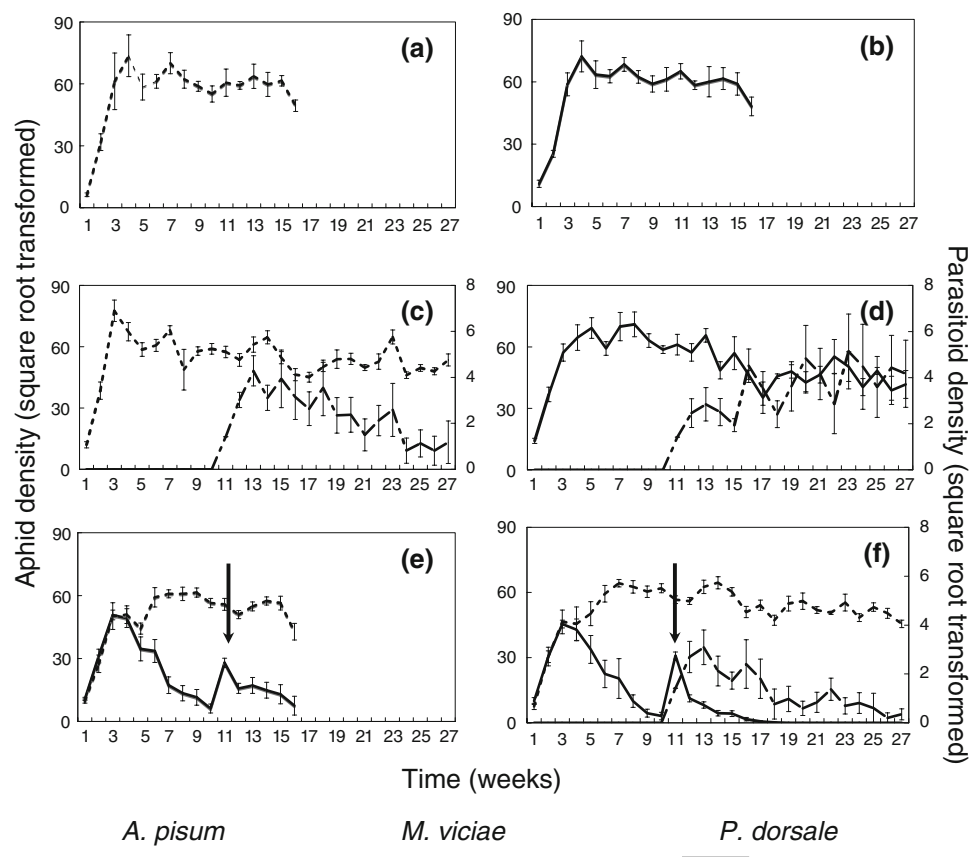

Table 1 Statistical tests of differences in the cumulative numbers of *Acyrthosiphon pisum* and *Megoura viciae* in the different communities

Comparison	Species	Treatment	Cumulative numbers, mean (SE)	F-test (significant in *bold*)
Single-species versus aphid competition communities	*A. pisum*	Single species	27,668 (1,232)	$F_{1,10} = 7.2$
		Aphid competition	22,043 (1,166)	$P = 0.02$
	M. viciae	Single species	55,031 (2,926)	$F_{1,10} = 109$
		Aphid competition	12,439 (1,731)	$P < 0.001$
Single-species versus aphid-parasitoid communities	*A. pisum*	Single species	10,704 (500)	$F_{1,8} = 1.6$
		Aphid-parasitoid	9,744 (508)	$P = 0.2$
	M. viciae	Single species	21,258 (2,577)	$F_{1,8} = 0.2$
		Aphid-parasitoid	19,774 (1,967)	$P = 0.65$
Aphid competition versus three-species communities	*A. pisum*	Aphid competition	18,420 (1,032)	$F_{1,13} = 4.5$
		Three species	20,857 (701)	$P = 0.053$
	M. viciae	Aphid competition	1,763 (544)	$F_{1,13} = 2.3$
		Three species	1,260 (108)	$P = 0.15$

ent in four cages (42 ± 12 individuals) and had gone extinct in the other two.

Aphid competition community

In the treatment where the two aphids competed for resources in the absence of parasitoids, the numbers of both species increased initially, but while *A. pisum* densities

reached an asymptote those of *M. viciae* then declined rapidly (Fig. 2e). Despite an additional introduction of *M. viciae* in week 10, by week 16 it was extinct in three out of eight cages. In the remaining cages, numbers had fallen to less than 60 *M. viciae* except in one cage where there were 1,424 individuals; *A. pisum* numbers were low in this cage (308 individuals at week 16). We do not have an explanation for the relative success of *M. viciae* in this single cage.

Table 2 Statistical tests of differences in the cumulative numbers of *Praon dorsale* in the different communities

Comparison	Host	Cumulative numbers, mean (SE)	F-test (significant in **bold**)
The two single aphid-parasitoid communities	*A. pisum*	166 (45.3)	$F_{1,10} = 2.7$
	M. viciae	327 (93.2)	$P = 0.12$
A. pisum single- versus three-species communities	*A. pisum*	166 (45.3)	$\mathbf{F_{1,11} = 5.4}$
	A. pisum	71.1 (16.0)	$\mathbf{P = 0.04}$
M. vicae single- versus three-species communities	*M. viciae*	327 (93.2)	$\mathbf{F_{1,11} = 13.6}$
	M. viciae	71.1 (16.0)	$\mathbf{P = 0.003}$

Three-species community

Finally we studied the effect of *P. dorsale* on resource competition between *A. pisum* and *M. viciae*. *P. dorsale* failed to establish in one replicate, so only seven were included in the analysis. Prior to parasitoid addition both aphid populations had increased in density with *A. pisum* numbers reaching a plateau and *M. viciae* numbers declining sharply after the initial peak. Following the addition of *P. dorsale* and a further introduction of *M. viciae*, *A. pisum* numbers remained constant. In contrast *M. viciae* numbers continued to decline; 6 weeks after *P. dorsale* was added *M. viciae* was extinct in five cages and at very low numbers (<40) in the remaining two cages (Fig. 2f). *P. dorsale* numbers increased to a peak before declining steadily (Fig. 2f). 17 weeks after *P. dorsale* was added, it was extinct in five cages and present in low numbers in the remaining cages (less than ten).

We compared the numbers of each aphid species from this treatment in the weeks following parasitoid introduction with the equivalent data from the treatment with both aphids present in the absence of the parasitoid. There was no effect of the presence of *P. dorsale* on *A. pisum* numbers (main effect of community, $F_{1,13} = 4.6$, NS; interaction with time, $F_{1,73} = 1.02$, NS; for analysis of cumulative aphid numbers see Table 1). Similarly, *P. dorsale* had no effect on *M. viciae* numbers (community, $F_{1,13} = 2.6$, NS; interaction, $F_{1,73} = 2.01$, NS; for cumulative numbers see Table 1).

We also compared the dynamics of *P. dorsale* in this treatment with the communities containing the parasitoid and a single species of aphid. In comparison with the treatment where *A. pisum* was the only aphid present, *P. dorsale* had lower cumulative numbers in the derived variable analysis (Table 2), but the treatment and interaction effects were not significant in the mixed-model ANOVA ($F_{1,11} = 2.6$, NS and $F_{1,206} = 0.07$, NS, respectively). In contrast, *P. dorsale* achieved significantly higher densities in communities where *M. viciae* was the only host (main effect of community, $F_{1,11} = 9.93$, $P = 0.009$; for analysis of cumulative parasitoid numbers see Table 2) and parasitoid populations persisted at higher densities for a longer period of time (interaction with time, $F_{1,206} = 8.11$, $P = 0.005$).

Parasitoid performance

Data were collected from 120 *A. pisum* and 120 *M. viciae* individuals exposed to *P. dorsale*. There was no difference in the percentage of aphids of each species that became mummified: 28% *A. pisum* compared to 29% *M. viciae* ($\chi_1^2 = 0.0$, NS). Of the aphids that did not mummify, significantly more *M. viciae* survived to the adult stage compared to *A. pisum* (48% versus 68%; $\chi_1^2 = 5.85$, $P = 0.016$).

Thirty-four *A. pisum* and 35 *M. viciae* mummified after being exposed to *P. dorsale*. Parasitised *M. viciae* took significantly longer to mummify than parasitised *A. pisum* (10.1 ± 0.11 vs. 8.4 ± 0.12 days respectively; $t = 11.3$, $P < 0.001$). There was no difference in the length of time between mummification and emergence of the adult parasitoid between the two aphid species ($t = 0.8$, NS). Significantly fewer juvenile parasitoids developing on *M. viciae*, having reached mummification, survived to emerge as adult parasitoids compared to those developing on *A. pisum* (85% of the mummies produced an adult parasitoid from *A. pisum* compared to 41% for *M. viciae*, $\chi_1^2 = 15.6$, $P < 0.001$). Note that we did not estimate rates of superparasitism on the two hosts and if they were not the same they might contribute to differences in parasitoid survival (though this would not be an issue if any such differences were a reflection of what also occurred in the microcosms).

Discussion

We have described an experiment that used replicated microcosm communities to examine interspecific resource competition and the effects of a shared parasitoid species on the population dynamics of two species of aphids. We found that interspecific resource competition was the major determinant of community structure and dynamics. The presence of the parasitoid had no effect on the outcomes of interspecific resource competition, and had very little influence on the population dynamics of either aphid species.

Microcosms are artificially simple assemblages of species maintained in unnatural environments, and it is important to consider the effects of any possible artefacts

introduced by the experimental protocol. In our experiments the aphids' food plant was replenished twice a week by replacing two out of eight pots of *V. faba* seedlings (with the aphids being shaken off and reintroduced to the cages). This renewal regime introduces some heterogeneity in the intensity of competition across plants (there are more aphids on plants nearing the end of the time in the cage). However, the heterogeneity will be experienced by both aphid species (and by any parasitoid larvae they contain) and we do not think this will affect the system dynamics. A fraction of aphids are disturbed during resource renewal, and it is possible that differential susceptibility to disturbance might influence the relative performance of the two species, though comparison of single- and two-aphid-species communities does not suggest this is important.

In the treatments containing just the single aphid species, the numbers of each species reached a plateau following an initial period of increase. *A. pisum* numbers were approximately 40% higher than those of *M. viciae*. Differences in the size of the two aphids [length of wingless adults: *A. pisum* 2.5–4.3 mm, *M. viciae* 3–5 mm (Blackman and Eastop 2006)], and differences in the age structure of *A. pisum* and *M. viciae* populations (an average of 7% of *A. pisum* individuals were adults compared to 11% for *M. viciae*) may explain the difference in the population sizes of these species.

In the treatment containing the two aphid species in the absence of the parasitoid, the numbers of both aphid species grew rapidly until they started competing for resources. Competition was asymmetrical; *A. pisum* had a negative effect on both the average abundance and rate of decline of *M. viciae* and excluded the latter within ten generations in all but one of the replicates. In contrast, there was no difference in the mean abundance of *A. pisum* in the two treatments, nor an interaction with time, though the analysis of cumulative numbers showed the presence of *M. viciae* had a small effect on *A. pisum* dynamics.

Comparing treatments that differed only in the presence of *P. dorsale* showed that the parasitoid had remarkably little effect on the mean densities of the aphid species and how they fluctuated over time. Inspection of the population trajectories (Fig. 2) suggested that there may be an increase in the variance of *M. viciae* numbers after week 13, but this was not confirmed by formal statistical tests. *P. dorsale* never became sufficiently abundant to be a major source of aphid mortality, and indeed struggled to persist on populations of *A. pisum*. *P. dorsale* numbers were lowest in the three-species community. This was partly due to *A. pisum*, the host on which *P. dorsale* persistence was most difficult, being dominant in this treatment. However, parasitoid densities were slightly lower in this treatment compared to when *A. pisum* was the only host. Possible reasons for this include longer handling times when the parasitoid has a

choice of hosts of different value, or stronger interspecific relative to intraspecific competition reducing the quality of *M. viciae* in the three-species community. Note that *M. viciae* is both a poorer interspecific competitor and a better host for *P. dorsale* compared to *A. pisum*. There is thus no evidence for the type of cross-species trade-off between competitive ability and natural enemy response that we hypothesised might lead to aphid coexistence.

Other studies that have investigated the structure of insect microcosm communities have demonstrated the potential importance of parasitoids. Using a system of aphid-parasitoid communities similar to the one described in this report, van Veen et al. (2005) showed that the addition of the parasitoid *Aphidius ervi*, which parasitises *Acyrthosiphon pisum* but not *M. viciae*, prevented competitive exclusion of *M. viciae*. Further, without the presence of *M. viciae* in the community, the interaction between *A. ervi* and *A. pisum* was unstable, with the host being driven to extinction by the parasitoid. The authors argued that the presence of *M. viciae* reduced the efficiency of the parasitoid and prevented it from overexploiting its host. Bonsall and Hassell (1997, 1998) studied a microcosm community composed of two moth species (*Ephestia kuehniella* and *Plodia interpunctella*) that were prevented from competing for resources, and the parasitoid *Venturia canescens*, which parasitizes both moth species. The individual host-parasitoid interactions were stable, but in the three-species community, *P. interpunctella* had an indirect negative effect on *E. keuhniella*, driving it to extinction via raised densities of *V. canescens*.

Why, in contrast to these studies, did the parasitoid *P. dorsale* have so little effect on the community structure or population dynamics of the aphid species in the simple communities we studied? The parasitoid performance experiment suggested that both species of aphids were suitable hosts for *P. dorsale* and this parasitoid is recorded from both aphid species in natural communities (Müller et al. 1999). A possible explanation has been suggested by Ives and Settle (1995), prompted by observations that *Aphidius ervi* failed to persist on a large population of *A. pisum* in a population cage. Aphid parasitoids typically attack early-instar nymphs and their larvae must remain in a state of suspended development until their hosts are large enough to provide them with sufficient resources for growth. During this period they are very susceptible to factors affecting their hosts' survival and quality. If host populations are experiencing high levels of resource competition affecting both individual survival and quality then the parasitoid too will suffer and its population growth rate may fall below zero so that it is unable to invade. This effect will be exacerbated if parasitised hosts are particularly susceptible to density-dependent mortality, as has been observed in some aphid parasitoid systems (Ives and Settle 1995),

though examples exist of interactions where parasitised hosts are at a competitive advantage (Spataro and Bernstein 2004; Cameron et al. 2007; White et al. 2007). By the time we released parasitoids into our microcosms, aphid densities were already high and intraspecific competition severe, and this may have hindered their ability to invade and persist. Parasitoids were more successful on *M. viciae* populations, despite this being the less suitable host, as suggested by the parasitoid performance experiment. This suggests that density-dependent mortality may have been less of a factor for parasitoids developing on this host than on *A. pisum.*

If high-density host populations are an unsuitable resource for parasitoids then this has a number of consequences. First, there may be a threshold host density above which parasitoid establishment does not occur. The system may thus have alternative stable states, a lower aphid equilibrium determined by interactions with natural enemies and an upper one determined by resource competition with the natural enemy absent or at a very low density. Such alternative stable states have been invoked to explain periodic outbreaks in pest insects, most notably the larch bud moth in North America (Ludwig et al. 1978). Second, it suggests that the timing of parasitoid arrival may affect whether it can enter the community. Applied biologists have stressed the importance of providing conditions where aphid parasitoids can overwinter near crops so that they can colonise aphid populations early before their densities reach damaging levels (Powell 1982). Early arrival will be even more important if parasitoids have difficulties establishing themselves on later, larger aphid populations. Finally, there may be interesting indirect interactions amongst the guild of natural enemies. For example, predators may reduce aphid populations below the threshold density that allows parasitoids to invade (although predators may also increase the mortality experienced by the parasitoid population). The order of arrival of different natural enemies is known to affect the dynamics of other insect microcosm model systems (Sait et al. 2000). In addition to the density-dependent effects on host quality, the order of introduction may also affect the success of parasitoid invasion through a population dynamic effect. Recently Noonberg and Abrams (2005), and earlier in a parasitoid context Wilson et al. (1996), showed that the nature of the transient population dynamics before an equilibrium (if it exists) is established may determine which natural enemy can invade. It would be interesting to repeat our experiments but alter the timing of the introduction of the two competitors and the natural enemy.

In conclusion, our microcosm experiments provide an example of a system where, though both resource competition and apparent competition are possible, community structure and dynamics seem largely determined by the former. We suggest this occurs because resource competition reduces the value of the aphids as hosts for parasitoids. Future work needs to explore whether these processes occur in the more complicated communities found in natural and agricultural environments, and whether they influence the structure of communities of temperate aphids and their natural enemies that are reassembled each season.

References

Begon M, Harper JL, Townsend CR (1996) Ecology, 3rd edn. Blackwell, Oxford

Blackman RL, Eastop VF (2006) Aphids on the world's herbaceous plants and shrubs: an identification and information guide. Wiley, Chichester

Bonsall MB, Hassell MP (1997) Apparent competition structures ecological assemblages. Nature 388:371–373

Bonsall MB, Hassell MP (1998) Population dynamics of apparent competition in a host-parasitoid assemblage. J Anim Ecol 67:918–929

Cameron TC, Metcalfe D, Beckerman AP, Sait SM (2007) Intraspecific competition: the role of lags between attack and death in host-parasitoid interactions. Ecology 88:1225–1231

Dempster JP (1963) The population dynamics of grasshoppers and locusts. Biol Rev 38:490–529

Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition re-examined and resurrected. Annu Rev Entomol 40:297–331

Dixon AFG (1958) The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). Trans R Entomol Soc London 110:319–334

Finke DL, Denno RF (2004) Predator diversity dampens trophic cascades. Nature 429:407–410

Gause GF (1934) The struggle for existence. Williams and Wilkins, Baltimore

Hairston NG, Smith EF, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425

Hanna R, Wilson LT, Zalom FG, Flaherty DL (1997) Effects of predation and competition on the dynamics of *Tetranychus pacificus* on grapevines. J Appl Ecol 34:878–888

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theor Popul Biol 12:197–229

Holt RD, Lawton JH (1993) Apparent competition and enemy-free space in insect host-parasitoid communities. Am Nat 142:623–645

Holt RD, Lawton JH (1994) The ecological consequences of shared natural enemies. Annu Rev Ecol Syst 25:495–520

Holt RD, Grover JP, Tilman D (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. Am Nat 144:741–771

Ives AR, Settle WH (1995) The failure of a parasitoid to persist with a superabundant host: the importance of the numerical response. Oikos 75:269–278

Janzen DH (1973) Host plants as Islands. II. Competition in evolutionary and contemporary time. Am Nat 107:786–790

Lawton JH, Strong DR (1981) Community patterns and competition in folivorous insects. Am Nat 118:317–338

Long ZT, Petchey OL, Holt RD (2007) The effects of immigration and environmental variability on the persistence of an inferior competitor. Ecol Lett 10:574–585

Ludwig D, Jones DD, Holling CS (1978) Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J Anim Ecol 47:315–332

McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman and Hall, London

Moran NA, Whitham TG (1990) Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. Ecology 71:1050–1058

Morin PJ (1999) Community ecology. Blackwell, Massachusetts

Müller CB, Adriaanse ICT, Belshaw R, Godfray HCJ (1999) The structure of an aphid-parasitoid community. J Anim Ecol 68:346–370

Noonberg EG, Abrams PA (2005) Transient dynamics limit the effectiveness of keystone predation in bringing about coexistence. Am Nat 165:322–335

Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. Nature 402:69–72

Pinheiro J, Bates DM (2000) Mixed effects models in S and S-plus. Springer, New York

Powell W (1982) The role of parasitoids in limiting cereal aphid populations. In: Cavalloro R (ed) Aphid antagonists. Balkema, Rotterdam, pp 50–56

R Development Core Team (2007) R: a language and environment for statistical computing. Version 2.5.0. R Foundation for Statistical Computing, Vienna

Sait SM, Liu W-C, Thompson DJ, Godfray HCJ, Begon M (2000) Invasion sequence affects predator-prey dynamics in a multi-species interaction. Nature 405:448–450

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Annu Rev Ecol Syst 16:269–311

Slobodkin LB, Smith FE, Hairston NG (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. Am Nat 101:109–124

Snyder WE, Ives AR (2001) Generalist predators disrupt biological control by a specialist parasitoid. Ecology 82:705–716

Snyder WE, Ives AR (2003) Interactions between specialist and generalist naturalist enemies: parasitoids, predators, and pea aphid biocontrol. Ecology 84:91–107

Spataro T, Bernstein C (2004) Combined effects of intraspecific competition and parasitoid attacks on the dynamics of a host population: a stage structured model. Oikos 105:148–158

Starý P (1966) Aphid parasites of Czechoslovakia. A review of the Czechoslovak Aphidiidae (Hymenoptera). Junk, The Hague

Strong DR, Lawton JH, Southwood TRE (1984) Insects on plants: community patterns and mechanisms. Blackwell, Oxford

Tilman D (1977) Resource competition between plankton algae: an experimental and theoretical approach. Ecology 58:338–348

Tilman D (1990) Mechanisms of plant competition for nutrients: the elements of a predictive theory competition. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic, San Diego

van Veen FJF, van Holland PD, Godfray HCJ (2005) Stable coexistence in insect communities due to density- and trait-mediated indirect effects. Ecology 86:1382–1389

van Veen FJF, Morris RJ, Godfray HCJ (2006) Apparent competition, quantitative food webs, and the structure of phytopageous insect communities. Annu Rev Entomol 51:187–208

van Veen FJF, Muller CB, Pell JK, Godfray HCJ (2008) Food web structure of three guilds of natural enemies: predators, parasitoids and pathogens of aphids. J Anim Ecol 77:191–200

White SM, Sait SM, Rohani P (2007) Population dynamic consequences of parasitised-larval competition in stage-structured host-parasitoid systems. Oikos 116:1171–1185

Wilson HB, Hassell MP, Godfray HCJ (1996) Host-parasitoid food webs: dynamics, persistence and invasion. Am Nat 148:787–806