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Herbivore identity mediates the strength of trophic cascades on individual plants

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Abstract. The strength of top-down indirect effects of carnivores on plants (trophic cascades) varies greatly and may depend on the identity of the intermediate (herbivore) species. If the effect strength is linked to functional traits of the herbivores then this would allow for more general predictions. Due to the generally sub-lethal effects of herbivory in terrestrial systems, trophic cascades manifest themselves in the first instance in the fitness of individual plants, affecting both their numerical and genetic contributions to the population.

We directly compare the indirect predator effects on growth and reproductive output of individual *Vicia faba* plants mediated by the presence of two aphid species: *Acyrtosiphon pisum* is characterised by a boom and bust strategy whereby colonies grow fast and overexploit their host plant individual while *Megoura viciae* appear to follow a more prudent strategy that avoids over-exploitation and death of the host plant. Plants in the field were infested with *A. pisum*, *M. viciae* or both and half the plants were protected from predators.

Exposure to predators had a strong impact on the biomass of individual plants and the strength of this effect differed significantly between the different herbivore treatments. *A. pisum* had a greater direct impact on plants and this was coupled with a significantly stronger indirect predator effect on plant biomass. Although the direct impact of predators was strongest on *M. viciae*, this was not transmitted to the plant level, indicating that the predator-prey interactions strength is not as important as the plant-herbivore link for the magnitude of the indirect predator impact. At the individual plant level, the indirect predator effect was purely due to consumptive effects on herbivore densities with no evidence for increased herbivore dispersal in response to presence of predators.

The nature of plant-herbivore interactions is the key to terrestrial trophic cascade strength. The two herbivores that we compared were similar in feeding mode and body size but differed their way how they exploit host plants, which was the important trait explaining the strength of the trophic cascade.

Key words: aphid; feeding mode; predator; Syrphidae; terrestrial; trophic cascade; *Vicia faba*.

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Introduction

Communities of interacting species are shaped not only by the direct interactions among species such as predation and interference competition, but also by indirect interactions. These are the effects of one species on another as mediated by at least one intermediate species. Examples

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include apparent competition (Holt 1977, Bonsall and Hassell 1997, van Veen et al. 2006), in which two prey species interact via a shared natural enemy, and various trait-mediated indirect effects in which induced chemical, morphological and behavioral defenses play a role (Beckerman et al. 1997, Abrams and Vos 2003, Dicke et al. 2003). The types of indirect interactions that have probably received the most attention are those that cascade up or down a chain of trophic interactions (Strong 1992, Polis 1999, Polis et al. 2000).

Top-down trophic cascades are the indirect effects of higher-level consumers on lower trophic levels, e.g., the indirect effects of predators on plant biomass by controlling herbivore populations. The term is used widely to refer to the effects of carnivore removal on whole producer communities, both in terms of diversity and total biomass, and on subsets of communities and single species populations (Strong 1992, Schmitz et al. 2000). The latter case is sometimes termed a species cascade (Polis 1999). Although earlier considered to be a feature mostly of aquatic systems (Strong 1992), there is also ample evidence for terrestrial trophic cascades (Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Mooney et al. 2010*a*).

In terrestrial systems, the effects of herbivory are often sub-lethal and hence the short-term effects of trophic cascades are likely to be on the growth and reproductive output of individuals. These effects on individual plants are rarely measured in this context (Tooker and Hanks 2006) but are crucial to understanding the mechanism of indirect predator effects on plant populations and communities (Knight et al. 2006, Mooney et al. 2010*b*). For individual plants, predators can affect both their contribution to recruitment, through seeds, and their genetic contribution to the population, through seeds and pollen.

Positive indirect effects of carnivores on producers can be caused by a reduction in the density of herbivores, due to their consumption by the carnivores, but it has also been shown that the presence of natural enemies can induce dispersal morphs and -behavior (Weisser et al. 1999, Sloggett and Weisser 2002, Kunert et al. 2005, Kunert et al. 2007) which, locally, can also result in a reduction in herbivore density. Alternatively, the presence of natural enemies may cause a change in the behavior or other traits of the herbivore, which reduce its per capita feeding rate and therefore its impact on the producers (Beckerman et al. 1997, Schmitz et al. 1997, Holt et al. 2010).

There is large variation in the strength of trophic cascades, much of which remains unexplained, especially in terrestrial systems (Borer et al. 2005). One explanation for weak effects is that positive indirect effects of predators on plants via herbivores may be counteracted by negative effects via mutualists, especially pollinators (Knight et al. 2006). Most other theories center on the idea that herbivore growth is limited by plant defenses and stoichiometric constraints (Polis 1999), which means that herbivores have little direct impact on plants and hence there is little potential for indirect effects from predators. It has indeed been demonstrated that the strength of indirect predator effects varies strongly among closely related plants and is positively associated with the plants response to soil fertility but not related to the strength of herbivore suppression (Mooney et al. 2010*b*).

As well as the plant species, the identity of the consumer species involved in a trophic (species) cascade may also have a major impact on its effects at the producer level (Polis and Strong 1996, Persson 1999, Shurin et al. 2002, Otto et al. 2008, Schmitz 2008). These effects of species identity suggest that the distribution of trophic cascade strengths among systems is idiosyncratic; however, if the effect strength is linked to functional traits of the herbivores then this would allow for more general predictions to be made. Within invertebrate herbivores, differences in feeding modes (e.g., sap feeders, leaf chewers, gall formers) are thought to be likely to play a role for shaping the strength of trophic cascades (Moon and Stiling 2002). However even within functional groups important traits such as the strategy of resource exploitation, susceptibility to predators or growth rate are likely to vary and might serve as better predictor for their impact on the community.

Part of the difficulty in testing the species-specific effects is the variety of experimental methods and systems that are compared in meta-analyses and a much more powerful method is to compare species-specific responses within a

single experiment (Beckerman et al. 1997, Mooney et al. 2010*b*). Here we directly compare the indirect predator effects on the growth and reproductive output of individual plants as mediated by two similar sap feeding herbivore species, within a single field experiment. These two species differ in two important traits: their susceptibility to predators and their impact on host plants. We expect that both higher susceptibility of the herbivore to predators and a stronger impact on host plants lead to a stronger trophic cascade. We further test whether reduced densities of herbivores in the presence of predators are due only to consumptive effects, or whether there is an additional effect caused by increased investment in dispersal morphs, i.e., a trait-mediated indirect effect.

Methods

Study organisms

Our focal plant species was *Vicia faba* var. 'de Sutton' (broad bean). We used the aphid species *Acyrthosiphon pisum* (Harris) and *Megoura viciae* (Buckton) as the herbivore species to mediate the indirect effects of the naturally occurring predator community (Fig. 1). Both species are sap-feeding herbivores of a similar body-size and weight (Fig. 1; Sutter, *unpublished data*). We have observed that *A. pisum* shows clear cycles of resource over-exploitation in population cage experiments, even when the resource is regularly renewed (van Veen et al. 2005) while, in similar experiments, *M. viciae* displays no such cycles, and despite reaching similar population densities to *A. pisum*, this rarely results in the death of the host plants. In natural populations, *M. viciae* suffers very low levels of attack by parasitoid wasps (Müller et al. 1999, van Veen et al. 2008), is rarely found infected with entomopathogenic fungi (van Veen et al. 2008) and it is poisonous to some generalist insect predators (Dixon 1958). In contrast, *A. pisum* is susceptible to a large community of parasitoids, pathogens and insect predators (Müller et al. 1999, van Veen et al. 2008). Thus, because of the way it exploits its host, we would expect that *A. pisum* has a bigger effect on its host plant than *M. viciae* and that natural enemies have a relatively larger indirect positive effect on the host plant when *A. pisum* is the intermediate species, because of its greater susceptibility.

All aphids used in the experiments came from laboratory populations maintained for approximately one year prior to the experiment. Both *A. pisum* and *M. viciae* populations consisted of a single clone, collected from the host plant *Lathyrus pratensis* in Silwood Park in the South East of England. Laboratory cultures were maintained on the host plant *Vicia faba* var. 'de Sutton' (broad bean) at 20°C and a 16:8 h light:dark cycle.

Field experiment

Sixty potted two-week old broad bean plants (*V. faba*) were placed out in a meadow in Silwood Park in the South East of England. The plants were arranged in a ten by six grid with a spacing of 5 m between plants. Plants were inoculated either with *A. pisum*, *M. viciae* or both species. We further included a treatment with both aphid species present to test whether the presence of *M. viciae* can protect the more susceptible species *A. pisum* from predation through a positive trait-mediated interaction and therefore reduces the strength of the trophic cascade (see van Veen et al. 2009). Half the plants were then protected from predators (see below), giving a total of six treatments. Each of the ten rows in the grid contained all six treatments and the position of the treatments within the row was randomized.

Aphids were introduced as five apterous adults per species 24 hours before the start of the experiment and were contained on the plant by means of plastic cylindrical cages (10 × 30 cm). These cages were removed at the start of the experiment. In the predator exclusion treatments the plants were covered with 60 × 60 cm cylindrical wire cages (5 mm mesh diameter) covered in fruit tree grease. This method has previously proven to be an effective means of excluding the majority of aphid predators while not affecting shading and airflow enough to have a significant effect on microclimate (Müller and Godfray 1999). The cages also exclude potential pollinators, however *Vicia faba* plants are known to have the ability to develop seeds through self-pollination with seed production being more limited by plant resources than pollinator presence (Holden and Bond 1960, Suso et al. 1996). The aphid colonies were allowed to develop for 42 days (starting 23 May 2003) after which all the

Fig. 1. The focal species *Vicia faba*, with the aphids *Acyrthosiphon pisum* (pale green) and *Megoura viciae* (dark green, black appendages) and the eggs of predatory Syrphidae. Note the similarity in size of the aphid species. Photo: Frank van Veen.

plants were collected. The plant roots were washed clean of soil after which each plant was divided into underground parts, above ground vegetative parts and reproductive parts (flowers and seed pods). To obtain dry weights the sections were placed in individual paper bags and placed in an oven at 60°C for three days and weighed to the nearest 0.01 g.

Aphids and predators were counted daily throughout the experiment. No natural enemies were observed until day 21 and there was no difference in numbers of aphids between exposed and protected colonies up to this point. The aphid population dynamics are analyzed in detail elsewhere (van Veen et al. 2009). Here we focus on the cumulative colony sizes (based on daily counts) after the arrival of predators and their effects on plant biomass. The relative number of disperser morphs (alatae), was also counted for each colony to test for species-specific responses to colony density and exposure to predators.

Statistical analysis

Since one would expect the greater biomass of plants exposed to predators to be due to a reduction in aphid numbers we performed an ANCOVA, with plant biomass as response variable and cumulative aphid numbers, aphid species (Ap, Mv or Ap + Mv) and exposure to predators as explanatory variables. Plants containing either just *A. pisum* or *A. pisum* + *M. viciae* were not significantly different from each other so these two factor levels were merged.

To test whether aphid number and species identity had an impact on reproductive output of

plants, we performed a similar ANCOVA as above but with reproductive tissue (flowers + seed pods) dry weight as response variable. After stepwise model simplification (using the Akaike Information Criterion) only the presence/absence of *A. pisum*, exposure to predators and the interaction between these two variables remained in the final model, which explained 65% of variation in reproductive tissue biomass.

In addition to the absolute amount we also tested for effects on reproductive biomass as a proportion of total biomass. The proportion data were arcsine square-root transformed and analysed as a function of the exposure to predators and the aphid species treatment.

We further tested for the effects of species identity, colony density (defined as the log of the number of individuals per gram plant dry-weight) and exposure to predators on the proportion of alates (dispersal morph) in each colony. The analysis was carried out on single-species colonies only. Because the data were overdispersed, we used quasibinomial errors with a dispersion parameter for the final model of 8.74.

Direct and indirect effect magnitudes of predator impact on aphids and plant biomass were calculated using the log ratio [ln(VP+/Vp−)] where VP+ and Vp− are community variables (herbivore abundance and plant biomass) in the presence (three-level treatment +) and absence (two-level treatment −) of predators (Schmitz et al. 2000), respectively.

Results

Total plant biomass

When protected from predators, mean cumulative population sizes in single-species colonies were significantly larger for *M. viciae* at 7448 ± 908 (mean ± SE) than for *A. pisum* at 4548 ± 1041 ($t_{1,18} = -2.1$, $p = 0.05$). Despite this, the mean total biomass of plants occupied by *A. pisum* was significantly lower than those occupied by *M. viciae* (mean 1.4 g vs. 6.2 g; $t_{1,18} = -6.5$, $p < 0.001$; Fig. 2A). For both single-species and mixed-species treatments, plant biomass was greater when the plants were exposed to predators (Fig. 2A). The effect was the greatest when *A. pisum* was the intermediate species with 3.3 times more plant biomass in the presence of predators, compared with 1.8 and 2.5 times for *M. viciae* and *A. pisum* + *M. viciae*, respectively. The effects were similar on above ground, below ground and reproductive tissue (Fig. 2B).

There was a clear effect of the exposure to predators and the presence of *A. pisum* on plant biomass and also a significant interaction between these two factors because the relative difference in biomass between protected and exposed plants was smaller for *M. viciae*-only colonies (Table 1). There was only a clear negative relationship between aphid numbers and plant biomass in the presence of predators (Fig. 3), indicated by the significant interaction between predator exposure and aphid numbers (Table 1). Thus, including aphid numbers in the model did not explain all the variation in plant biomass caused by exposure to or protection from predators. This model explained 75% of variation in plant biomass.

Reproductive tissues

Plants in all treatments produced flowers but only those that were occupied by *M. viciae* alone and were exposed to predators produced seed pods. The significant interaction between the presence/absence of *A. pisum*, and the exposure to predators term indicated a greater absolute difference in reproductive tissue between plants exposed to or protected from predators when they hosted only *M. viciae* than when they hosted either just *A. pisum* or both species (Table 2).

The proportion of reproductive tissue was significantly greater in the presence of predators ($F_{1,58} = 32.4$, $p < 0.001$; Fig. 2B) in all aphid treatments and was significantly greater in the *M. viciae* treatments than when *A. pisum* was present ($F_{1,58} = 20.1$, $p < 0.001$). The interaction between these factors was not significant ($F_{1,56} = 0.3$, $p > 0.5$).

Aphid dispersal morph production

M. viciae produced a significantly greater proportion of alates than *A. pisum* ($F_{1,37} = 244.4$, $p < 0.001$) and for both species the proportion of alates increased with colony density ($F_{1,37} = 37.4$, $p < 0.001$; Fig. 4). Species and density together explained 87% of deviance and no further significant deviance was explained by either their interaction ($F_{1,36} = 0.20$, $p > 0.6$) or the exposure to predators ($F_{1,36} = 0.49$, $p > 0.4$).

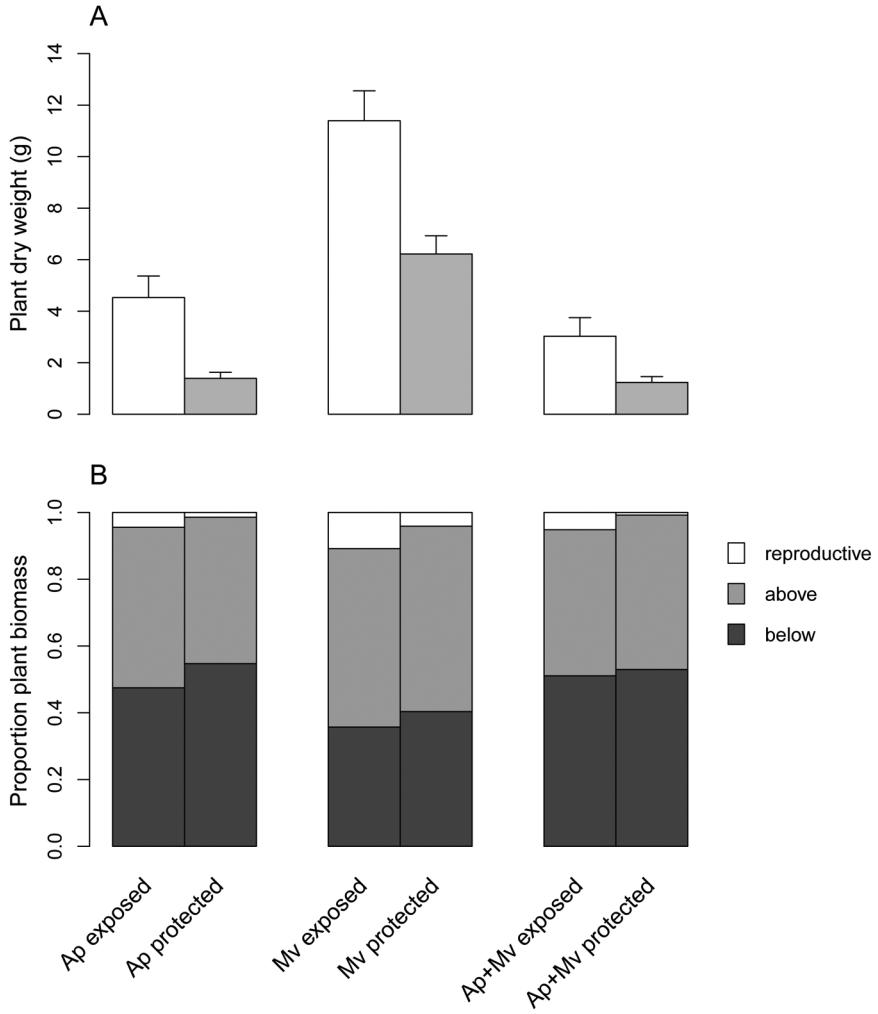

Fig. 2. (A) Mean (±SE) individual plant total biomass in the six experimental treatments. Grey bars represent plants protected from predators and white bars represent unprotected plants. (B) Mean relative contribution of above and below ground vegetative parts and reproductive parts. Ap = *Acyrthosiphon pisum*; Mv = *Megoura viciae*.

Predator densities and predator impact

The only predators present at the aphid colonies were hoverfly larvae (Syrphidae). We found no differences in hoverfly density between treatments (Ap: 6.3 ± 1.3, Mv: 3.9 ± 0.6, Ap + Mv: 5.1 ± 1.0, $F_{2,27} = 1.47$, $p = 0.24$). The predator numbers per aphid were 40% lower when *M. viciae* was present on the plants (Mv and Ap +

Table 1. ANCOVA on total plant biomass with cumulative aphid density, aphid species (*M. viciae* vs. *A. pisum* and *A. pisum* + *M. viciae*) and exposure to predators as explanatory variables.

Variable	df	Deviance	Residual df	Residual deviance	F	p
Null			59	1013.85		
Aphid density	1	31.15	58	982.70	6.56	0.013
A. pisum present	1	606.13	57	376.58	127.59	7.70e−16
Exposure to predators	1	69.12	56	307.45	14.55	0.00035
Aphid:predator	1	26.51	55	280.94	5.58	0.022
A. pisum:predator	1	24.42	54	256.53	5.14	0.027

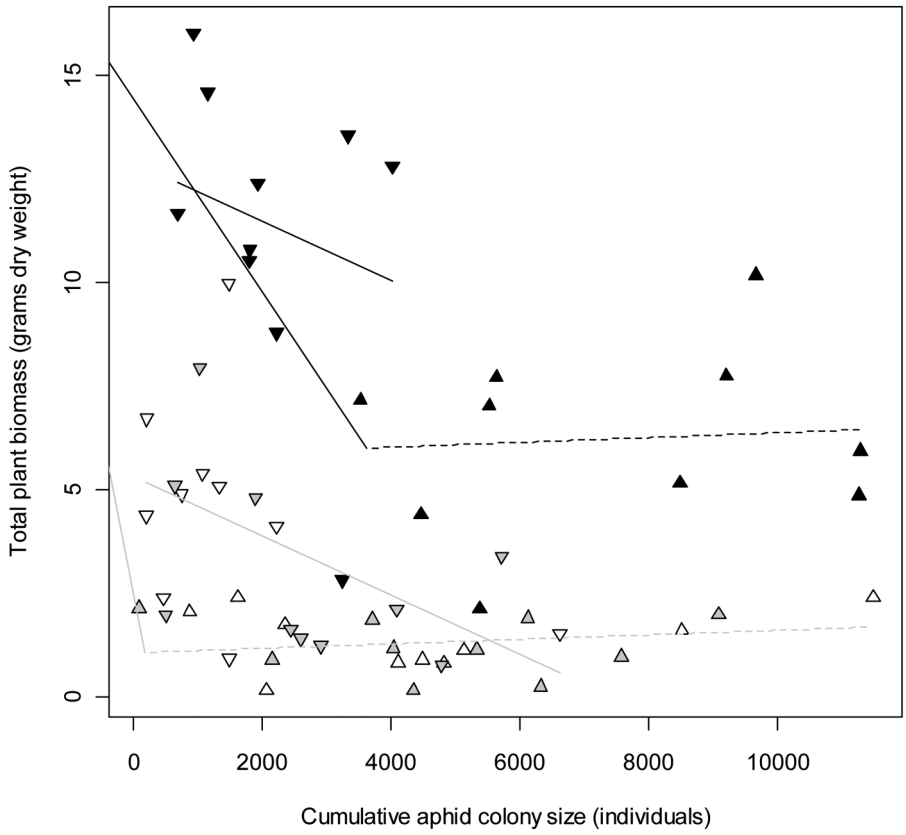

Fig. 3. Results of ANCOVA on total plant biomass. Downward pointing triangles represent plants exposed to predators, upward pointing triangles represent plants protected from predators. Plants with *M. viciae* are in black, with *A. pisum* in white and plants with both species grey. Fitted lines are solid for predator exclusion plants and dashed for plants exposed to predators. Black lines give model fit for *M. viciae* plants, grey lines for plants containing both species and those containing just *A. pisum*, as these were not significantly different.

Mv: 0.0011 ± 0.0002) than on plants with *A. pisum* only (0.0019 ± 0.0003, $F_{1,27} = 5.16$, $p = 0.031$). The direct predator impact on herbivores was biggest for *M. viciae* only and least when both were species together on one plant (Fig. 5). The indirect predator impact on plant biomass was strongest for plants with *A. pisum* only, which was reduced when adding *M. viciae*, and lowest for *M. viciae* only plants.

Discussion

Our results show that two herbivore species with identical feeding modes and similar body

Table 2. ANCOVA on reproductive plant biomass (flowers and seed pods). After model simplification only the presence/absence of *A. pisum*, exposure to predators and the interaction between these two variables remained in the final model.

Variable	df	Deviance	Residual df	Residual deviance	F	p
NULL			59	16.36		
A. pisum present	1	5.83	58	10.53	57.62	3.65e−10
Exposure to predators	1	3.01	57	7.52	29.78	1.14e−06
A. pisum:predator	1	1.86	56	5.66	18.40	7.15e−05

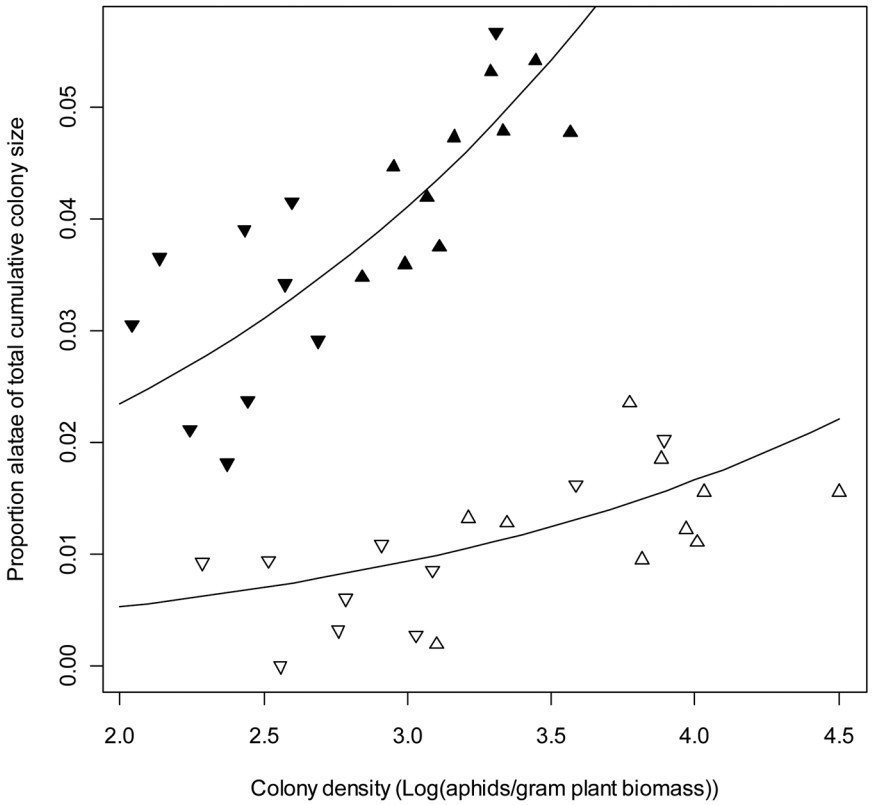

Fig. 4. The proportion of dispersal morphs (alatae) of total cumulative aphid colony size as a function of colony density. Black triangles represent *M. viciae*, white triangles represent *A. pisum*. Downward pointing triangles are used for exposed colonies and upward pointing triangles for colonies that are protected from predators Predator exposure had no effect while species identity and colony density explain 87% of deviance.

sizes, but differences in their susceptibility to predators and their strategy to exploit host plants lead to very different strengths of indirect predator effects on plant biomass. In the absence of predators, plants with a colony of *M. viciae* attained a 4.5 times greater biomass than plants with an *A. pisum* colony, despite *M. viciae* colonies being larger. Thus despite a much greater depletion of the resource, less biomass is accumulated at the herbivore level when *A. pisum* is present. The greater per capita impact of *A. pisum* is coupled with a significantly stronger indirect predator effect on the host plants as indicated by the significant species:predator interaction term for both total and reproductive plant biomass (Tables 1 and 2). It has been suggested that terrestrial trophic cascades are generally weak due to weak effects of herbivores on plants (Shurin et al. 2002). Our results suggest that terrestrial trophic cascades can be very strong but that indeed the difference in strength with the different herbivores is mainly due to the different effects that these species have on their host and not to different effects of the predators on the different herbivores. This is in agreement with results from an experiment comparing plant-species effects that also found that variation in trophic cascade strength is determined by plant-herbivore interactions rather than herbivore-predator interactions (Mooney et al. 2010*b*). We found more predators per aphid on plants with *A. pisum* only then on those with *M. viciae*, however the direct impact of predators on aphid populations was strongest for *M. viciae* as a single species (Fig. 4). Therefore the stronger direct impact on *M. viciae* is not transmitted to the producer level, indicating that the predator-prey interactions strength is not as important as the plant-herbivore link (Fig. 5). Combining the two aphid species reduced the direct predator impact

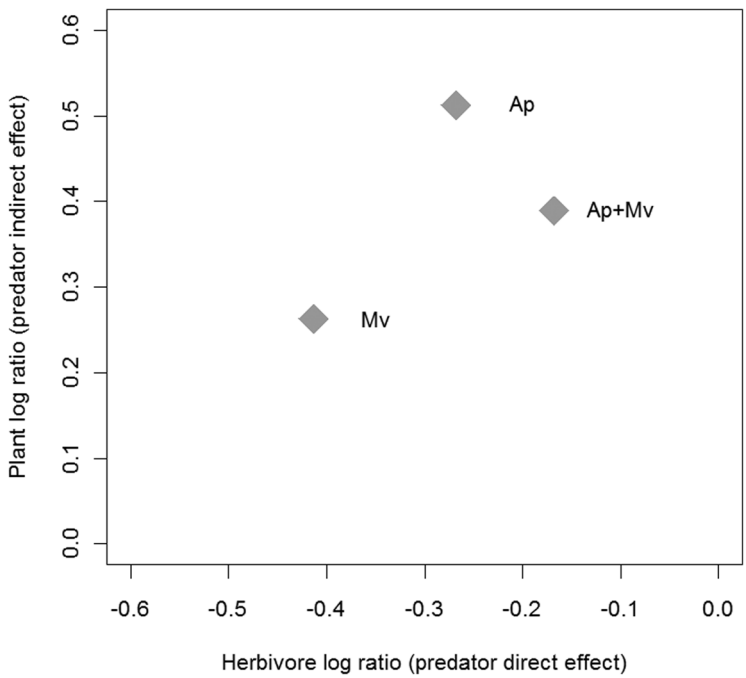

Fig. 5. Relationship between the magnitude of direct effects of predators on aphids and indirect effect of predators on plant biomass mediated by the different aphid communities. Ap = *Acyrthosiphon pisum*; Mv = *Megoura viciae*.

on aphids and also weakened the predator indirect effects on plant biomass as compared to plants with *A. pisum* only (Fig. 5). As syrphid larvae have longer development times and lower survival rate when feeding on *M. viciae*, its inclusion in the diet of syrphids may lead to a reduced predation of nearby *A. pisum* colonies (van Veen et al. 2009) and thus a reduction in the predator indirect effects.

We measured the indirect predator effect on individual plants rather than on population or community level biomass. The results indicate that although the effect on plant biomass is strongest when *A. pisum* is present, the effect at a population level is likely more significant when *M. viciae* is the intermediate species. This is because in the latter case, plants exposed to predators produced seeds while those shielded from predators did not. In this case, there is therefore a clear potential for a numerical response at the plant population level. In the presence of *A. pisum*, no plants produced seeds, whether exposed to predators or not. The effect of the predators on the reproductive output of individual plants is therefore confined to their genetic contribution to the population via pollen. For annual plants, the numerical response of the plant population to a trophic cascade may therefore contain a stepwise element that depends on whether the effect allows plants to reach a threshold biomass for seed production. In perennial and predominately vegetatively producing species the effects are likely to follow a more continuous trajectory.

We found no evidence for a predator effect on the proportion of dispersers that aphid colonies produced, and therefore we conclude that, at the individual plant level, the indirect predator effect is purely due to consumptive effects on herbivore densities with no additional dispersal-mediated effect. The proportion of dispersers appeared to be largely determined by a species-specific response to density, expressed as cumulative number of aphids per unit biomass. This is in contrast to laboratory studies that have demonstrated an increased production of dispersal morphs in response to predators and parasitoids (Weisser et al. 1999, Kunert et al. 2005, Kunert et al. 2007). It may be that the cumulative population numbers that we used did not allow us to

pick up subtle predator effects at particular stages of colony development. However, the fact that species identity and cumulative colony density explained 87% of variation in the proportion of alatae indicates that there is little room for an additional predator effect at this scale. This does of course not exclude the possibility that predators affect aphid dispersal at a larger spatial scale with aphids responding to alarm pheromones at a population scale.

Although we attribute the trophic cascade to consumptive effects of predators on aphids, plant biomass was only partly explained by aphid numbers: There was a negative relationship between aphid number and biomass in the presence of predators, as expected, but not in their absence. In the absence of predators, part of the variation in aphid numbers is likely itself due to plant health resulting in a bottom-up effect obscuring the negative effects of the aphids. In the presence of predators, control of the aphid population is top-down and now there is a clear effect on biomass. Therefore, aphid density needs to be regarded with some caution as an explanatory variable for plant biomass because it is itself a response variable to the experimental treatment and causality can be in both directions.

Why the different effects on the host plant from the two aphid species? *M. viciae* affects the plant far less (but still enough to record a clear trophic cascade), despite greater abundance and similar body weight (Sutter, *unpublished data*). A similar difference in ratio of plant biomass lost to aphid biomass gained has been found among aphid species on cereals (Migui and Lamb 2007). Some species appear to be characterized by a boom and bust strategy whereby colonies grow fast and overexploit their host plant individual while other species appear to follow a more prudent strategy that avoids over-exploitation and death of the host plant. The latter strategy is possible in aphids, from an evolutionary point of view, due to the clonal reproduction during the summer months which, in some species at least, may lead to monoclonal colonies in which cooperation can occur without cheats (Hodgson 2002). From our results we therefore hypothesize that *M. viciae* forms predominately mono-clonal colonies while *A. pisum* occurs mostly in multi-clonal colonies.

Conclusion

We found large indirect effects of predators on plant individual biomass and reproductive output. These depend on the nature of the interaction between herbivore and plant and in particular the species-specific negative effect of herbivores on their host plant which, between these two herbivores, does not appear to be related to energy transfer between the trophic levels. This corroborates previous work that indicated that the nature of plant-herbivore interactions is the key to terrestrial trophic cascade strength (Mooney et al. 2010*b*). Since the two herbivores that we compared are ecologically very similar (feeding mode, body size) but differ in two important traits (susceptibility to predators and their per capita effects on host plants), this indicates that detailed knowledge of species interactions, rather than general 'functional' traits, is required to make predictions on the strength of trophic cascades in ecological communities.

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