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REVIEW

A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning

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Abstract

The last 15 years has seen parallel surges of interest in two research areas that have rarely intersected: biodiversity and ecosystem functioning (BEF), and multispecies predator–prey interactions (PPI). Research addressing role of biodiversity in ecosystem functioning has focused primarily on single trophic-level systems, emphasizing additive effects of diversity that manifest through resource partitioning and the sampling effect. Conversely, research addressing predator–prey interactions has focused on two trophic-level systems, emphasizing indirect and non-additive interactions among species. Here, we use a suite of consumer-resource models to organize and synthesize the ways in which consumer species diversity affects the densities of both resources and consumer species. Specifically, we consider sampling effects, resource partitioning, indirect effects caused by intraguild interactions and non-additive effects. We show that the relationship between consumer diversity and the density of resources and consumer species are broadly similar for systems with one vs. two trophic levels, and that indirect and non-additive interactions generally do little more than modify the impacts of diversity established by the sampling effect and resource partitioning. The broad similarities between systems with one vs. two trophic levels argue for greater communication between researchers studying BEF, and researchers studying multispecies PPI.

Keywords

Biodiversity, indirect effect, intraguild predation, resource partitioning, sampling effect, trophic interactions.

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INTRODUCTION

There is a long and rich history of ecological studies that examine predator–prey interactions (PPI) and the role of predators in the suppression of prey populations (Hairston *et al.* 1960; Paine 1966; Hassell & May 1986; Murdoch & Briggs 1997; Polis 1999). Much of this work has been motivated by biological control efforts, in which predators or herbivores are introduced to suppress pest species. While there is long-standing appreciation that predator diversity potentially affects prey density (Walsh & Riley 1868; Pimentel 1961; Root 1973; Snyder *et al.* 2004), in the last 15 years there has been an explosion of interest in the complexities that arise from interactions within diverse predator–prey assemblages (Polis 1991; Polis & Holt 1992; Rosenheim 1998; Sih *et al.* 1998). This, in turn, has spawned a growing subdiscipline in ecology focused on multispecies predator–prey systems, which we term PPI.

Another subdiscipline generating much recent attention focuses on the role that biodiversity plays in ecosystem functioning (Chapin *et al.* 1998; Tilman 1999; Loreau *et al.* 2001; Naeem 2002), or biodiversity and ecosystem function (BEF). While community ecology has historically focused on how ecological processes maintain species diversity, the central question of BEF is how diversity affects, rather than responds to, ecological processes. While BEF has not developed in strict isolation from PPI (Wilby & Thomas 2002; Cardinale *et al.* 2003; Chalcraft & Resetarits 2003), the two research areas clearly have distinct histories and different emphases (Duffy 2002). Studies of BEF generally focus on additive mechanisms of diversity where the per capita effects of all species are assumed to be independent of the number of species in a community. In contrast, PPI studies have focused more on indirect interactions among predator species, and the nonlinearities that exist in PPI.

The aim of this article is to show that the emphases of BEF and PPI are complementary and can be merged into a general theoretical framework that describes the influence of consumer diversity in consumer-resource systems. Here, we use the terms 'consumer' and 'resource' broadly to encompass systems such as predators feeding on herbivores, herbivores feeding on plants, or plants 'consuming' (i.e. absorbing) nutrients. To highlight the similarities and differences between PPI and BEF studies, we compare systems with two trophic levels, in which the resources have density-dependent dynamics, to systems where non-dynamic resources effectively render a single trophic level of consumers. The former is the mainstay of PPI studies, whereas the latter is typical of BEF studies of plants consuming nutrients (Tilman *et al.* 1996; Hector *et al.* 1999) or detritivores consuming detritus (Jonsson & Malmqvist 2000; Duffy *et al.* 2001; Cardinale *et al.* 2002).

We centre our discussion on two related questions. First, how does consumer diversity affect the total density (or biomass) of resources? This question has its roots in PPI and biological control where the primary objective is often pest suppression. Second, how does consumer diversity influence the combined density (or biomass) of consumers? This question resonates with the BEF tradition, in which the production of biomass at the consumer trophic level is typically the response variable of interest. We structure our discussion around a set of models that illustrate four mechanisms through which consumer diversity can influence the combined densities of consumer species and their resources: (i) the sampling effect, (ii) resource partitioning, (iii) indirect effects caused by intraguild interactions, and (iv) non-additive effects. Mechanisms (i) and (ii) dominate the BEF literature, while (iii) and (iv) dominate the PPI literature. Following each model we synthesize ideas from theoretical and empirical studies of PPI and BEF, acknowledging that our review of the literature is not exhaustive; comprehensive reviews of PPI and BEF as separate subdisciplines are published elsewhere (Polis *et al.* 1989; Rosenheim *et al.* 1995; Johnson *et al.* 1996; Sih *et al.* 1998; Schmid *et al.* 2001; Holt & Loreau 2002).

Base models

As we designed the models to provide a scaffolding for the article, they do not contain the details needed to depict any specific, real system. They do, however, contain many qualitative features that apply broadly across consumer-resource systems. The basic model uses discrete time Lotka-Volterra-like equations, with the dynamics of M consumer species using N different resources given by

$$y_j(t+1) = y_j(t)\exp\left[\sum_{i=1}^{N} c_j b_{ij} x_i(t) - d\right], \tag{1}$$

where $x_i(t)$ and $y_j(t)$ are the densities of each resource i ($i = 1,\ldots,N$) and consumer species j ($j = 1,\ldots,M$) at time t. The per capita capture rate of consumer j on resource i is b_{ij}, the assimilation efficiency by which consumer j converts resource into new consumers is c_j, and the per capita consumer death rate is d, which is assumed to be the same for all species. Although we will refer to the values of $x_i(t)$ and $y_j(t)$ as densities, they could equally well be considered biomasses or any similar measure of abundance or standing stock.

To compare systems with one vs. two trophic levels, we use two different equations to describe resources. For resources having density-dependent dynamics, such as would occur in two trophic-level (i.e., predator–prey) systems, we use

$$x_i(t+1) = x_i(t)\exp\left[r\left(1 - \frac{x_i(t)}{K}\right) - \sum_{j=1}^{M} b_{ij} y_j(t)\right] \tag{2}$$

where r is the intrinsic rate of increase and K is the carrying capacity, both of which are assumed to be the same for all resources. For non-dynamic resources producing one trophic-level (plant–nutrient) systems, we use

$$x_i(t) = \max\left\{R - \sum_{j=1}^{M} b_{ij} y_j(t), 0\right\}, \tag{3}$$

where R is the renewal rate assumed to be the same for all resources and $x_i(t)$ is constrained to be non-negative. In eqn (3) the density of resources is simply that proportion of new resources renewed at each time step that remains following consumption. Note that resource densities $x_i(t)$ are simple functions of consumer densities $y_j(t)$; thus, eqn (3) can be used to remove explicit dependence on resource densities from eqn (1) leading to a model with a single trophic level.

A key feature of these basic models (eqns 1–3) is that the per capita population growth rate of any species (or resource) depends on a linear combination of the densities of the other species with which it interacts. In other words, we assume that species have additive effects on per capita population growth rates. In the discussion that follows, we consider several modifications to this basic model that illustrate four different ways in which consumer diversity can influence both resource and consumer densities.

The sampling effect

We begin by mathematically describing what is perhaps the simplest mechanism by which consumer diversity can impact consumer and resource densities. The mechanism has been called the 'sampling', 'selection' or 'selection-probability' effect in the BEF literature (Huston 1997; Tilman 1999; Fridley 2001; Loreau *et al.* 2001), and the 'lottery model' in biological control (Denoth *et al.* 2002). To illustrate how the mechanism works, consider a scenario in which there is a single resource, and m consumer species are chosen randomly from a pool of M possible consumers. Given the assumption that consumers have additive effects on resource abundance, only a single consumer species can persist in the system – the species which depresses the resource to its lowest equilibrium density. This is an old and well-known result (Nicholson & Bailey 1935), and is familiar in the community ecology literature as the R* principle (Tilman 1982). Although only one consumer species can persist, the probability that the most effective consumer will dominate the system is proportional to the number of consumer species added. This, in turn, causes the equilibrium resource density to decrease as consumer diversity m increases (Fig. 1a). It can be shown analytically (Appendix 1) that this result is true with either dynamic resources (two trophic-level systems) or non-dynamic resources (one trophic-level systems); hence, it represents a generality for both PPI and BEF.

Not only is the effect of consumer diversity on the equilibrium resource density via a sampling effect the same for both PPI and BEF systems, so is the effect of consumer diversity on the equilibrium consumer density (Appendix 1). Nonetheless, the effect of consumer diversity on consumer density is not a simple one (Fig. 1b). When consumer species differ in their assimilation efficiencies c_j, the most successful consumer is the species that most efficiently converts resources into new biomass, ultimately outcompeting other species because it achieves a high population density. This leads to a positive effect of consumer diversity m on consumer density (Fig. 1b). Conversely, if consumers differ in their capture rates, b_j, then the competitively superior species is the one that has the greatest per capita impact on resource density. A dominant consumer with a high capture rate depresses resource density, which in turn causes lower equilibrium consumer density. This leads to a negative effect of diversity on consumer density (Fig. 1b). Thus, the sampling effect of consumer diversity on consumer density depends on whether consumer species vary in assimilation efficiency or capture rates.

Synthesis

The sampling effect is commonly observed in both PPI and BEF studies. We have modelled the sampling effect for the case of a single resource, which leads to competitive exclusion of all but a single consumer species. This creates a particularly strong form of sorting process, with only one consumer species surviving from the m introduced species, and hence illustrates the sampling effect in its purest form. Although extreme, this type of pure sampling process is common in biological control. For example, in a recent meta-analysis of 167 biological control projects, Denoth *et al.* (2002) concluded that 'while the success of biological control frequently increases with the number of agents

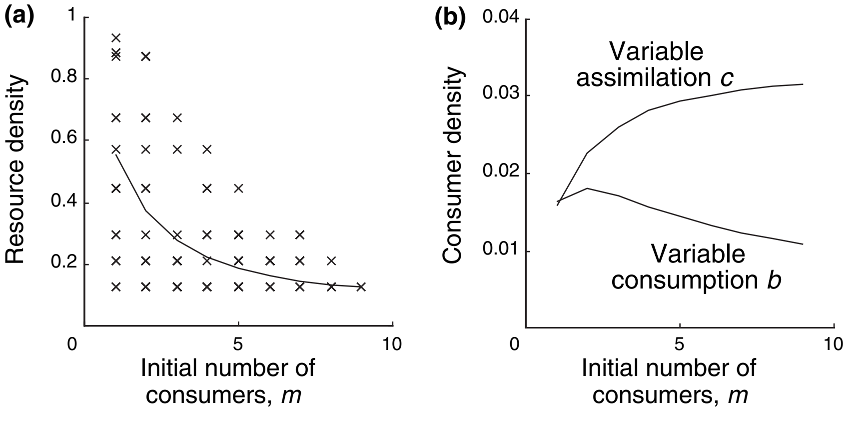

Figure 1 The sampling effect, in which m consumers are selected at random from a pool of nine consumer species and introduced into a system with a single resource species. (a) Equilibrium density of the resource species as a function of m, where x's mark the realization of 10 random selections of consumer species at each level of m, and the line gives the theoretical expectation for resource density vs. m (Appendix 1, eqn A1). (b) Equilibrium density of the surviving consumer species as a function of m for the cases in which consumers differ in capture rates, b_j, or assimilation efficiencies, c_j (Appendix 1, eqns A2, A3). For the case of variable capture rates, b_j were selected for the nine consumers in the species pool by assuming $1/b_j$ follows a uniform distribution, and all values of c_j were set to 1. For the case of variable assimilation efficiencies, c_j were given the same values as b_j in the case of variable capture rates, and b was set to the mean value of the variable b_js. This produces the same relationship between m and the expected density of the resource species given in (a). Other parameters are $r = 0.1$ and $K = 1$.

released, in more than 50% of the successful multiple-agent projects against weeds and insect pests, a single species was responsible for the success of control efforts'. The prevalence of strong sampling effects in the PPI literature may be, at least in part, the result of the fact that most biological control programmes introduce specialist natural enemies and thus are predisposed to find strong competitive sorting among control agents.

Although often less extreme, the sampling effect is common in BEF studies (Huston 1997). Although multiple introduced species coexist in typical BEF studies, the sorting process that increases the dominance of a subset of the m introduced species is no less important to produce the sampling effect (Loreau & Hector 2001; Holt & Loreau 2002; Cardinale *et al.* 2004). To prove this, consider the situation where m consumers are selected randomly from a pool of M species differing in some attribute, for example, productivity. In the absence of a sorting process, the expected productivity of the m species is simply the mean of the M species pool. Thus, increasing m alone cannot influence productivity, and the sampling effect only occurs after competition or some other sorting process accentuates the performance of the best species.

In our model, consumer diversity decreases resource density regardless of whether resources have density-dependent dynamics or not (Fig. 1a). This is consistent with numerous empirical studies of both BEF and PPI (Hector *et al.* 1999; Tilman *et al.* 2001; Cardinale & Palmer 2002; Denoth *et al.* 2002). Our second result, that consumer diversity may either increase or decrease consumer density (Fig. 1b), may be a surprise to BEF researchers, and we know of no BEF study showing decreased consumer density because of a sampling effect. However, this is familiar to PPI researchers because a common observation is that as more biological control agents are released, densities of both pest and control agents are reduced (Bess *et al.* 1961). In our model, the contrast between BEF and PPI is not the result of PPI systems having two trophic levels and BEF systems having just one; rather, it is because of consumer species varying in either their assimilation efficiencies or capture rates. This begs the question, do typical PPI and BEF systems differ fundamentally in which attributes make consumer species the competitive dominants? We suspect that, as a general rule, consumer species in PPI systems (predators) differ in capture (attack) rates, but there is little reason to expect that they differ widely in assimilation efficiency. In contrast, competitively dominant consumers in BEF systems (plants) tend to use their resources (nutrients) to achieve greater biomass, with greater biomass increasing their competitive impact on other species. There are, however, a number of possible exceptions to these generalities, such as phytoplankton that differ in nutrient uptake rates yet have comparable assimilation efficiencies, thereby possibly making them more similar to the predators in PPI studies than the plants in BEF studies. The impact of a sampling effect on consumer density warrants investigation in a broader range of systems.

Resource partitioning

A second mechanism that can affect the relationship between consumer diversity and the densities of resources and consumer species is resource partitioning. When consumer species use different resources, partitioning will give rise to more complete resource consumption in more diverse consumer assemblages (Tilman *et al.* 1997; Loreau 2000). To explore the effects of resource partitioning, we consider an assemblage of N resources to which are added m consumer species selected from a pool of M species. We structure the consumer species pool so that each consumer has a different preferred resource for which it has the highest capture rate, and consumer diet breadth is controlled by the parameter σ which ranges from 0 (complete specialists) to infinity (complete generalists). The capture rate of consumer j on resource i is described by

$$b_{ij} = \frac{w(\sigma)}{\sqrt{2\pi}\sigma}\exp\left[-\frac{(i-j)^2}{2\sigma^2}\right]$$

which reaches a maximum when $i = j$. We use the scaling term $w(\sigma)$ to compare systems with different consumer diet breadths; we assume $w(\sigma)$ decreases as σ increases so that the total capture rate of each consumer species, $\sum_{i=1}^{N} b_{ij}$, is independent of σ. This implies that there is an inherent trade-off so that consumers can capture a lot of one resource or a little of many different resources, but not a lot of all resources.

Note that within any system, we assume that the peak capture rates of all consumer species on their preferred resource are the same, and that all consumers have the same diet breadth. Although this symmetry is artificial, it eliminates the possibility of results being driven by individual species traits. Despite the symmetry, when generalist consumers are added sequentially to a system, with enough time between additions to allow the system to equilibrate, the order in which they are added influences which consumer species persist. For example, an added consumer that prefers a similar resource to several pre-existing consumer species is more likely to go extinct than an added consumer with different resource preferences from pre-existing consumers. To average out this variability and focus on diversity *per se*, we simulated 1000 'experiments' in which m consumer species were selected and introduced to the system in random order, with enough time between introduction to allow the system to equilibrate. From this we calculated the mean effect of adding m

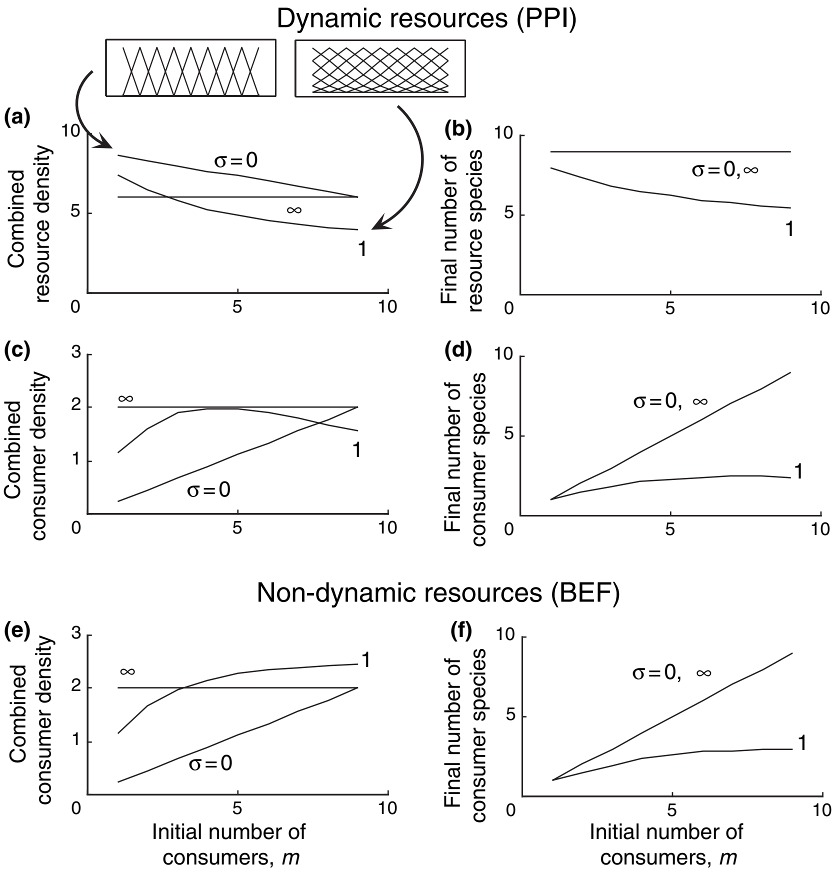

Figure 2 Resource partitioning and the effect of consumer diversity *m* on a community of nine resource species. For the system with two trophic levels, (a) gives the combined resource equilibrium density, (b) gives the number of persisting resource species, (c) gives the combined consumer equilibrium density, and (d) gives the number of persisting consumer species. For the system with one trophic level, (e) gives the combined consumer equilibrium density and (f) gives the number of persisting consumer species. In each panel, lines for specialist ($\sigma = 0$), moderate generalist ($\sigma = 1$), and extreme generalist ($\sigma = \infty$) consumers are labelled when they are sufficiently different. Lines represent the average of 1000 simulations at each level of *m* in which the order of consumer species added to the community was selected at random, and enough time is allowed between introductions for the population densities to equilibrate. The 'thumbnail' panels illustrate the distributions of b_{ij} for the cases of complete specialists and moderate generalists. Model parameters are $r = 1$, $K = 1$, $R = 1$, $d = 1$, and $c = 1$. Values of b_{ij} were scaled so that $\Sigma_{i=1}^{N} b_{ij} = 1.5$.

consumers on combined resource and combined consumer densities for those species that survive at equilibrium.

For systems with dynamic resources, increasing consumer diversity *m* leads to a decrease in the combined density of resources when consumers are specialists ($\sigma = 0$) (Fig. 2a). There is no effect when consumers are complete generalists ($\sigma = \infty$), however, because in this artificial case the consumers are identical to each other. Interestingly, resource density is reduced to the lowest levels when consumers are moderate generalists ($\sigma = 1$). This is caused by apparent competition (Holt 1977); consumer densities augmented by some resource species lead to higher consumption rates on other resource species, ultimately driving them extinct (Fig. 2b). When resource species go extinct, the total available resource density decreases correspondingly.

The influence of consumer diversity on combined consumer density reflects its effect on combined resource density. When consumers are specialists ($\sigma = 0$), increasing consumer diversity increases consumer density, but there is no effect of consumer diversity when species are complete generalists ($\sigma = \infty$) (Fig. 2c). When consumers are moderate generalists ($\sigma = 1$), the relationship between consumer diversity and the combined density of consumers is hump-shaped (Fig. 2c). This can be explained in terms of two opposing processes. First, increasing the number of consumer species increases the number of resource species that are heavily consumed, thereby increasing the spectrum of resources used by all consumers combined. This acts to increase combined consumer density. Second, increasing the number of consumer species increases the number of resource species that go extinct (Fig. 2b). With these extinctions, the total pool of resources diminishes, and this smaller resource pool acts to decrease the combined density of consumers. Thus, increasing consumer density simultaneously increases the completeness with which the consumers as a group use the pool of resources and decreases the size of the pool. With increasing diversity from low to moderate, the former process outweighs the latter, leading to an increase in combined consumer density, whereas the latter outweighs the former as diversity increases further, leading to a decrease in combined consumer density.

In comparison with the case of dynamic resources (PPI), there is one main difference when resources are non-dynamic (BEF); consumer density is a monotonically increasing function of consumer diversity when consumers are moderate generalists ($\sigma = 1$) (Fig. 2e). This is because extinction cannot occur for non-dynamic resources that are continuously renewed. Therefore, although pressure from consumers becomes greater with increasing consumer diversity, all resources continue to be renewed and remain available to support increasing consumer densities. This contrast between PPI and BEF systems occurs despite the fact that a comparable fraction of consumer species ultimately go extinct from both types of system (Fig. 2d, 2f).

Synthesis

The model illustrates a key difference between the typical BEF system with one trophic level and the typical PPI system with two: in systems with two trophic levels and a dynamical resource, the resource species may go extinct. This reduces the net availability of resources to consumer species and may create a hump-shaped relationship between consumer diversity and combined consumer density. In contrast, in systems with one trophic level, non-dynamic resources do not go extinct, and the continuous availability of resources leads to a monotonic increase in combined consumer density with increasing consumer diversity. This is the only inherent difference between systems with one vs. two trophic levels that we found in all of the analyses in this article.

Given the likely ubiquity of resource partitioning in nature (Chesson 1991) and the large literature on resource partitioning as a mechanism for species coexistence, it is surprising that few empirical studies on consumer diversity provide evidence of resource partitioning. A small number of BEF studies have claimed evidence of resource partitioning, but the evidence is indirect, based on the observation that the impact of consumer diversity on resources exceeds that which can be explained by a sampling effect alone (Norberg 2000; Fridley 2001; Loreau & Hector 2001; Duffy *et al.* 2003). The lack of evidence of resource partitioning in the BEF literature is perhaps understandable, because resource use is not easily quantified in the typical plant systems studied. Additionally, BEF studies have generally been performed at such small spatial scales, in experimental units chosen for spatial homogeneity, that resource partitioning is unlikely (Covich *et al.* 2004). Recent theoretical (Cardinale *et al.* 2004; Loreau 2004) and empirical (Dimitrakopoulos & Schmid 2004) evidence suggests that the likelihood of detecting a diversity effect caused by resource partitioning increases with spatial and temporal scales as niche differences among species are more fully realized.

It is also uncommon for PPI studies to examine resource partitioning among consumer species. In one of the rare examples, Bogran *et al.* (2002) studied three species of parasitoid attacking a whitefly pest in cotton. Although there was only a single prey species, resource partitioning occurred as different parasitoid species attacked hosts of different sizes and in different locations on plants, and this resource partitioning led to greatest prey suppression when all three parasitoids were present. Despite the rarity of examples of studies of resource partitioning, we expect that PPI could provide useful model systems for studying resource partitioning in the context of biodiversity. In contrast to the canonical BEF system of plants where all species depend on a relatively small number of common resources (e.g. light, water and nutrients), specialization by predators and herbivores is common. Host–parasitoid systems in which parasitoids attack distinct subsets of host species (Memmott *et al.* 1994; Muller *et al.* 1999), and plant–herbivore systems with specialist herbivores (Schoenly *et al.* 1991; McEvoy *et al.* 1993), could prove especially useful for studies of diversity and resource partitioning.

Indirect effects: intraguild interactions among consumers

In diverse systems with multiple species of consumers and resources, interactions between species can give rise to numerous types of indirect effects. Here, we follow the terminology of Sih *et al.* (1998), using the term 'indirect effect' to refer to the situation when one species changes the density of a second species which, in turn, alters the per capita population growth rate of a third species; thus, the first species has an indirect effect on the third. While there are many different types of indirect effects, here we focus on indirect effects caused by intraguild interactions among consumer species, because intraguild predation has received much interest in the recent PPI literature. Intraguild predation arises when the predator trophic level is not clearly delineated, and predators feed not just on the trophic level below, but also on other predators (Polis *et al.* 1989; Rosenheim *et al.* 1995). Intraguild interactions lead to positive indirect effects of a consumer species on a given resource; as the density of the consumer increases, it suppresses the density of other consumers, thus partially freeing the resource from consumption. While intraguild interactions may be more prevalent in PPI systems, a number of analogues occur in BEF systems, such as when plants exhibit chemical allelopathy.

We modified the basic model (eqns 1–3) to include intraguild interactions among consumer species. To retain the symmetry of consumers established in the model for resource partitioning, we assume that all consumers share a common attack rate g on other consumers and also themselves (i.e. cannibalism):

$$y_j(t+1) = y_j(t)\exp\left[\sum_{i=1}^{N} c_j b_{ij} x_i(t) - g\sum_{k=1}^{m} y_k(t) - d_j\right]. \quad (4)$$

To facilitate comparison of results with those from the resource partitioning model, we assume that the consumer species exhibit moderate specialization with $\sigma = 1$. As

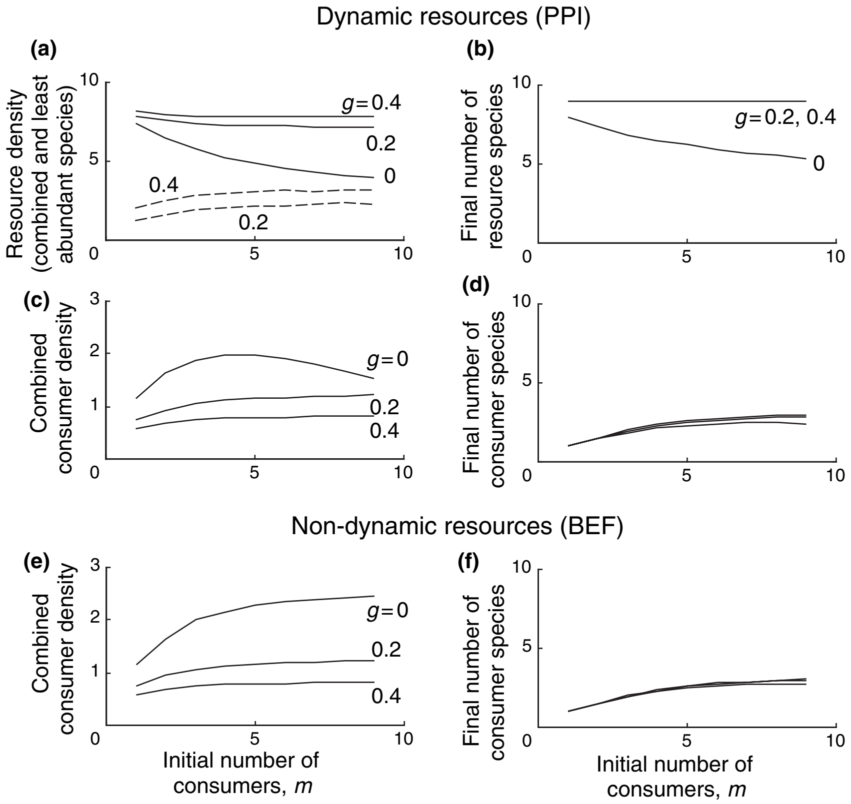

Figure 3 Intraguild consumer interactions and the effect of consumer diversity *m* on a community of nine resource species. For the system with two trophic levels, (a) gives the combined resource equilibrium density (solid lines) and the equilibrium density of the species that is the preferred resource for the initial consumer species in the community (dashed lines for the cases of $g = 0.2$, 0.4) multiplied by five to be visible in the panel, (b) gives the number of persisting resource species, (c) gives the combined consumer equilibrium density, and (d) gives the number of persisting consumer species. For the system with one trophic level, (e) gives the combined consumer equilibrium density and (f) gives the number of persisting consumer species. In each panel, lines for no ($g = 0$), moderate ($g = 0.2$), and strong ($g = 0.4$) intraguild interactions are labelled when they are sufficiently different. Other details are as in Fig. 2.

before, we allow time for the systems to equilibrate and report the densities of resources and consumers at equilibrium.

For the system with dynamic resources, intraguild interactions diminish the negative relationship between consumer diversity, *m*, and combined resource density (Fig. 3a, solid lines). This occurs because intraguild interactions limit the ability of consumers to reach high densities and greatly suppress their resources. Despite the increase in combined resource density with intraguild interactions, the relationship between consumer diversity and combined resource density remains negative. The monotonic decrease in resource density might appear to contradict recent studies showing that intraguild predation can cause increasing predator diversity to disrupt the suppression of a pest species; as more predators occur, intraguild predators inhibit the primary predators on a pest species, thus leading to higher pest densities (Rosenheim *et al.* 1993; Brodeur & Rosenheim 2000; Snyder & Ives 2001). Our model results do not, however, contradict this expectation; we find the same pattern in the model if we change focus from combined resource density to the density of a single focal resource species. The dashed lines in Fig. 3a give the densities of that resource species which is the preferred resource for the first consumer species present in the community (i.e. when $m = 1$). As the number of additional consumer species increases, the density of this focal resource species increases, because the additional consumers act as intraguild predators on the first consumer. Thus, intraguild predation disrupts the control of the focal resource species. Nonetheless, because the additional consumers also consume other resource species, the combined density of resources decreases with increasing consumer diversity.

Another effect of intraguild interactions is to reduce the impact of consumers on resources and hence reduce the extinctions of resource species (Fig. 3b). In the absence of resource species extinctions, the combined consumer density changes from a hump-shaped to a monotonically increasing function of consumer diversity for the case of moderate generalists ($\sigma = 1$) (Fig. 3c). However, because intraguild interactions between consumers are symmetrical, the strength of these interactions has little impact on the extinction of consumer species (Fig. 3d).

The impacts of intraguild interactions in systems with non-dynamic resources are similar, tending to reduce the increase in combined consumer density with increasing consumer diversity (Fig. 3e) but have little effect on the number of consumers persisting (Fig. 3f). The similarity of these results to those obtained with dynamic resources suggests that we might expect comparable effects of indirect interactions in both BEF and PPI systems.

Synthesis

Two results from the model stand out. First, intraguild interactions diminish, but do not qualitatively alter the effects of consumer diversity on combined resource density. Thus, the fundamental effects of consumer diversity on resource density do not depend on the nature of indirect interactions. Second, intraguild interactions may qualitatively change the effect of consumer diversity on combined consumer density when indirect interactions stop resource species from going extinct. In our model, this causes the relationship between consumer diversity and combined consumer density to converge for the cases of dynamic and non-dynamic resources (Fig. 3).

Recent PPI studies have reported the loss of prey suppression by predators because of intraguild predation, causing increasing predator diversity to increase the density of a focal prey species (Rosenheim *et al.* 1993; Brodeur & Rosenheim 2000; Snyder & Wise 2001; Finke & Denno 2004). Our model gives a similar pattern when focusing on a resource species that is initially controlled by a single consumer species (Fig. 3a, dashed lines). Despite the disruption of control of a focal resource species, the combined density of resources decreases with increasing consumer diversity as the additional consumers take an increasing portion of the spectrum of resources. The disruption of control of one resource species occurs because the presence of other resource species subsidizes the density of intraguild predators. If these other resource species were not present, intraguild predators could not reach sufficient densities to reduce the consumer population that is responsible for suppressing the density of the focal resource.

Is it possible for intraguild predation to produce a positive relationship between consumer diversity and combined resource density? Studies showing negative effects of intraguild predation on prey suppression often involve some predators that feed almost exclusively on particularly efficient predators, thereby producing effectively a three trophic-level system (prey–predator–top predator). We explicitly excluded this possibility from our model, which constrains consumers to have symmetrical intraguild interactions with each other. Strong asymmetries in intraguild predation are needed to overcome the decrease in combined resource density with increasing consumer diversity, implying that disruption of top–down control of combined resource species is more influenced by trophic diversity than by consumer diversity within a trophic level. The important question is, how common are sufficiently extreme asymmetries to disrupt the negative relationship between consumer diversity and combined resource density? Recent meta-analyses of trophic cascades all demonstrate the prevalence of top–down control across a variety of terrestrial and aquatic systems (Schmitz *et al.* 2000; Halaj & Wise 2002; Shurin *et al.* 2002), suggesting that intraguild interactions are rarely strong and asymmetrical enough to disrupt the negative relationship between consumer diversity and combined resource density.

While indirect interactions caused by intraguild predation have played a prominent role in the PPI literature, they are rarely mentioned in the BEF literature. We suggest that BEF researchers could benefit by considering intraguild interactions. While the mode of resource capture in plant and detritivore systems may make intraguild interactions less obvious, any type of direct competition between consumers that is not mediated through the focal resources, such as shading in plants or territoriality in detritivores, has the potential to generate positive indirect interactions of consumers on resources. Thus, we expect certain forms of intraguild interactions among plants and detritivores to have similar effects as the intraguild interactions described above.

Non-additive effects

In the basic model (eqns 1–3), the per capita population growth rates of resource and consumer species are assumed to be additive functions of resource and consumer densities. However, many forms of non-additivity occur in nature. Here we consider two forms: (i) when the presence of one consumer influences the per capita capture rate of another consumer on their shared resource species, and (ii) when the presence of one resource influences the per capita rate at which another resource is captured. These two types of non-additive interactions encompass the most likely non-additive effects in natural systems. Note that what we term 'non-additive effects' are subsumed within the category of 'indirect effects' by some authors (Wootton 1994) along with the type of indirect effects we described in the preceding section. We prefer to separate non-additive effects into their own category and use a more restrictive definition of indirect effects.

We first consider non-additive effects resulting from consumers either decreasing (antagonism) or increasing (synergism) the per capita capture rates of other consumer species. We incorporated non-additive effects by introducing the parameter a that governs the effect of the density of a consumer on the per capita capture rate of all other consumers:

$$b_{ij} = \hat{b}_{ij} \exp\left[a \sum_{k \neq j}^{m} y_k(t)\right]$$

where $\hat{b}_{ij}$ is the nominal capture rate that is modified by the exponential term including the combined densities of all other consumers. If $a < 0$, increasing the density of a consumer species decreases the per capita capture rate of a second consumer, giving antagonistic non-additive effects

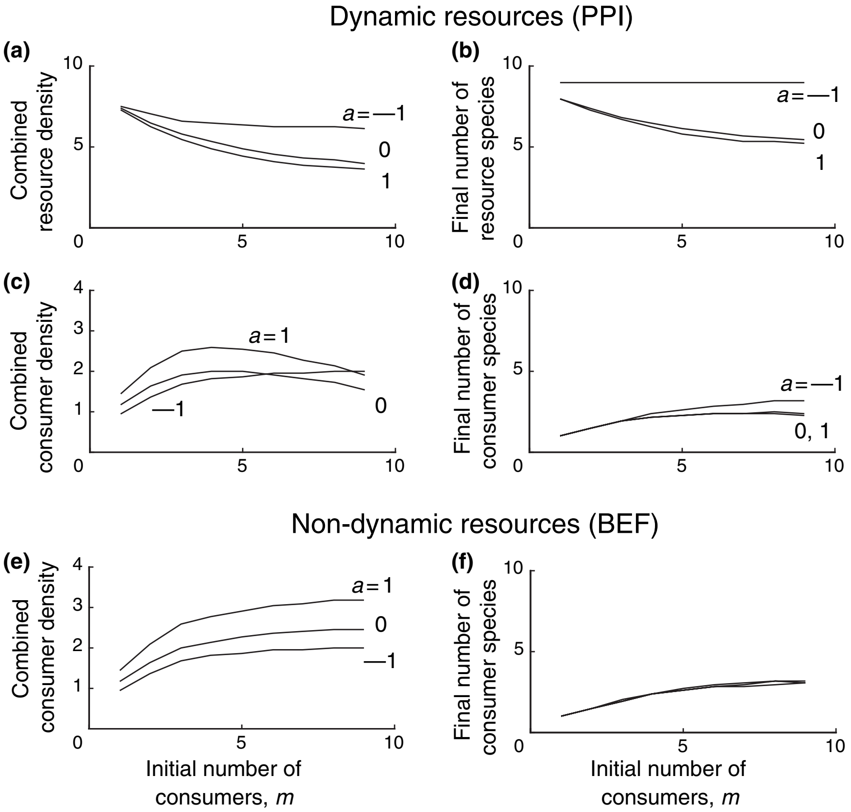

Figure 4 Non-additive effects of consumers on the capture rates by other consumer species. For the system with two trophic levels, (a) gives the combined resource equilibrium density, (b) gives the number of persisting resource species, (c) gives the combined consumer equilibrium density, and (d) gives the number of persisting consumer species. For the system with one trophic level, (e) gives the combined consumer equilibrium density and (f) gives the number of persisting consumer species. In each panel, lines for antagonistic ($a = -1$), no ($a = 0$), and synergistic ($a = 1$) interactions among consumers are labelled when they are sufficiently different. Other details are as in Fig. 2.

between consumer species. The converse is true if $a > 0$, which leads to synergistic non-additive effects. To facilitate comparison with previous models of resource partitioning and indirect effects, we assume that consumers are moderate generalists ($\sigma = 1$), and we analyse the model in terms of equilibrium resource and consumer densities.

In the system with dynamic resources, antagonistic interactions ($a < 0$) between consumers weaken the relationship between consumer diversity and the combined density of resource species, whereas the opposite is true for synergistic interactions ($a > 0$) (Fig. 4a). Furthermore, because antagonistic interactions among consumers inhibit the extinction of resource species (Fig. 4b), the combined density of consumer species changes from a hump-shaped to a monotonically increasing function of consumer diversity (Fig. 4c). In contrast, synergistic interactions simply augment the impacts of consumer diversity on combined resource density (Fig. 4a) and the hump-shaped relationship between consumer diversity and combined consumer density (Fig. 4c).

For the system with non-dynamic resources, the combined density of consumer species remains a monotonically increasing function of consumer diversity, with antagonistic and synergistic interactions only decreasing and increasing, respectively, combined consumer density (Fig. 4e). For the case of antagonistic interactions ($a < 0$) the relationship between consumer diversity and combined consumer density converges for systems with both dynamic and non-dynamic resources (Fig. 4c vs. 4e). Finally, for neither dynamic nor non-dynamic resources do non-additive interactions among consumers have a strong effect on the number of consumer species that persist (Fig. 4d and 4f).

The second type of non-additive interaction we consider – when the presence of one resource influences the per capita rate at which another resource is captured – arises whenever consumers have nonlinear functional responses. For example, suppose consumers exhibit type II functional responses, in which capture rates increase at a decelerating rate with the combined density of resource species. If consumer species all have type II functional responses and if the addition of more consumer species to a system decreases resource density, then one would expect that the resulting lower resource density will increase per capita consumer capture rates, thereby suppressing resource density even further.

We incorporated a type II functional response into the basic model by making the per capita capture rate of all consumers decrease as they capture more resources:

$$b_{ij} = \frac{\hat{b}_{ij} w(h)}{1 + h \sum_i \hat{b}_{ij} x_i(t)}.$$

Here, $h = 0$ gives a type I functional response, and increasing h makes the capture rate saturate as resource

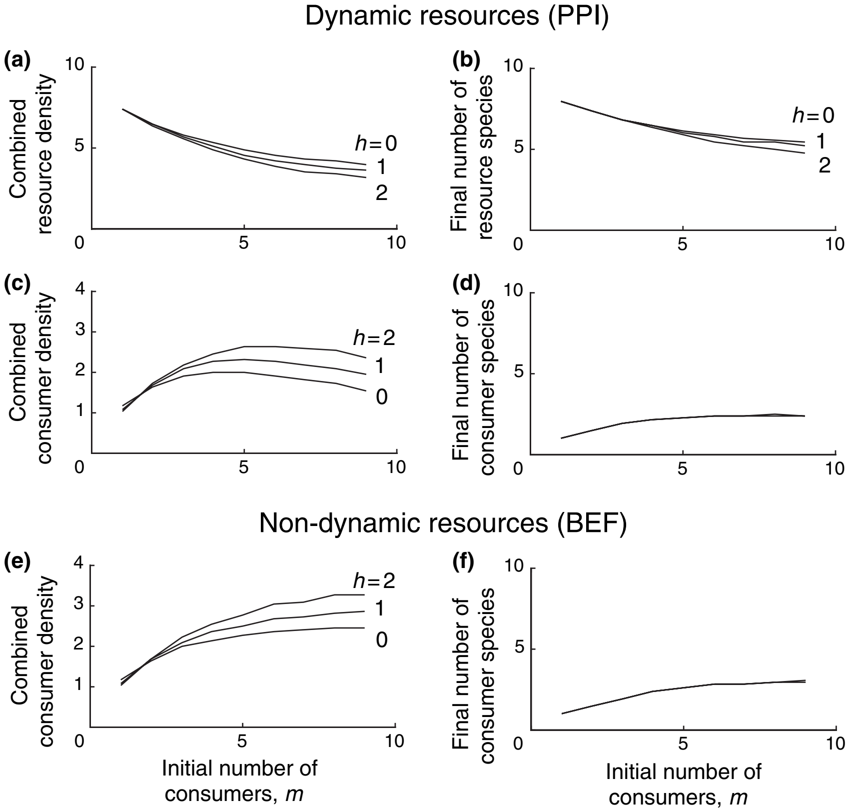

Figure 5 Non-additive effects of resources caused when consumer species have a type II functional response. For the system with two trophic levels, (a) gives the combined resource equilibrium density, (b) gives the number of persisting resource species, (c) gives the combined consumer equilibrium density, and (d) gives the number of persisting consumer species. For the system with one trophic level, (e) gives the combined consumer equilibrium density and (f) gives the number of persisting consumer species. In each panel, lines for type I (h = 0), weakly saturating type II (h = 0.1), and strongly saturating type II (h = 0.2) functional responses are labelled when they are sufficiently different. Other details are as in Fig. 2.

density increases. The constant $w(h)$ is used to standardize the comparison of systems with different values of h; $w(h)$ is selected so that the average capture rate among all consumer species is independent of h.

For the system with dynamic resources, non-additive effects created by a type II functional response accentuate the relationship between consumer diversity and the combined density of resource species, causing greater reductions in total resource density (Fig. 5a). This occurs because adding consumer species reduces resource density, which in turn reduces the saturation of capture rates that occurs with a type II functional response. There is a concomitant decrease in the average number of resource species persisting (Fig. 5b), which serves to accentuate the hump-shaped relationship between consumer diversity and combined consumer density (Fig. 5c). There is little influence of non-additive effects on the number of consumer species persisting (Fig. 5d). For the system with non-dynamic resources, non-additive effects also increase the combined consumer density (Fig. 5e) but have little impact on the persistence of consumer species (Fig. 5f).

Synthesis

As was the case in the previous section on indirect effects, non-additive effects changed the magnitude but not the shape of the relationship between consumer diversity and densities of combined resources and combined consumer species. The one exception to this generality occurred when non-additive interactions decreased extinctions of dynamic resources, for example, when antagonistic interactions between consumer species caused the relationship between consumer diversity and combined consumer density to change from hump-shaped to monotonically increasing (Fig. 4c). This emphasizes again the importance of extinction of resource species in explaining differences in patterns seen between systems with one vs. two trophic levels.

In the PPI literature, there are several good examples of both negative (Wissinger & McGrady 1993; Crowder *et al.* 1997) and positive (Losey & Denno 1998) non-additive effects in which consumer species influence capture rates of each other. A common feature to many of these examples is that they involve behavioural responses on the part of the resources (prey). This suggests that it is more likely for non-additive consumer effects on capture rates to be observed in the two trophic-level systems typical of PPI. However, it is possible for non-behavioural processes to drive similar non-additive effects in systems with a single trophic level. For example, Cardinale *et al.* (2002) showed that more diverse collections of suspension-feeding caddisfly species had higher collective feeding efficiency in streams. Different species created feeding nets of different sizes, and the resulting turbulent water flow over the stream bed increased particle capture by all species.

Given the large number of studies documenting non-type I functional responses, it seems surprising that few BEF or PPI studies have investigated the consequences of non-type I functional responses in systems with multiple consumer species. One exception is the study by Ruesink & Srivastava (2001), who investigated non-additive effects of detritivores in the decomposition of leaf litter. Their experiments included both removal treatments in which one of two dominant insect detritivores was eliminated, and replacement-series treatments, in which the biomasses of remaining species were increased to maintain the combined consumption rate of the reduced-diversity community. Although there was an increase in per capita detritivore processing following the simple removal treatments, this increase was not sufficient to compensate for the species removal. Thus, despite the increased availability of detritus, consumption rates did not increase proportionally, which suggests a type II functional response. This study highlights the value of combining both simple removal and replacement-series experimental designs to separate additive from non-additive effects among species (Sih *et al.* 1998).

Avenues for future research

We have brought together ideas from the BEF and PPI literatures to address the common impacts of consumer diversity on the densities of combined resources and consumer species. We initially expected that the key difference between the typical BEF and PPI studies – that BEF systems involve single trophic levels, whereas PPI systems involve two trophic levels – would cause very different effects of consumer diversity in BEF vs. PPI systems. However, a pattern that pervades our results is that systems with one or two trophic levels respond to consumer diversity in similar ways under most circumstances. The only situation in which this was not the case was when resource species are forced to extinction in systems with two trophic levels. The striking similarities between systems with one vs. two trophic levels implies that many of the ideas generated in BEF and PPI subdisciplines should be readily transferable.

The first two mechanisms we discussed, the sampling effect and resource partitioning, have been the primary focus of BEF. Our models suggest that these are, in fact, the primary mechanisms that dictate the range of possible relationships between consumer diversity and the densities of combined resources and consumer species. Both these mechanisms cause systems with more diverse consumer assemblages to have lower combined resource density. The effect of consumer diversity on combined consumer density is, however, more complex. For the sampling effect, this relationship may be positive or negative depending on which biological traits differ among consumer species (Fig. 1), and for resource partitioning it can be flat, monotonically increasing, or hump-shaped depending on the extent of niche overlap (Fig. 2). These results suggest that there are a number of theoretically plausible relationships between consumer diversity and combined consumer density, although BEF studies have generally showed a positive relationship between consumer diversity and combined consumer density.

The remaining mechanisms that we investigated, indirect and non-additive effects, are generally only modifiers that change the quantitative, but not qualitative effects of consumer diversity created by the sampling effect or resource partitioning. There are some exceptions to this. For example, indirect effects can change a hump-shaped relationship between consumer diversity and combined consumer density to a monotonically increasing one if the indirect effects reduce the extinction of resource species (Fig. 2b and c). Nonetheless, the sampling effect and resource partitioning tend to dictate system behaviour, and other processes play only secondary roles.

Our work raises a number of questions that point to avenues that may be fruitful for further research:

1. Is resource partitioning the primary mechanism by which consumer diversity influences resource and consumer density?

We know of no conclusive evidence from empirical studies that resource partitioning is the mechanism underlying an effect of consumer diversity on resource and consumer density. Nonetheless, we believe that resource partitioning should be viewed as central to any discussion of consumer diversity, because resource partitioning is a ubiquitous explanation for the coexistence of diverse species assemblages (Chesson 2000). Why have few studies on diversity found evidence for resource partitioning? Most studies have been performed at spatial and temporal scales that are smaller than the scale at which resource partitioning likely occurs. These small-scale experiments are biased towards detecting sampling effects rather than resource partitioning. Small-scale experiments might find rampant evidence of a sampling effect but not resource partitioning, even when resource partitioning at larger scales is responsible for coexistence in the regional species pool, which is itself a prerequisite for a sampling effect to occur (Mouquet *et al.* 2002; Cardinale *et al.* 2004; Loreau 2004).

We need to scale-up studies of diversity and study resource partitioning more directly. The types of systems used for typical PPI studies may be particularly valuable for this, because communities of natural enemies typically span the spectrum from specialists to generalists. Thus, PPI systems with strong resource partitioning among specialists can be compared with systems with weaker partitioning among generalists. BEF plant or detritivore systems typically have consumers with limited specialization (Hutchinson 1961) and hence less obvious small-scale resource partitioning.

2. Do indirect and non-additive effects serve only to modify the relationships between consumer diversity and combined resource or consumer density, or can they qualitatively change these relationships?

In our simple models, indirect and non-additive effects generally only modified the effects of consumer diversity established by resource partitioning. One exception occurred when indirect and non-additive effects change the extinction probabilities of resource species, leading to qualitative changes in the relationship between consumer diversity and consumer density. It would be interesting to test empirically whether indirect and non-additive effects can change the extinction risk of species, and whether changes in local extinction risks of resource species may in turn alter the effects of diversity in natural systems with two trophic levels.

We are sceptical of our results about the relatively small qualitative effects of indirect and non-additive effects on diversity relationships. A limitation of our models including indirect and non-additive effects is that they impose potentially unrealistic symmetries in interaction strengths among species. These assumptions give a reasonable place to start investigating indirect and non-additive effects on diversity relationships; there are so many asymmetries that could be incorporated into the models, it seems worthwhile first to understand the simplest case of strong symmetries. Nonetheless, strong asymmetries, such as a group of strong intraguild consumers that effectively act as a third trophic level, are common in natural systems. Such strong asymmetries may qualitatively change the relationship between consumer diversity and combined resource density driven by the sampling effect or resource partitioning. The theoretical consequences and the empirical cataloguing of asymmetrical interactions both deserve more attention in investigations of diversity. This is especially true for BEF studies that have in general ignored indirect and non-additive effects.

3. How does consumer diversity affect the suppression of single vs. multiple resource species?

Most PPI studies focus on a single prey species, particularly studies of biological control. This is in part because it is often a single pest species that is of interest, and in part because many biological control programmes focus on extremely specialized consumers to minimize the risk of impacts on non-target species. Nonetheless, awareness that generalists may be important in biological control (Root 1973; Riechert & Lockley 1984; Symondson *et al.* 2002; Snyder & Ives 2003) argues for studying multiple prey species because the abundance of generalist predators is determined not only by a focal prey species, but also by a variety of other prey species. Similarly, BEF studies that explicitly address resources typically only consider one or a few resource types, such as soil nutrient concentrations. Explicitly investigating multiple resources might increase our understanding of resource partitioning and possible interactions among consumer species (such as shading among plants) that have potentially similar effects as intraguild predation among animal predators.

One of our results demonstrates the contrasting perspectives that arise from looking at one vs. many resource species. In our model with intraguild interactions, increasing consumer diversity disrupted control of one of the resource species, leading to increasing densities; yet simultaneously, increasing consumer diversity decreased the combined density of resource species (Fig. 3a). This result argues for investigating the effects of diversity both on individual species and on collections of species in a community.

4. How can multiple effects of diversity be identified in real systems?

In our presentation, we have separated different mechanisms that are involved in diversity relationships, yet in natural systems multiple mechanisms likely operate in concert. A sampling effect, resource partitioning, indirect interactions, and non-additive effects could all occur in the same system, or operate concurrently for the same species at different spatial scales (Mouquet *et al.* 2002; Loreau *et al.* 2003; Cardinale *et al.* 2004). When this happens, how can multiple processes be separated and quantified?

To study multiple processes empirically, we believe that multiple experimental approaches should be used in combination. BEF studies have typically employed 'replacement-series' experimental designs, in which experimental communities are assembled that differ in initial diversity but preserve the total initial density or biomass of the manipulated trophic level. This design is particularly appropriate to identify the role of species-specific differences in performance on future total community density or biomass, because all communities start with the same total density or biomass and differ only in species composition (Jolliffe *et al.* 1984; Connolly 1986, 1988, Jolliffe 2000). Thus, replacement-series designs are best to identify sampling effects. In contrast, PPI studies often use an 'additive-series' design in which diversity is manipulated while preserving the initial density or biomass of individual species; thus, more diverse communities will have higher initial total density or biomass of the manipulated trophic level. This design is appropriate to identify indirect and non-additive effects on the species within the community, because the initial density of a given species is the same across all diversity treatments (Connolly 1988; Sih *et al.* 1998; Jolliffe 2000). This design may also be more relevant to tests of resource partitioning because when there is resource partitioning, total consumer density will increase with consumer diversity. Our take-home message is that replacement-series and additive-series designs have complementary strengths and weaknesses. Therefore, running replacement-series and additive-series designs in concert is a powerful approach in separating the various effects of diversity.

In addition to highly manipulated experiments in which communities are constructed by assembling species across a range of diversity, we need experiments that more naturally reproduce diversity effects at biologically relevant spatial and temporal scales. For example, removal experiments have advantages over designs based upon assembling communities because removals can be performed at relatively large spatial scales and start with communities that represent natural assemblages of species (Diaz *et al.* 2003). Similarly, whole-ecosystem manipulations, such as the addition or removal of entire trophic levels (Carpenter & Kitchell 1993), can be used to identify the main direct and indirect interactions among species, and from this predict the consequences of species loss (Ives *et al.* 1999). While large-scale manipulations may not provide the precision of designs based on the assembly of communities differing in diversity, they complement community assembly designs by more accurately representing the consequences of loss of diversity from real communities.

5. Do more complex trophic structures overturn the generalities we have described?

Throughout this article, we have been rather dogged in our focus on the diversity only of consumers and only in communities with one or two trophic levels. However, just as consumer diversity can have top–down effects on resources, resource diversity can have bottom–up effects on consumers (Root 1973; Andow 1991; Hillebrand & Cardinale 2004; Aquilino *et al.* 2005). Similarly, when there are more than two trophic levels, effects of diversity can cascade either up or down trophic levels (Holt & Loreau 2002; Petchey *et al.* 2004). More complex communities than those considered here will present new challenges, but a more complete understanding of biodiversity requires future work on complex, multi-trophic food webs.

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APPENDIX 1

Here we derive relationships for the sampling effect in which m consumer species from a pool of M species are added to a system with a single resource species. For systems with either one or two trophic levels (eqn 1–3), the equilibrium resource density caused by a single consumer species i is $x_i^* = d_i/(c_i b_i)$, and the consumer species that produces the lowest x_i^* outcompetes all other consumer species. The expected density of the resource caused by the addition of m consumer species, $E[x^*]$, can be derived from the resource densities that occur with the most effective consumer, x_1^*, the second-most effective consumer, x_2^*, etc.:

$$E[x^*] = \frac{m}{M}x_1^* + \left(1-\frac{m}{M}\right)\left(\frac{m}{M-1}\right)x_2^* + \left(1-\frac{m}{M}\right)\left(1-\frac{m}{M-1}\right)\left(\frac{m}{M-2}\right)x_3^* + \ldots \quad (A1)$$

As m increases, $E[x^*]$ decreases, with $E[x^*]$ equalling the lowest x_1^* with certainty when all M species in the consumer pool have been added.

The equilibrium density of consumer species i when alone is $y_i^* = (R - x_i^*)/b_i$ for the system with a single trophic level, and $y_i^* = (r/K)(K - x_i^*)/b_i$ for the system with two trophic levels. Note that these two expressions differ only by the constant (r/K) if the resource renewal rate R is equated to the carrying capacity K; thus, the systems with one and two trophic levels have the same relationship between m and the expected density of consumers, $E[y^*]$. This relationship, however, depends on whether consumers differ amongst each other in the assimilation efficiencies c_i or the capture rates b_i. In the former case,

$$E[y^*] = \begin{cases} \frac{R-E[x^*]}{b} \\ \frac{r}{K}\frac{K-E[x^*]}{b} \end{cases} \quad (A2)$$

whereas in the latter case

$$E[y^*] = \begin{cases} \frac{c}{d}\left(RE[x^*] - E\left[(x^*)^2\right]\right) \\ \frac{rc}{Kd}\left(KE[x^*] - E\left[(x^*)^2\right]\right) \end{cases} \quad (A3)$$

where $E[(x^*)^2]$ is the expectation of $(x^*)^2$ calculated from eqn (A1) by replacing x_i^* with $(x_i^*)^2$.

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ERRATUM

The lead author of Ives *et al.* (2005) made a programming error in the models that affected the results reported in the article. Specifically, eqn 1

$$y_j(t+1) = y_j(t)\exp\left[\sum_{i=1}^{N} c_j b_{ij} x_i(t) - d\right] \qquad (1)$$

was incorrectly coded in such a way that b_{ji} replaced b_{ij}. While we originally reported that our model had symmetric interactions among species (p. 105), the error results in a model with asymmetries in competition among consumer species. These asymmetries cause resource species to go extinct in the models with two trophic levels. For the model originally reported in the paper in which we assumed symmetric interactions among species, resource species do not go extinct for the parameter values used to produce Figures 2–5. As a result, the relationship between consumer diversity and consumer density is identical for systems with one and two trophic levels.

While the programming error changed Figures 2–5, it does not change the general conclusions described in the article. We concluded that when resource species go extinct with increasing numbers of consumer species, the relationship between consumer diversity and consumer abundance will differ between systems having one vs. two trophic levels, whereas when there is no extinction, the relationship is the same. Comparing the asymmetrical model caused by the programming error and the correct, symmetrical model substantiates this claim.

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