

**IDEA AND
PERSPECTIVE**

Understanding biodiversity effects on prey in multi-enemy systems

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Abstract

Biodiversity–ecosystem functioning theory would predict that increasing natural enemy richness should enhance prey consumption rate due to functional complementarity of enemy species. However, several studies show that ecological interactions among natural enemies may result in complex effects of enemy diversity on prey consumption. Therefore, the challenge in understanding natural enemy diversity effects is to predict consumption rates of multiple enemies taking into account effects arising from patterns of prey use together with species interactions. Here, we show how complementary and redundant prey use patterns result in additive and saturating effects, respectively, and how ecological interactions such as phenotypic niche shifts, synergy and intraguild predation enlarge the range of outcomes to include null, synergistic and antagonistic effects. This study provides a simple theoretical framework that can be applied to experimental studies to infer the biological mechanisms underlying natural enemy diversity effects on prey.

Keywords

Additive effects, biological control, complementarity, ecosystem functioning, intraguild predation, phenotypic niche shifts, predator diversity, redundancy, resource partitioning, synergy.

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INTRODUCTION

Determining the relationship between biodiversity and ecosystem functioning has become a major thrust in contemporary ecology. Biodiversity and ecosystem functioning studies typically analyse the extent to which an ecological process is affected by variations of species richness and composition, i.e. what happens to ecosystem process rates if species are taken out of or added to a community (Hooper *et al.* 2005). Much of the seminal work in this area has focussed on interactions at a single trophic level considering, for example, effects of plant species richness on measures of primary productivity. While not without exceptions, much of this research indicates a positive effect of biodiversity (generally species richness) on measures of ecosystem functioning (Hooper *et al.* 2005 and references therein). Generally, it has been suggested that increasing species diversity should enhance ecosystem process rates via complementarity of species resource use until some saturation is reached (Loreau *et al.* 2001; Hooper *et al.* 2002).

Somewhat independent to the biodiversity–ecosystem functioning literature, a body of research has been devel-

oped exploring predator–prey interactions and the effects of multiple natural enemies on the process of overall prey consumption rate (Sih *et al.* 1998; Ives *et al.* 2005). Until recently (e.g. Wilby & Thomas 2002b; Cardinale *et al.* 2003; Finke & Denno 2005; Ives *et al.* 2005; Wilby *et al.* 2005), this research has tended not to be viewed in a biodiversity–ecosystem functioning context; this in spite of the fact that the concepts are inherently similar (i.e. effects of diversity on process rate) and that natural pest control is a key ecosystem service provided by biodiversity (Wilby & Thomas 2002b; Kremen 2005; Tscharntke *et al.* 2005). Similar to the positive effects of diversity suggested above, from a predator–prey perspective high diversity of natural enemies should offer more ‘solutions’ for consuming prey in different environmental conditions (Altieri 1999; Wilby & Thomas 2002b; Tscharntke *et al.* 2005). However, several studies show that adding more natural enemies to a system does not necessarily ensure higher consumption rates of prey and can actually result in lower consumption rates due to antagonistic interactions between enemies (Rosenheim *et al.* 1995; Rosenheim 1998; Finke & Denno 2004, 2005). On the other hand, synergistic interactions are also possible

such that overall consumption rate is more than the sum of single species consumption rates (Losey & Denno 1998, 1999; Cardinale *et al.* 2003). In fact, empirical studies show that adding natural enemies to a system may result in a full spectrum of outcomes including null, additive, antagonistic or synergistic effects (e.g. Losey & Denno 1998; Bogran *et al.* 2002; Finke & Denno 2004; Rosenheim *et al.* 2004; Wilby *et al.* 2005). That is, prey consumption rates may show an idiosyncratic pattern (Johnson *et al.* 1996; Wilby & Thomas 2002a) with irregular variation of process rate in relation to changes in species richness and composition.

In summary, it appears that patterns of prey consumption are determined by resource partitioning together with ecological interactions among natural enemies (Sih *et al.* 1998; Ives *et al.* 2005). Therefore, the challenge in understanding enemy diversity effects on prey mortality is to predict overall prey consumption rates taking into account effects arising from patterns of prey use together with species interactions (Ives *et al.* 2005). In this paper we develop the multiplicative risk model (Soluk 1993; Sih *et al.* 1998) to explore the effect of prey use patterns and interspecific interactions on consumption rates of prey in multiple enemy assemblages. We show how complementary and redundant prey use patterns result in additive and saturating effects, respectively, and how ecological interactions, such as phenotypic niche shifts, synergy, interference and intraguild predation (IGP), enlarge the range of effects. The simple theoretical framework developed here can be applied to experimental studies to infer the biological mechanisms underlying enemy diversity effects on prey.

PREY USE PATTERNS: REDUNDANCY AND COMPLEMENTARITY OF NATURAL ENEMIES

Functional redundancy of species refers to the degree to which organisms do similar things (Rosenfeld 2002a), while functional complementarity refers to the degree to which organisms do different things. For example, species of natural enemies feeding on the same prey may use the resource during different life stages (e.g. Bogran *et al.* 2002; Wilby & Thomas 2002b) or in different microhabitats (Losey & Denno 1998; Sih *et al.* 1998; Borer *et al.* 2004). Indeed, sympatric organisms may differentiate their action or place as a result of ecologically based divergent selection, a process that arises through ecological interactions between individuals and the environment, and evolution of population gene pools (Rundle & Nosil 2005). In general, species can do different things as a consequence of genetic differences, or they can differentiate their action by changing the phenotype.

Phenotypic plasticity in resource use patterns can be particularly relevant in changing environments, where individuals must be able to keep functioning, coexist and

survive in a vast array of environmental conditions (Agrawal 2001; Piersma & Drent 2003). Individuals change behaviour, physiology and morphology in relation to the ecological conditions that they experience or are able to forecast. For example, individual specialization of feeding habits is distributed across a broad range of taxonomic groups, including invertebrates (Bolnick *et al.* 2003). Also, niche shifts in space and time can be a behavioural consequence of IGP (Polis & Holt 1992). Interestingly, it has been shown that parasitoid species can show phenotypic plasticity in host use depending on the level of competition (Bogran *et al.* 2002).

In synthesis, the evolution of sympatric enemies and their ecological interactions may result in functional complementarity in prey use. By acknowledging the importance of past and present ecological interactions in community assembly (Rosenzweig 1995; Chesson 2000), many researchers assert that complementarity of species is rather common in ecosystems (Wellnitz & Poff 2001; Hooper *et al.* 2002, 2005; Rosenfeld 2002a,b; Tschardtke *et al.* 2005), and we should perhaps expect that natural enemies are often functionally complementary to some extent (e.g. Soluk & Collins 1988; Tschardtke 1992; Losey & Denno 1998; Paine *et al.* 2000; Bogran *et al.* 2002; Chalcraft & Reserits 2003; Borer *et al.* 2004; Van Son & Thiel 2006).

PREDICTING PREY CONSUMPTION RATE IN MULTI-ENEMY SYSTEMS

In general, experimental studies on multi-enemy effects are performed by adding natural enemies/predators (for simplicity, hereafter we will refer to predators only) of different species to a prey system. However, it is often difficult to disentangle the relative influence of density vs. species richness in producing variation of consumption rates (e.g. Sih *et al.* 1998; Vance-Chalcraft *et al.* 2004) as adding a new predator species to a system produces a simultaneous increase in richness and density. It is therefore useful to treat density and biodiversity effects under the same framework. In fact, individuals of the same species can differ in their predatory behaviour and effectiveness, while individuals belonging to different species could have the same predatory action (Sih *et al.* 1998). In ecological systems, predators with different genotypes, physiological states and histories in general, can aggregate in the same location and use the available prey. Each individual can have a consumption rate that is to some extent unique (Bolnick *et al.* 2003). Therefore, at least as a starting point, it seems reasonable to assume that each individual has a given predatory rate on prey, no matter if predators belong to the same species or not. We also assume in the first instance that predators and prey behave independently (we consider how more realistic ecological interactions among individuals can be incorporated later).

If predators have independent effects, the proportion of prey that survive predation is:

$$S = (1 - p_1)(1 - p_2)(1 - p_3) \dots (1 - p_x) = \prod (1 - p_i), \quad (1)$$

where p_i is predation risk, i.e. the probability of prey being killed from each given predator P_i ($i = 1, 2, 3, \dots, x$), and $(1 - p_i)$ is the probability of prey surviving predation from predator P_i during a given interval (Royama 1981; Wilbur & Fauth 1990; Soluk 1993; Sih *et al.* 1998). This model is generally applied in multipredator studies to generate expected consumption rates of predator assemblages (Sih *et al.* 1998).

The number of prey surviving one time interval can be calculated as:

$$N_{t+1} = N_t \prod (1 - p_i), \quad (2)$$

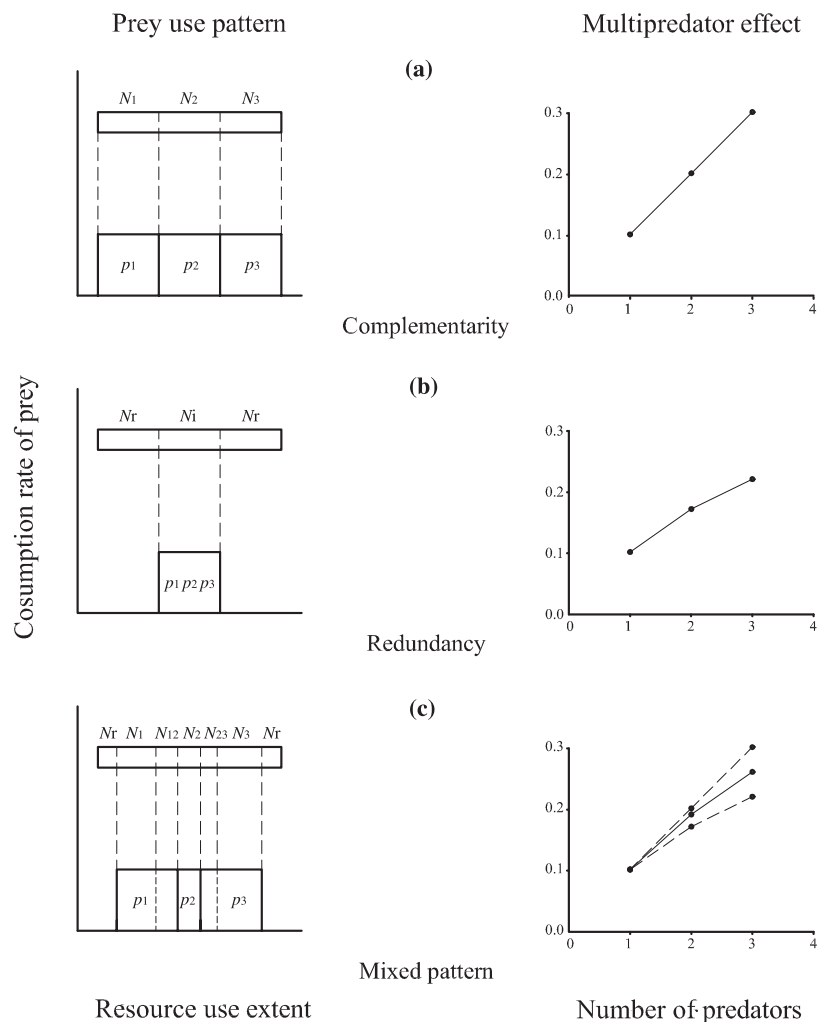
where N_t and N_{t+1} are total prey population size before and after predation respectively.

If predators are thought to have similar predation rates and resource use patterns, they can be grouped. In this case p'_i refers to the per capita average predation rate of predators belonging to a given group i (e.g. a species) of NP_i predators, and the formula can be generalized as below:

$$N_{t+1} = N_t \prod (1 - p'_i)^{NP_i}. \quad (3)$$

In this way, predator identity effects (e.g. Straub & Snyder 2006) arising from different per capita predation rate of predators (p'_i) can be separated from predator density (NP_i). This model assumes that the prey population under risk N_t is equally exposed to predation from all predators; that is, there is maximum redundancy among predators along the whole resource space exposed to predation. In reality, it is more likely that some part of the prey population under risk will be differently exposed to the action of different predators. Figure 1 shows patterns of resource use along one niche axis for a three-predator system, ranging from maximum

Figure 1 Effect of resource use patterns on consumption rates of prey. (a) Maximum complementary: three predators with similar individual consumption rate p_1, p_2 and p_3 , predate on different portion of the prey population, N_1, N_2 and N_3 respectively (left). The graph on the right shows that total prey consumption rate varies additively with increasing predator richness. (b) Maximum redundancy: three predators with similar individual consumption rate p_1, p_2 and p_3 , predate on the same portion of the prey population N_i . The relationship between total prey consumption rate and predator richness follows a saturating curve. (c) Mixed prey use patterns: three predators use different portions of the prey population and partially overlap in prey use. The relationship between total consumption rate of prey and predator richness lies in between the additive and the saturating curves (dotted lines).



complementarity (Fig 1a) to maximum redundancy (Fig 1b). When predation risk changes along a niche axis, the proportion of the population surviving predation can be calculated as:

$$N_{t+1} = \sum N_{i'}(1 - p_i)^{NP_i}, \quad (4)$$

where $\sum N_{i'}(1 - p_i)^{NP_i}$ is the sum term of the individuals belonging to prey subpopulations $N_{i'}$, exposed to predation risk p_i , that survive one time interval. By specifying differential prey use patterns in the model ($\sum N_{i'}$), effects arising from complementary prey use can be disentangled. Model 4 assumes that there is no overlapping in resource use by predators, which is, again unlikely. When predators overlap in their action to some extent, total prey consumption rate can be calculated by considering the extent of overlapping.

It can be noted that all above models are special cases of the following general model:

$$N_{t+1} = \sum N_{i'} \prod (1 - p_i)^{NP_i}, \quad (5)$$

where $\sum N_{i'} \prod (1 - p_i)^{NP_i}$ is the sum term of the individuals belonging to prey subpopulations $N_{i'}$, exposed to a set of predators P_i that survive one time interval. When a part of the prey population is not under risk, i.e. there is a refuge population (N_r), the respective p_i will be zero. If the prey subpopulations are at different levels of risk and predators overlap, the $N_{i'}$ s are subpopulations exposed to different combinations of predators (e.g. Fig. 1c).

EFFECT OF PREY USE PATTERNS ON CONSUMPTION RATES

Now, using the framework developed above, we show how different resource use patterns of predators are expected to affect multipredator consumption rates of prey. Specifically, we analyse in the first instance the cases of maximum complementarity, redundancy, and the more likely case of mixed patterns. In all scenarios, multipredator consumption rates are calculated by specifying in the model prey use patterns ($N_{i'}$) and the values of single-predator consumption rates (p_i). We also assume an additive design, where intraspecific predator densities are kept constant as predator richness increases (Sih *et al.* 1998; Ives *et al.* 2005).

Complementarity

Figure 1a shows a case where three predators are completely complementary in their predatory action. For simplicity predators are assumed to have the same predation rate (0.3) and to attack 1/3 of the prey population. If predation is independent, the expected overall consumption rate is

calculated using model 4, where $N_{i'}$ is N_1 , N_2 and N_3 , and $N_r = 0$. Figure 1a also shows the relationship between consumption rate and biodiversity when 1, 2 or 3 complementary predators are added. The relationship is additive and reaches a maximum at 0.30, which results from the constant predation rate of 0.30 exerted over the whole exposed prey population. This result shows that additive effects arise when additional predators use different portions of the prey population. Therefore, the mechanism underlying additive effects of multiple predators on prey is complete complementarity in prey use of predators.

Redundancy

We now consider a case where three predators are completely redundant in their predatory action. For simplicity, predators are assumed to have the same predation rate (0.3) and to attack 1/3 of the prey population (here N_r is 2/3). If predation is independent, the expected consumption rate is calculated using model 3, where $N_{i'}$ refers to the population under risk and N_r to the refuge population. Figure 1b shows also the relationship between consumption rate and biodiversity when 1, 2 or 3 redundant predators are added. The effect is saturating and, if more predators were added, would tend to reach an asymptote at 0.333, which corresponds to the total proportion of the population exposed to predation, 1/3. Note that adding redundant predators of different species and increasing the density of one predator species would produce the same effect. In this case, increasing interspecific or intraspecific density would produce identical outcomes because higher taxonomic richness does not correspond to higher functional richness; that is, $p'_1 = p'_2 = p'_3$ and $N_{i'1} = N_{i'2} = N_{i'3}$: the general model becomes $N_{t+1} = N_r + N_{i'}(1 - p')^{NP}$ and the curve depends only on the overall predator density (NP). In other words, density and biodiversity effects would show the same pattern resulting from the same process – complete redundancy of resource use, and they should perhaps be considered as *de facto* density effects.

Mixed prey use patterns

In Fig. 1c we present a more likely case where predators are both complementary and redundant to some extent. If predation is independent, the expected consumption rate can be calculated using model 5. For example, for a three-predator system with predator P_2 partially overlapping with P_1 and P_3 , as in Fig. 1c, the proportion of the population surviving after one time interval is given by:

$$N_{t+1} = N_r + N_{i'1}(1 - p_1) + N_{i'2}(1 - p_2) + N_{i'3}(1 - p_3) + N_{i'12}(1 - p_1)(1 - p_2) + N_{i'23}(1 - p_2)(1 - p_3), \quad (6)$$

where N_{r1} , N_{r2} , N_{r3} are the parts of the prey population exposed only to predator P_1 , P_2 and P_3 , respectively, while N_{r12} and N_{r23} are prey subpopulations simultaneously exposed to both predators P_1 and P_2 or P_2 and P_3 respectively. Expected values of consumption rates will result from a mixture of saturating and additive effects due to mixed patterns of resource use. Therefore, depending on the level of overlap, consumption rates of multipredator systems showing mixed patterns of resource use will lie somewhere in between the extremes of additive and saturating effects.

ECOLOGICAL INTERACTIONS EXTEND THE RANGE OF EFFECTS

The above scenarios show how different resource use patterns can produce saturating, additive or mixed effects. However, the models so far assume independence in predator and prey behaviour and as such do not capture effects such as phenotypic niche shifts, interference, IGP or

synergy that have been demonstrated empirically. We now consider more realistic scenarios where we expect not only mixed resource use patterns, but also interactions among predators and prey such that the basic model assumption of independence is violated.

Phenotypic niche shifts

Studies on the whitefly parasitoids *Eretmocerus mundus*, *Encarsia formosa* and *Encarsia pergandiella* (Aphelinidae, Hymenoptera) indicate that in the absence of competition, there is no preference in the size or position of whitefly nymphs selected for parasitism between the three species (Bogran *et al.* 2002). Such single species resource use patterns would suggest redundancy between parasitoids and should lead to a saturating rate of parasitism as species are added. However, when the parasitoids were combined *Encarsia formosa* tended to use larger whitefly individuals and *Encarsia pergandiella*, while still using whitefly individuals of

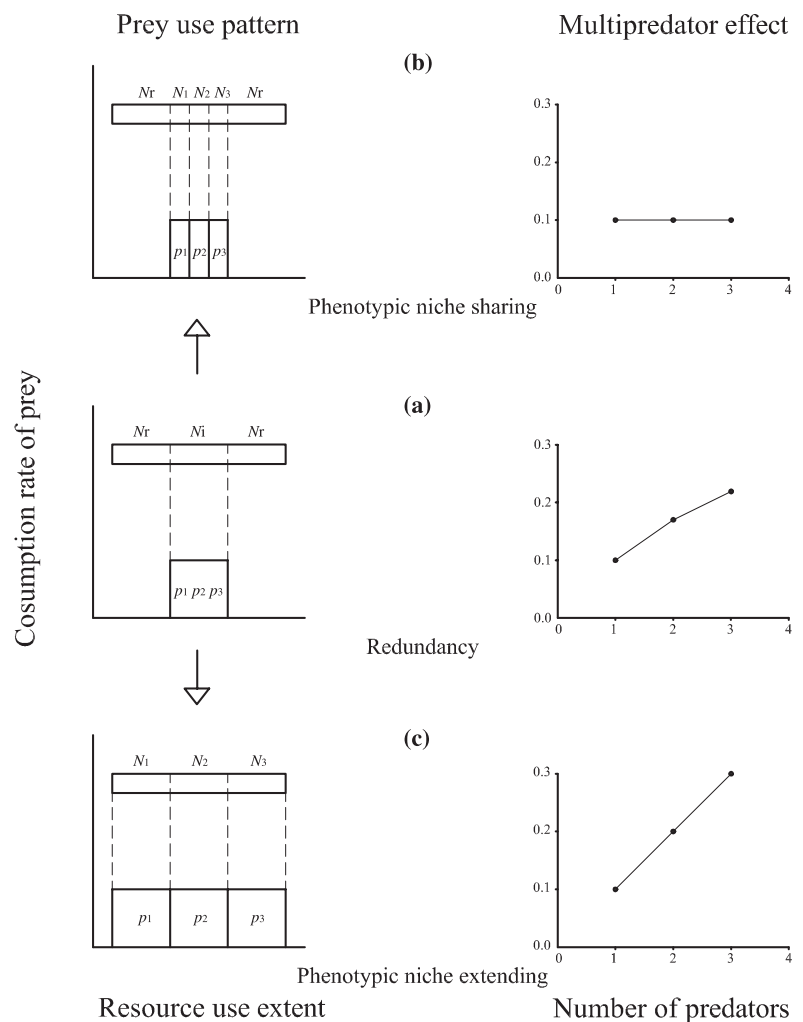


Figure 2 Phenotypic niche shifts may result in null to additive predator diversity effects. (a) Three redundant predators with similar individual consumption rate p_1 , p_2 and p_3 , predate on the same portion of the prey population N_r . The graph on the right shows the relationship between total prey consumption rate and predator richness. (b) The interaction among predators results in phenotypic niche sharing: predators avoid overlapping by further partitioning the prey population exposed to predation, N_r , in three prey subpopulations N_1 , N_2 and N_3 that are complementarily predated. If predation rates do not change as consequence of this interaction, total prey consumption rate does not vary with increasing predator richness, resulting in null effects. (c) Phenotypic niche extending: predators avoid overlapping by extending resource use to portions of the population previously unexploited. In such an ideal situation, we go back to the previous case of complete complementarity (Fig. 1a) and overall consumption rate is again additive.

the same size, shifted the distribution of parasitism on the host plants (Bogran *et al.* 2002). This demonstrates phenotypic plasticity in host use of parasitoids along two niche axes, induced by competitive interactions.

The effects of such phenotypic changes in prey use pattern are explored in Fig. 2. Let us start from three redundant predators that completely overlap in prey use (Fig. 2a). After a behavioural interaction, the three predators shift in prey use. Two possible outcomes are illustrated: in Fig. 2b predators simply share the resource and do not extend total prey use, whereas in Fig. 2c predators extend prey use to portions of the population previously unexploited (N_r). If predation rates do not change as a consequence of this interaction, the expected consumption rate can be calculated using model 4, where N_{ii} represents different portion of the population exposed to predation. Consider that N_r is 2/3 or 0 when the outcome of the interaction is niche sharing (Fig. 2b) or niche extending respectively (Fig. 2c). For simplicity, predators have the same consumption rate (0.3). When predators extend prey use and avoid overlapping, we go back to the previous case of complete complementarity (Fig. 1a). In such an ideal situation, overall consumption rate would again be additive. In the case of niche sharing (Fig. 2b) predators further partition the prey population previously exposed to predation (N_{ii}) and do not overlap. Consequently, there is no redundancy. However, as the total proportion of the prey population under risk and consumption rates do not change, the effect of adding predators is null. This range of effects from null to additive highlights the importance of understanding species interactions and consequent phenotypic shifts in prey use.

Intraguild predation and functional synergy

As indicated previously, one of the marked features of natural enemy diversity studies that adds complexity over many of the single trophic level biodiversity–ecosystem functioning studies is the potential for negative effects as species are added. That is, predator species may not act in an independent way and negative interactions such as IGP and interference can lead to reductions in prey consumption rate with increasing diversity (Rosenheim *et al.* 1993; Finke & Denno 2004). For example, lacewing predation on aphid populations can be dramatically reduced by adding true bugs into the system (Rosenheim *et al.* 1993). Indeed, true bugs respond strongly to moving prey, preferentially predating on lacewing larvae (Cisneros & Rosenheim 1997). Moreover, lacewing larvae escape from an attacking predator by running to the bottom of the plant (J. Rosenheim, personal communication). This behavioural interference would likely reduce the foraging activity of lacewings.

We explore this in Fig. 3a. Imagine p_1 as the predation rate on aphids of a population of lacewings, NP_1 , and p_2 as the predation rate on aphids of a population of true bugs, NP_2 . Predators have different predation rates and mixed resource use patterns. In this case, expected consumption rates can be calculated using the following model:

$$N_{t+1} = N_t + N_{t1}(1 - p'_{t1})^{NP_1} + N_{t12}(1 - p'_{t1})^{NP_1}(1 - p'_{t2})^{NP_2} + N_{t2}(1 - p'_{t2})^{NP_2},$$

where p'_i is the per capita predation rate of predators. However, if we allow asymmetric IGP of true bugs on lacewings, then overall consumption rates will be affected by the reduction in population NP_1 due to predation from NP_2 . That is, NP_1 becomes a function of NP_2 such that $NP_1 = f(NP_2)$ where f describes a level of intraguild predation. Even the per capita predation rate, p'_1 , and the extent of resource use, N_{t1} , could be reduced by true bugs as a consequence of inhibition of lacewing activity; that is, $p'_1 = f(NP_2)$ or $N_{t1} = f(NP_2)$ where f describes a level of interference. In all cases, the result is a decline in overall prey consumption rate as predator richness increases.

In contrast to negative interactions such as IGP, synergistic interactions are also possible whereby the total consumption rate of multiple predators is more than additive (Sih *et al.* 1998). For example, coccinellid larvae feeding on aphids on leaves may cause aphids to drop from plants and in so doing, increase the effective predation rate of ground based predators such as carabid beetles (Losey & Denno 1998, 1999). Again it is possible to capture this type of functional synergy within the modelling framework. Imagine a predator P_1 that facilitates the action of a second predator P_2 by changing the distribution of prey along the resource space axis, as pictured in Fig. 3b. The prey population under risk from P_2 , N_{t2} , increases as a consequence of P_1 activity. Observed mortality is consequently higher than expected. However, higher mortality is not due to a truly higher predation rate of P_2 but rather to the higher proportion of the prey population under risk. In this case, the assumption that prey distribution is independent from predator P_1 density is not met and instead $N_{t2} = f(NP_1)$.

DISCUSSION

Empirical studies on natural enemies show a much greater variation in response to changes in diversity than reported in most of the biodiversity–ecosystem functioning literature. This study reveals how these observed patterns can be explained in terms of variations of prey use patterns, per capita prey use rates, population size of predators, and predator and prey distribution. It also provides novel insights into well-established mechanisms such as complementarity: additive effects have often been explained with

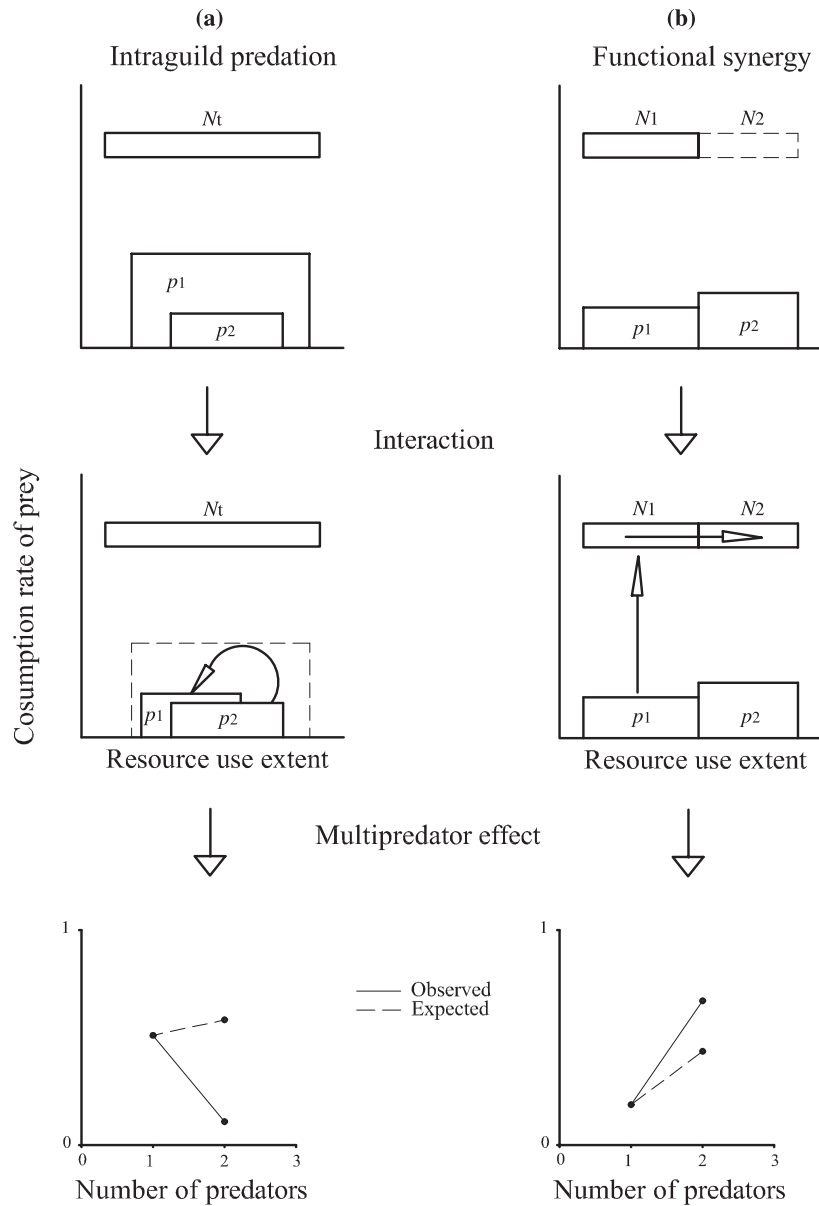


Figure 3 Intraguild predation and functional synergy enlarge the range of predator diversity effects. (a) Negative effects due to intraguild predation: two predators with different predation rates p_1 and p_2 , use the same resource, N_t , with some degree of overlapping. The ecological interaction between predators produces a reduction of predator P_1 abundance and activity, resulting in a lower p_1 and resource use extent. The observed multipredator effect (solid line) is consequently lower than expected (dotted line). (b) More than additive effects due to functional synergy: two predators with different predation rates p_1 and p_2 use different portion of the prey population, N_1 and N_2 respectively. The variation of prey distribution, due to avoidance of predator P_1 , results in a higher abundance of prey population N_2 under risk from predator P_2 . The multipredator effect is more than additive (solid line).

complementarity but the underlying mechanism has not been clarified in terms of simple mathematical consequences of prey population partitioning. Moreover, the study investigates the effect on consumption rate of prey of two types of phenotypic niche shift, prey use sharing and prey use extending (producing null and additive effects respectively). Despite the potential importance of phenotypic plasticity on predator diversity effects, this process has seldom been considered in experimental (but see Bogran *et al.* 2002) or theoretical studies of consumer diversity effects. While confirming the importance and the general positive effect of resource partitioning on ecosystem processes (Hooper *et al.* 2005; Ives *et al.* 2005), this study underlines that functional complementarity can be a

consequence of short-term phenotypic changes in resource use. In such cases, we showed that when complementarity arises from prey use sharing, positive effects might not emerge at all. Similar to Ives *et al.* (2005), we further identify that additional ecological interactions, such as IGP, can modify the expected effects of consumer diversity. Given the non-dynamical nature of our approach, we cannot explore the implications of prey use patterns, phenotypic shifts or other interactions for population processes such as species coexistence and stability (cf. Ives *et al.* 2005). Nonetheless, the study helps elucidate mechanisms by which prey use patterns and ecological interactions affect the short-term net predation rate of multiple enemy assemblages.

In this context the framework provides a useful tool for disentangling the relative importance of different process in generating the range of patterns observed in multiple enemy studies. Many predator diversity studies apply the multiplicative risk model to generate expectations of total predation (e.g. Soluk 1993; Losey & Denno 1998; Sih *et al.* 1998; Cardinale *et al.* 2003; Rosenheim *et al.* 2004; Vance-Chalcraft *et al.* 2004; Wilby *et al.* 2005); discrepancies between observed and expected values are then used to infer the presence of emergent effects. However, such discrepancies can be caused by various mechanisms that are not accounted for in the simple multiplicative risk model (Sih *et al.* 1998), but that are considered in the general model developed here. For example, complementarity, phenotypic niche shifts, and synergy can be modelled by properly specifying the N_{iS} (prey use patterns). Similarly, variation in predator density due to intraguild predation can be accounted for with an appropriate variation of NP_i . Note that the variation of NP_i could also be used to generate expectations adjusted for variation of predator density due to substitutive experimental designs, where total density of predators is kept constant across treatments (Sih *et al.* 1998; Finke & Denno 2005; Ives *et al.* 2005; Straub & Snyder 2006), as attempted in other studies (Van Son & Thiel 2006). Moreover, the framework could be applied to study other mechanisms responsible for diversity effects that have not been taken into account here. For example, the species identity or sampling effect, an important alternative mechanism that can result in positive predator diversity effects on prey (Hooper *et al.* 2005; Ives *et al.* 2005; Straub & Snyder 2006), could be studied by assuming different per capita predation rates (p'_i) among predators. Additionally, analysing the variation of the p'_i could be a valid way to study possible effects of intra- and interspecific predator density variations on per capita consumption rates.

However, it is important to stress that understanding the mechanisms underlying biodiversity effects by simply contrasting observed and expected values has some limits. Indeed, even apparently straightforward patterns obtained from simple systems where no interaction amongst enemies occurs, could be well explained by alternative models. For example, in Fig. 4 we generate biodiversity–consumption rate relationships obtained by adding one to 10 predators that are either functionally redundant or complementary. We consider three cases corresponding to three different predation rates (0.1, 0.3 and 0.9). Each predator uses the resource along 1/10 of a hypothetical axis of resource distribution. At high predation rates there is a clear differentiation between patterns generated by complementarity vs. redundancy, even when very few predators are added (Fig. 4a). In contrast when predation rates are low (or as would occur also when resources are abundant) it becomes difficult to discern which model best

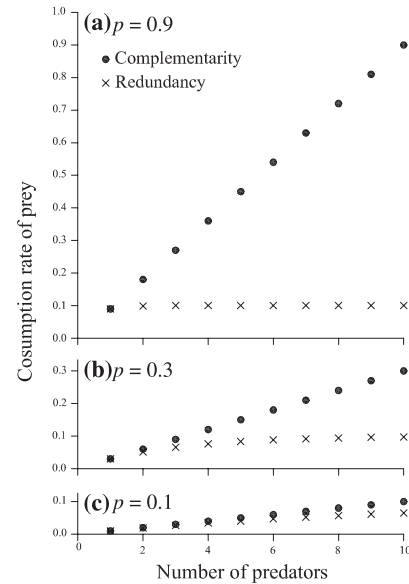


Figure 4 Biodiversity–consumption rate relationships obtained by adding one to 10 predators that are either functionally redundant (crosses) or complementary (dots). We consider three cases corresponding to three different predation rates: (a), 0.9; (b), 0.3; (c), 0.1. Each predator uses the resource along 1/10 of a hypothetical axis of resource distribution. At high predation rates (a, b) there is a clear differentiation between patterns generated by complementarity vs. redundancy, even when very few predators are added. In contrast, when predation rates are low (c) the two patterns are very similar.

describes the data, in spite of the fact that redundancy and complementarity represent such contrasting mechanisms. This suggests that the impact of prey use patterns on the emergence of species diversity effects will vary depending on the attack rates, which will be influenced by factors such as predator–prey ratio and functional response among others. Therefore, the framework could be used both to inform experimental design (few empirical studies appear to consider the potential importance of prey abundance and density of predators *a priori*) and to link auxiliary observations on prey use patterns (e.g. Bogran *et al.* 2002), occurrence of intraguild predation (e.g. Finke & Denno 2005) or variation of prey distribution (e.g. Losey & Denno 1998) to the variation of the correspondent model parameters, as discussed above. By identifying the most appropriate model, the relative importance of different processes in generating observed patterns could be better understood (Sih *et al.* 1998; Johnson & Omland 2004; Van Son & Thiel 2006).

Given the importance of natural enemies in providing natural pest control services, this study could also have utility in understanding and improving biological control. Effective biocontrol (whether through classical introduction

or conservation of natural enemies) relies on selecting the best species or combination of species, for maximizing consumption rates of prey (Ehler 1990). Our findings suggest that resource use complementarity should maximize net consumption rates as long as this is not a consequence of phenotypic prey use sharing (where there may be no net effect). Consumption rate can be increased further if additional enemies lead to refuges being broken and the utilization of previously unexploited parts of the prey population (see also discussion in Pedersen & Mills 2004 where a similar conclusion was obtained using an alternative modelling approach). On the other hand, the framework also reveals that if the prey refuge is small and the predation rate of a single predator species is high across the prey resource axis, then there might be little to be gained by adding more species over maximising abundance of existing species. The importance of refuge magnitude and the fact that refuge breaking could be achieved with phenotypic niche shifts of apparently redundant natural enemies point to the need to estimate the proportion of the prey population that is not at risk and to determine patterns of prey use both as single- and multispecies combinations (cf. Bogran *et al.* 2002). While clearly challenging, this type of mechanistic framework is rarely considered, particularly in conservation biocontrol (but see Kean *et al.* 2003).

Overall, this study reveals how patterns of prey use should determine net consumption rates, with interactions among species enlarging the range of effects. In order to understand the consequences of biodiversity change in natural enemy assemblages it is therefore important to disentangle effects arising from patterns of prey use and the numerical and behavioural consequences of ecological interactions among species. The framework presented here provides a useful tool that can be applied in that direction.

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