COMMUNITY ECOLOGY

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Relative importance of fertiliser addition to plants and exclusion of predators for aphid growth in the field

Abstract Herbivore dynamics and community structure are influenced both by plant quality and the actions of natural enemies. A factorial experiment manipulating both higher and lower trophic levels was designed to explore the determinants of colony growth of the aphid *Aphis jacobaeae*, a specialist herbivore on ragwort *Senecio jacobaea*. Potential plant quality was manipulated by regular addition of NPK-fertiliser and predator pressure was reduced by interception traps; the experiment was carried out at two sites. The size and persistence of aphid colonies were measured. Fertiliser addition affected plant growth in only one site, but never had a measurable effect on aphid colony growth. In both habitats the action of insect predators dominated, imposing strong and negative effects on aphid colony performance. Ants were left unmanipulated in both sites and their performance on the aphid colonies did not significantly differ between sites or between treatments. Our results suggest that, at least for aphid herbivores on *S. jacobaea*, the action of generalist insect predators appears to be the dominant factor affecting colony performance and can under certain conditions even improve plant productivity.

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Introduction

An interesting question in community ecology is whether food web structure is purely determined by resource or energy inputs, or whether the response is modulated by the action of higher trophic levels. Theoretical arguments point towards an interplay between enrichment and the effects of higher trophic levels, for example suggesting greater inputs lead to longer food chains, but that adding an extra top predator can reverse the relative abundance of lower trophic levels (Fretwell 1977; Oksanen et al. 1981; DeAngelis 1992; Hunter and Price 1992; Abrams 1993). Experiments on resource limitation show that primary productivity is a major determinant of consumer abundance and through that the abundance of predators (Wootton and Power 1993; Schmitz 1993; Roininen et al. 1996; Kaunzinger and Morin 1998; Hulot et al. 2000; Price 2002), but that prey edibility may also play a critical role in influencing the consequence of enrichment (Leibold et al. 1997). Most studies testing these ideas have focused on aquatic systems where food chains may be more linear (less omnivory) than in terrestrial systems (Strong 1992). Terrestrial food webs are more complex, with more species feeding on prey from multiple trophic levels, and general conclusions about the consequences of increased productivity have yet to emerge Polis and Strong 1996.

In many cases, elevating plant quality by the addition of fertiliser leads to an increase in herbivore densities through functional and numerical responses. There are, though, examples where fertilisation has the reverse effect (e.g. Scriber 1984), for which there may be several explanations. Some plant species attacked by herbivorous insects respond by increasing investment in effective quantitative defences that reduce palatability (Crawley 1983), while in other species insect herbivory can induce

the production of defensive alkaloids and other toxins (Karban and Carey 1984; Karban 1993; Karban et al. 1997; Agrawal 1998), either by the plant alone or together with closely associated fungal symbionts (Clay 1990; Omacini et al. 2001). Enrichment can change the energy or nutrient budget of the plant to make effective defence either more achievable or more profitable (the concomitant observation being that stressing a plant may make defences less profitable triggering increased insect attack, e.g. White (1993)). Alternatively, as most herbivorous insects are themselves attacked by insect predators, parasitoids and fungal pathogens, improved resource quality could increase herbivore population growth rates at first but subsequently reduce the populations through the attraction and retention of natural enemies to plants with high herbivore abundance.

Similar processes may occur at the next trophic level. For example, aphids can successfully resist parasitoids (Henter and Via 1995; Ferrari et al. 2001), pathogens (Brobyn et al. 1987) and insect predators (Dixon 1959, Roitberg and Myers 1979, Losey and Denno 1998) through a variety of intrinsic defence mechanisms, or may obtain protection through a mutualistic association with ants (Dixon 1998). The interaction between plants, aphids and their natural enemies is complex because plant quality may affect prey quality in unpredictable ways. For example, aphid population growth typically depends on plant quality. Natural enemies tend to aggregate on large aphid colonies and while it is possible that more nutritious plants may allow aphids to grow better, this may still not be enough to compensate for losses to predation (Lawton and McNeil 1979).

In addition to direct effects on herbivore fitness through their defensive chemistry, plants may also indirectly affect herbivores via their natural enemies (e.g. Sunderland et al. 1997; Müller and Godfray 1999a). For example, some plants have been shown to release volatile chemicals after insect attacks that attract the herbivore's specific natural enemies (Vinson 1976; Dicke and Sabelis 1988; Turlings et al. 1990; Vet and Dicke 1992; Takabayashi and Dicke 1996). If volatiles are costly, healthier plants of high nutritional quality may be more successful at producing such cues. In contrast, specialised herbivores may also use plant defence compounds to become themselves unpalatable for predators or parasitoids. Such acquired defences have been shown, for example, in the moth *Tyria jacobaeae* that lives and feeds on ragwort, *Senecio jacobaea*, a plant toxic to vertebrate grazers (Aplin et al. 1968).

Here, we manipulate the top and bottom levels of a tri-trophic system comprising ragwort (*S. jacobaea*), a specialist aphid (*Aphis jacobaeae*) and its natural enemies. We ask how the abundance of the herbivore is influenced by changes in potential plant quality and natural enemy abundance through a factorial experiment replicated in two different habitats. In a previous experiment with this system (in one of the two habitats used here) we found that aphid growth and persistence were strongly and negatively affected by the presence of

the guild of local insect predators (Müller and Godfray 1999b). Part of the motivation for this experiment was to investigate whether elevated potential plant resource quality could modify such a strong predator effect by allowing the aphid populations to increase fast enough to escape destruction by predators, at least temporarily. We worked at two sites because they contained different communities of plants and aphids supporting different guilds of specialist aphid predators.

Materials and methods

Biology of the system

Ragwort (*S. jacobaea* L.) is a monocarpic perennial plant that normally produces one flowering stem of between 50 cm and 170 cm height. It is highly toxic to most vertebrate grazers due to its production of pyrrolizidine alkaloids, a type of secondary metabolite. Cattle, horses and sheep may die because of an even more toxic compound that is produced in their stomachs after feeding on ragwort (Crawley 1997, p 136). Specialised insect consumers such as the moth *T. jacobaeae* L. and the aphid *A. jacobaeae* Schrank have become adapted to feeding on this plant and can tolerate the toxins and sequester them for their own defence (Aplin et al. 1968; van der Meijden et al. 1989). Despite these adaptations, *A. jacobaeae* is commonly attacked by natural enemies (Müller et al. 1999; Müller and Godfray 1999b) and often uses the services of tending ants (especially *Lasius niger* L.) for protection. The interactions between *S. jacobaea*, the two herbivores, *T. jacobaeae* and *A. jacobaeae*, and aphid-tending ants, are complex and may result in polymorphisms for pyrrolizidine concentration in the plant (Vrieling et al. 1991). *Aphis jacobaeae* does not show host alternation and is thought to be monophagous on *S. jacobaea*; it forms dense colonies of wingless parthenogens on growing parts of the plant, and produces a more limited number of winged individuals that disperse to form new colonies (Blackman 1975). Sexual morphs are produced late in the season and the species overwinters as eggs.

Study sites

Two different but adjacent field sites at Silwood Park (Berkshire, Southern England) were chosen for this study. The first is a flat, damp, botanically diverse meadow (Rush Meadow) in which a long-term study on aphid-parasitoid food webs is being carried out (Müller et al. 1999). In Rush Meadow, *S. jacobaea* occurs in small patches and appears not to be colonised by aphids through the action of resident predators that persist on other species of aphids (Müller and Godfray 1999b). The adjacent site is a much dryer, sandy slope dominated by *S. jacobaea* and short grass that is heavily

grazed by rabbits (Nursery Field). Here there have been large colonies of *A. jacobaeae* for at least 8 years.

Experimental design

We manipulated potential food plant quality and predator density to determine their relative effects on aphid population levels. We did not manipulate the ants that tend *A. jacobaeae* but treated them as a feature of the habitat.

In each site, we selected 11 groups of four plants that were likely to produce flowering stems and assigned randomly each of the four plants within each group to one of the following treatments (with codes):

Fertiliser application and predator exclusion (+F−P)
Fertiliser application without predator exclusion (+F+P)
No fertiliser application with predator exclusion (−F−P)
No fertiliser application without predator exclusion (−F+P)

The fertiliser treatment consisted of 6.8 g NPK (Growmore) granules dissolved in 50 ml water and applied to the base of each fertilised plant at weekly intervals between 11 May 1999 and 26 July 1999. Unfertilised plants received 50 ml of water at the same times. Predator exclusion was achieved by constructing a cylindrical cage of chicken wire (mesh size 0.6 cm^2) that was coated with a sticky gel (Tanglefoot) and placed around the plants. The tangle foot intercepts the flying predators when they approach a plant and land on the cage first. All plants within 20 cm of the experimental ragwort stem were cut back to make the trap more effective; equally, plants were cut back around uncaged experimental plants. As the plants grew, the cages were raised on bamboo canes and muslin netting was placed around the base to intercept insects. The temperature within the cages was approximately one degree lower than that around uncaged plants (through increased shading: mean (±SE) was 24.0°C (±0.8) inside the cage and 25.1°C (±0.8) outside).

At the start of the experiment five adult and five nymphal aphids were placed on each plant to initiate colonies that simulate a natural age-structured colonies (and any aphids already present were removed). The aphids were collected from nearby sites and transferred onto the experimental plants on 3 June in Nursery Field and on 7 June in Rush Meadow. Every second day we recorded the number of aphids per plant and the number and identity of ants and predators present. Some predators and ants were able to enter our exclusion treatment and all those predators found on plants in the predator-exclusion treatment (−P) were removed manually. The ants were counted but otherwise left undisturbed because they are able to build their nest entry at the base of the plants. In addition, all *T. jacobaeae* larvae were removed from experimental plants (though

their densities were not very high in 1999 in our study sites). The development of the colonies was followed over 18 days by which time most colonies in Rush Meadow were extinct in all treatment.

As some colonies grew to very large size and persisted in Nursery Field, at day 18 we decided to study the decline of aphid colonies previously protected from predation. In this site, we switched between the two predator treatments (i.e. now (+F−P) becomes (+F+P) and (−F−P) becomes (−F+P) and vice versa) and then sampled colony size for a further 45 days. If there were fewer than ten aphids on the plant at day 18, we added insects until colonies were of this size. The development of declining colonies was then analysed in the same way to show if the build-up and the declining phase of colony development are equally affected by fertiliser and predator additions.

At the end of the experiment, all plants were cut at ground level and the height of the stem measured. We also recorded the number and fresh weight of flowers, and the fresh weight of vegetative plant tissue. This enabled us to test the effects of the fertilisation and possible effects caused indirectly by predators. Plants from Rush Meadow were measured on 30 July and those of Nursery Field between 4 and 11 August.

Statistical analysis

To analyse aphid and ant counts over time and interactions between treatments, we used repeated measure ANOVA (SPSS). All analyses used univariate techniques on log- or arcsin-transformed count data (Crowder and Hand 1990). As assumptions of sphericity were violated in all cases, we corrected the degrees of freedom with Greenhouse-Geisser adjustments. The eleven blocks were originally included as cofactors but never showed significant effects. The measures of plant performance and the persistence time of aphid colonies were analysed by one-way ANOVAs as the data met normality assumptions. All graphs show population means and standard errors.

Results

Plant performance

Adding fertiliser to half of the experimental plants had no statistically significant effect on any of the plant traits measured in Rush Meadow (Height: $F_{1,42} = 0.85$, $P = 0.36$; Biomass: $F_{1,42} = 0.45$, $P = 0.51$; Weight of flowers: $F_{1,42} = 0.55$, $P = 0.46$; Number of flowers: $F_{1,42} = 0.13$, $P = 0.72$). In Nursery Field, the addition of fertiliser resulted in significantly increased aboveground biomass ($F_{1,42} = 7.99$, $P = 0.007$), higher investment in total flower mass ($F_{1,42} = 9.06$, $P = 0.004$) and number of flowers ($F_{1,42} = 10.76$, $P = 0.002$) but not an increase in plant height ($F_{1,42} = 1.61$, $P = 0.21$). In this site, it thus

appears that fertiliser treatment influences aspects of plant architecture such as branching rather than simply height.

Cascading effects

We also asked how both fertiliser and predator treatments affected plant growth and the number of flowers produced by the plant, which we used as surrogate measure of fitness. In Rush Meadow, a complex pictures with a significant interaction between the two main effects emerged: plant performance appears to be highest either with fertiliser and no predators, or without fertiliser but with predators (Table 1a). In Nursery Field, fertiliser application and the presence of predators had an additive effect on our measures of plant performance (Table 1b).

Aphid performance

Rush Meadow

Predator exclusion but not fertiliser addition influenced aphid colony size at this site (Fig. 1a). In the repeated measures ANOVA the main effect of predator exclusion was significant ($F_{1,40}=45.9$; $P<0.0001$) but not the fertiliser treatment ($F_{1,40}=0.23$; $P=0.63$) nor the interaction ($F_{1,40}=0.84$; $P=0.36$). Block effects were not significant and were omitted from the analysis ($F_{1,39}=0.41$; $P=0.53$). Aphid colony size declined significantly over time, but more strongly when predators were present giving rise to a significant time–predator interaction term. Neither the interaction between fertiliser addition and time nor the three-way interaction were

significant (Table 3a1). The effect of the two treatments on mean colony persistence time was very similar (Table 2). Colonies protected from predation survived for a significantly longer time than unprotected colonies ($F_{1,40}=58.78$; $P<0.0001$), but there was no effect of fertiliser application ($F_{1,40}=0.26$; $P=0.61$), nor was there an interaction between the two treatments ($F_{1,40}=1.42$; $P=0.24$). More migrating winged morphs were counted in colonies protected against predation though the difference in cumulative number of winged morphs was only statistically significant between predators exclusion and predator access in fertilised treatments (Fig. 3; $F_{3,40}=3.27$, $P=0.031$).
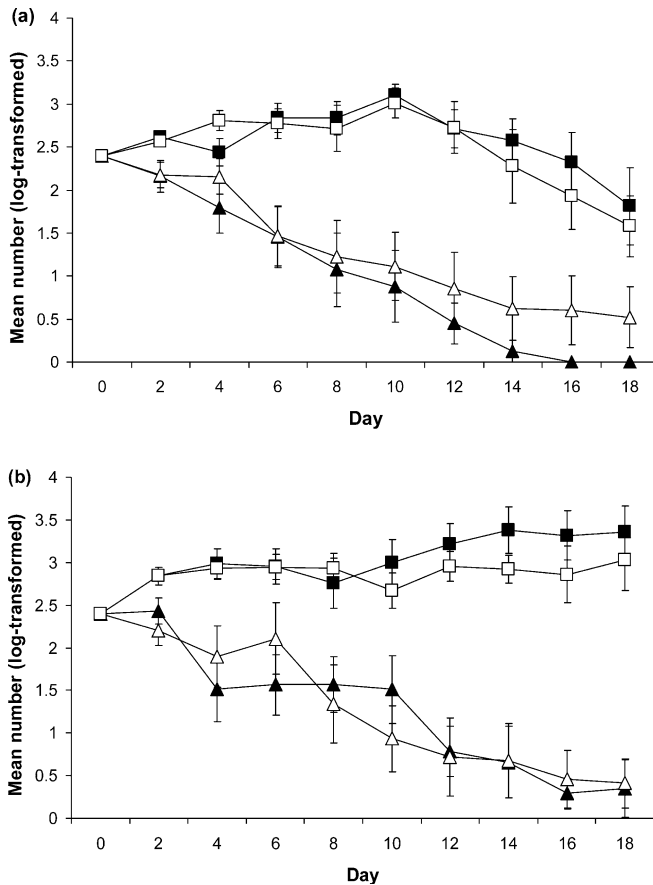
Nursery Field (day 1–18)

Again, colony size was influenced by the predator exclusion but not the fertiliser treatment (Fig. 1b). The main effect of predator exclusion was significant ($F_{1,40}=59.0$; $P<0.0001$) but not the fertiliser treatment ($F_{1,40}=0.15$; $P=0.70$) or the interaction ($F_{1,40}=0.18$; $P=0.67$). Again, block effects were not significant and were omitted from the analysis ($F_{1,39}=0.003$; $P=0.96$). Overall, aphid colony size changed with time, but colonies from which predators were excluded declined in density while those that were protected tended to increase in size, which was reflected in a strongly significant time–predator exclusion interaction. The interaction between time and fertiliser application and the three-way interaction were not significant (Table 3b1). All colonies with predator exclusions persisted for 18 days (Table 2). Persistence time was influenced only by the predator exclusion treatment ($F_{1,40}=4.9$; $P<0.0001$) but not by the fertiliser treatment ($F_{1,40}=0.02$; $P=0.89$) or the interaction ($F_{1,40}=0.02$;

Table 1 The effect of treatment on measures of *S. jacobaea* structure (plant height, plant weight, weight and number of flowers; mean ± SE) in Rush Meadow (a) and Nursery Field (b)

Treatment	Height (cm)	Weight aboveground (g)	Weight of flowers (g)	Number of flowers
(a) Rush Meadow				
+F−P	108.5±4.7	211.9±28.6	49.5±4.8	518.0±51.2
+F+P	114.2±9.8	169.1±17.5	37.5±4.6	391.6±57.5
−F−P	103.9±3.7	120.0±13.0	26.6±2.4	287.2±39.8
−F+P	106.6±7.1	222.2±40.3	51.4±8.1	563.3±124.8
$F_{3, 40}$	0.41	2.97	4.55	2.71
P	0.74	0.043	0.008	0.058
Significant contrasts ($P<0.05$)	–	–	(+F−P)>(−F−P) (−F+P)>(−F−P)	–
(b) Nursery Field (second)				
+F−P	103.8±3.6	106.0±16.5	31.6±5.4	360.4±47.6
+F+P	111.9±5.5	148.3±22.8	49.4±6.9	560.6±66.0
−F−P	96.4±4.8	74.9±12.1	20.4±4.7	258.4±50.5
−F+P	107.4±4.0	83.9±12.9	27.1±3.7	299.8±39.6
$F_{3, 40}$	2.08	3.88	5.47	6.67
P	0.12	0.016	0.001	0.001
Significant contrasts ($P<0.05$)	–	(+F+P)>(−F−P) (+F+P)>(−F+P)	(+F−P)>(−F−P) (+F+P)>(−F+P)	(+F−P)>(−F−P) (+F+P)>(−F+P) (+F+P)>(+F−P)

The results of a one-way ANOVA with different treatments and results of Tukey tests are shown. Plants in Rush Meadow were harvested on 30 July 1999 and those in Nursery Field between 4 and 8 August 1999

Fig. 1 Mean and standard errors of log-transformed numbers of *A. jacobaeae* per plant in **a** Rush Meadow and **b** Nursery Field over the first 18 days of the experiment. *Square symbols* indicate predator exclusion and *triangles* predator access to aphid colonies. *Solid symbols* are fertilised and *open symbols* unfertilised plants. Each treatment was replicated on 11 plants

$P = 0.89$). Again more winged morphs were found on plants with predator exclusions, reflecting the higher number of aphids on this treatment (Fig. 3).

Nursery Field (day 20–65)

On day 18, plants in the predator exposure and exclusion treatment were swapped and then aphid densities were tracked for a further 45 days. Again, predator

Table 2 Mean ($\pm$ SE) persistence time (in days) of experimental aphid colonies with and without predators, on plants that were either fertilised or not

Treatment	Rush Meadow (1–18)	Nursery Field (1–18)	Nursery Field (20–65)
+ F − P	17.27 ± 1.1	18	30.4 ± 4.9
+ F + P	7.8 ± 1.1	9.6 ± 1.9	10.9 ± 3.9
− F − P	16.54 ± 1.1	18	27.1 ± 5.1
− F + P	9.64 ± 1.1	10.0 ± 1.6	10.9 ± 3.1

Every treatment was replicated on 11 plants. The first phase of the experiment was terminated at day 18 by which time some of the colonies protected from predation were still persistent

effects dominated any influence of fertilisation (Fig. 2). Colonies protected from predators survived on average three times longer than those open to predation (Table 2, $F_{1,40} = 16.99$; $P < 0.0001$) while there were no significant effects of fertilisation ($F_{1,40} = 0.15$; $P = 0.70$) or of an interaction ($F_{1,40} = 0.15$; $P = 0.70$). The repeated measures analysis of aphid densities again gave similar results with significant predator main ($F_{1,40} = 10.99$; $P < 0.002$) and predator–time interaction effects, but with no significant main or interaction effects involving the fertiliser treatment (Table 3c1; Fig. 3).

Ants and natural enemies

Two species of ants were identified tending aphids in our experiment: *L. niger* (L.) and *Myrmica ruginodis* Nylander. Seventy three percent of colonies in Rush Meadow and 64% in Nursery Field were tended by ants. The

Table 3 Within subject effects of repeated-measure ANOVAs for number of aphids [ln $(x + 1)$-transformed] and ants per aphid (arcsin-square root-transformed) over the course of the experiment. (a1, a2) Rush Meadow, (b1, b2) Nursery Field, day 1–18, (c1, c2) Nursery Field, day 20–68

Effect	df	MS	F	P
(a1) Number of aphids: Rush Meadow				
Day	2.98	29.0	24.70	0.0001
Day×Predation	2.98	10.97	9.35	0.0001
Day×Fertiliser	2.98	0.45	0.38	0.76
Day×Pred×Fert	2.98	0.95	0.81	0.49
Error	119.0	1.17		
(a2) Number of ants per aphid: Rush Meadow				
Day	3.54	0.40	4.41	0.003
Day×Predation	3.54	0.10	1.15	0.33
Day×Fertiliser	3.54	0.002	0.28	0.87
Day×Pred×Fert	3.54	0.002	0.25	0.89
Error	134.4	0.009		
(b1) Number of aphids: Nursery Field, day 1–18				
Day	4.43	6.79	10.13	0.0001
Day×Predation	4.43	12.95	19.32	0.0001
Day×Fertiliser	4.43	0.88	1.32	0.26
Day×Pred×Fert	4.43	0.76	1.14	0.34
Error	177.2	0.67		
(b2) Number of ants per aphid: Nursery Field, day 1–18				
Day	4.44	0.008	1.13	0.34
Day×Predation	4.44	0.005	0.68	0.62
Day×Fertiliser	4.44	0.003	0.43	0.80
Day×Pred×Fert	4.44	0.106	1.53	0.19
Error	177.57	0.007		
(c1) Number of aphids: Nursery Field, day 20–59				
Day	1.67	162.35	9.46	0.001
Day×Predation	1.67	98.29	5.73	0.008
Day×Fertiliser	1.67	6.52	0.38	0.65
Day×Pred×Fert	1.67	2.01	0.12	0.85
Error	66.85	17.16		
(c2) Number of ants per aphid: Nursery Field, day 20–59				
Day	4.64	0.54	7.80	0.000
Day×Predation	4.64	0.006	0.82	0.53
Day×Fertiliser	4.64	0.002	0.30	0.90
Day×Pred×Fert	4.64	0.003	0.54	0.73
Error	180.90	0.007		

The fractional degrees of freedom are derived from the Greenhouse-Geisser correction for non-sphericity

Fig. 2 Mean and standard errors of log-transformed numbers of *A. jacobaeae* per plant in Nursery Field between day 20 and 65 after the treatment exchange (see Materials and methods). Colony monitored daily until day 56 by which time only colonies from which predators had been excluded persisted. Thereafter, colony size was measured every 3 days. *Square symbols* indicate predator exclusion and *triangles* predator access to aphid colonies. *Solid symbols* are fertilised and *open symbols* unfertilised plants. Each treatment was replicated 11 times
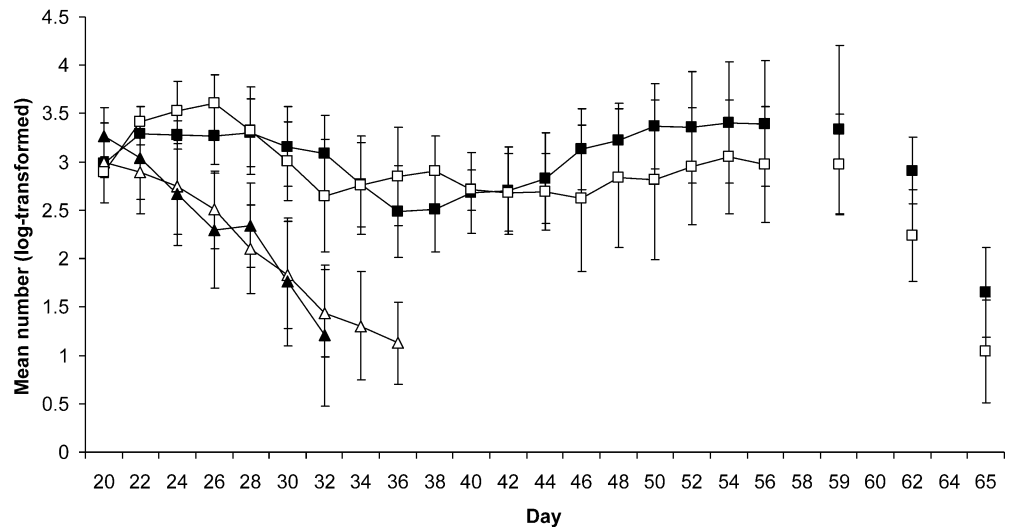
number of individual ants recorded on each plant was correlated with aphid colony size ($R_P = 0.62$; $n = 88$, $P < 0.001$), but was unaffected by the presence of the predator exclusion traps (Table 3a2, b2, c2). The two species of ants were of approximately equal abundance in Nursery Field, whilst in Rush Meadow *M. ruginodis* was dominant, and found at 94% of those colonies with ants. The intensity of ant-attendance (number of observed ants per aphid) was not different among treatments (Rush Meadow: $F_{3,40} = 0.054$; $P = 0.98$; Nursery Field, day 1–18: $F_{3,40} = 0.093$; $P = 0.96$; Nursery Field, day 20–65: $F_{3,40} = 0.056$; $P = 0.64$; Table 3a2, b2, c2).

During the experiment, no mummified aphids were found indicating that parasitoids were not a significant natural enemy in this system. The main predator groups observed on our target plants were spiders, anthocorid bugs, earwigs (*Forficula* sp.) and small predatory mites; very few aphid-specific predators were observed (Table 4). In the second phase (day 20–65) of the experiment in Nursery Field, predatory midges (*Aphidoletes aphidimyza* (Rond.): Diptera; Cecidomyiidae) that specialise on aphids became the dominant predators.

Discussion

We have previously shown that establishment of the aphid *A. jacobaeae* on ragwort *S. jacobaea* in Rush Meadow is prevented by the action of generalist predators that are maintained on other, earlier colonising species of aphids (Müller and Godfray 1999b). We hypothesised that this process of 'diffuse apparent competition' (Holt and Lawton 1994) may be modified by altered resource quality (Lawton and McNeil 1979; Hacker and Bertness 1995). Surprisingly, the results of this second field experiment showed that fertilisation played a negligible factor affecting aphid colony growth. That fertilisation had so little impact in Rush Meadow may be partly explained by the fact that none of the plant traits we measured seemed to be affected by our fertiliser treatment. Possibly the relatively fertile soil in the damp meadow meant the plants growing there were not nutrient limited, though measures of soil and foliar nitrogen in the experimental plants would be needed to confirm such a claim.

In Nursery Field, where plants responded to the addition of fertiliser by increased productivity, this treatment still had no effect on the course of colony growth of *A. jacobaeae*. In all sites and phases of the experiments predator effects dominated and determined aphid populations, and we found no evidence of an interaction between the predator exclusion and fertilisation treatments on aphid colony size.

We also found some evidence for an effect of aphid predators on plant performance (see Table 1). In Nursery Field, fertilisation increased plant performance positively, but for both groups, fertilised and unfertilised
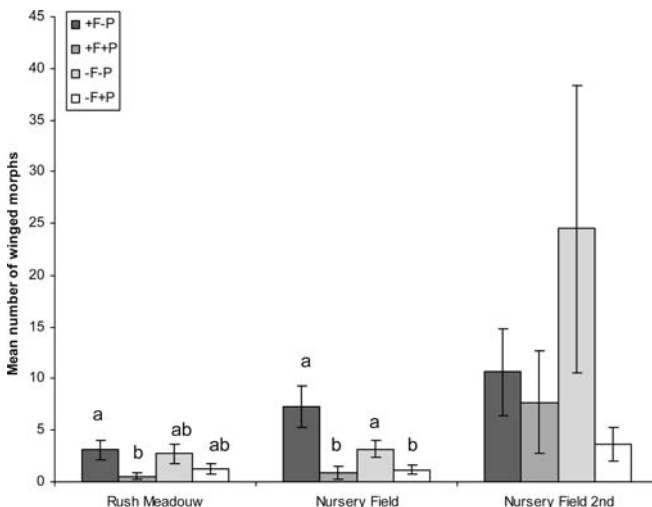
Fig. 3 Mean and standard errors of the cumulative number of winged morphs produced by each treatment group in Rush Meadow, Nursery Field, day 1–18, and Nursery Field second, day 20–68. The *small letters* above the bars indicate contrasts by Tukey tests

Table 4 Collected and observed predator groups on the experimental plants for the two phases of the experiment

	Total predators	Spiders	Bugs	Mites	Beetles	Midges	Earwigs	Syphids	Ladybirds
Rush Meadow	316	112	79	77	8	0	34	2	4
Nursery Field	232	76	64	37	2	17	34	0	2
Nursery Field (day 20–65)	711	56	98	16	26	403	81	4	9

The most abundant predators were generalists, while aphid specialists were relatively rare, except for predatory midges (*Aphidoletes aphidimyza* (Diptera: Cecidomyiidae)) that became abundant in the second phase of the experiment

plants, predator addition leads to a further positive effect on plant performance. A more complicated pattern was found in the other field site, Rush Meadow (see Table 1), possibly because the experiment at this site was terminated earlier than at Nursery Field and aphid herbivores could not have similar effects. Cascading effects of predators, as the ones within fertilised and unfertilised plants in Nursery Field, have been found in other natural terrestrial systems (reviewed by Schmitz et al. 2000) and can be caused by vertebrate or invertebrate predators.

Ants were present in our system, though they were not manipulated. However, we found no effects of ants on aphid colony performance, possibly because in this system ants are facultative mutualists and can use aphids as a protein resource as well as for honeydew production (Seifert 1996). Further study is required to confirm this, but casual observations suggest in particular that *M. ruginodis* in Rush Meadow may act more as a predator. Interestingly, the commonest type of interaction in which positive effects of predators on plants have been observed involve ants where the plant and the ant have a mutualistic relationship with the ant protecting the plant from herbivores and the plant providing shelter or some other resource (Schmitz et al. 2000).

The content of defensive pyrrolizidine alkaloids in our experimental plants could have been changed by the fertiliser addition. Unfortunately, we did not measure such potential changes in plant chemistry in this study. However, if nutrient addition reduces alkaloid concentration in plants (Hol et al. 2003), possible influences on aphid growth should have been measured as a fertiliser effect. We could not detect any strong fertiliser effects on growth of the specialist *A. jacobaea* and therefore believe that such effects via plant defence compounds are very small if they exist. In addition, it has been suggested that performance of specialist herbivores may be improved dependent on environmental factors, such as sandy soils compared to humid clay and peat soils (Vrieling and de Boer 1999). This latter fact could explain why aphids show overall poorer colony growth in Rush Meadow compared to Nursery Field.

For the last 10 years, we have been studying a community of aphids and their natural enemies on wild plants in an abandoned meadow (Müller and Godfray 1997; Rott et al. 1998; Müller et al. 1999; Müller and Godfray 1999b; Morris et al. 2001). The results of this earlier work plus the experiments presented here suggest how both lower and higher trophic levels combine to determine aphid community structure. Most of the aphid species at our field site are highly host specific, and of course a primary determinant of aphid community structure is the spectrum of plants available for colonisation. But the presence of a nutritionally suitable host plant is not sufficient to enable a species to persist. *A. jacobaeae* is absent from the Rush Meadow site, even though trapping studies show it to be a relatively common component of the aerial insect plankton (Müller and Godfray 1999b). It fails to colonise because the guild of aphid natural enemies present in the site, particularly, the predators prevent it (Müller and Godfray 1999b; this study).

It would be highly desirable to know more about the guild of predators that exclude *A. jacobaeae* from the site. In our earlier experiment, we designed interception traps to exclude crawling and crawling plus flying predators and found that they combined roughly additively to influence aphid colony parameters. This suggests that quite complex interactions may be involved. Studies of aphid predators, largely in crop situations suggest other still more complex interactions may come into play, for example intraguild predation that can interfere with a simple trophic cascade model of community dynamics (Polis et al. 1989; Rosenheim et al. 1995; Ferguson and Stiling 1996; Müller and Brodeur 2003; Finke and Denno 2004).

A further interesting question is why some species of aphids get excluded, while others are able to persist. One possibility is that some species have refuges from predation. For example, one of the commonest aphids at our study site is *Capitophorus carduinis* that feeds on thistle, *Cirsium* sp. Though attacked by predators, a certain fraction of the population seem to be protected by feeding in the densely appressed leaves of the plant's growing shoots. *A. jacobaea* is a colony-forming aphid and as such may be relatively easy to discover by natural enemies. Species that feed in more dispersed aggregations may enjoy a probabilistic refuge from predation (Hassell 2000) that allows them to survive in the face of strong predator attack.

Another way of saying an aphid species persists at a site is that population growth due to reproduction more than counterbalances loss due to predation. Part of the motivation for this study was to find out whether fertilising the plant led to greater aphid population growth rates that allowed persistence. We found no evidence of that here. Nevertheless, we suspect population growth rates do play an important role in aphid community

structure. In particular, comparisons of our old-field aphid community with those on crop plants suggest predators are far more important in natural habitats (Hawkins et al. 1999), and this may be due to the higher growth rates of aphids in agricultural environments where their host plants are fast growing and normally fertilised.

Predator induced cascades (Schmitz et al. 2000; Schmitz 2003), interspecific competition among herbivores (Gurevitch et al. 2000; Chase et al. 2002) and apparent competition via natural enemies (Holt 1977; Holt and Lawton 1994; Wootton 1994; Chaneton and Bonsall 2000) all play important roles in structuring natural food webs. In some cases, resource limitations will constrain the action of natural enemies on herbivore populations (Abrams and Schmitz 1999; Petersen and Hunter 2001; Gonzales et al. 2002; Bonsall and Holt 2003), while in other cases apparent competition prevails (Settle and Wilson 1990; English-Loeb et al. 1993; Hanna et al. 1997; Bergeson and Messina 1997, 1998; Müller and Godfray 1997; Morris et al. 2004). To understand the conditions when either of the two structuring forces is dominant, experiments have to be designed that manipulate both, resources and the predator community. This has only been done convincingly in microcosms (Balciunas and Lawler 1995) and microbial communities (Bohannan and Lenski 2000) and remains a challenge for terrestrial invertebrate systems.

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