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12-11-2002

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**MINI-
REVIEW**

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Biodiversity and ecosystem function: the consumer connection

J. Emmett Duffy

Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. – *Oikos* 99: 201–219.

Proposed links between biodiversity and ecosystem processes have generated intense interest and controversy in recent years. With few exceptions, however, empirical studies have focused on grassland plants and laboratory aquatic microbial systems, whereas there has been little attention to how changing animal diversity may influence ecosystem processes. Meanwhile, a separate research tradition has demonstrated strong top-down forcing in many systems, but has considered the role of diversity in these processes only tangentially. Integration of these research directions is necessary for more complete understanding in both areas. Several considerations suggest that changing diversity in multi-level food webs can have important ecosystem effects that can be qualitatively different than those mediated by plants. First, extinctions tend to be biased by trophic level: higher-level consumers are less diverse, less abundant, and under stronger anthropogenic pressure on average than wild plants, and thus face greater risk of extinction. Second, unlike plants, consumers often have impacts on ecosystems disproportionate to their abundance. Thus, an early consequence of declining diversity will often be skewed trophic structure, potentially reducing top-down influence. Third, where predators remain abundant, declining diversity at lower trophic levels may change effectiveness of predation and penetrance of trophic cascades by reducing trait diversity and the potential for compensation among species within a level. The mostly indirect evidence available provides some support for this prediction. Yet effects of changing animal diversity on functional processes have rarely been tested experimentally. Evaluating impacts of biodiversity loss on ecosystem function requires expanding the scope of current experimental research to multi-level food webs. A central challenge to doing so, and to evaluating the importance of trophic cascades specifically, is understanding the distribution of interaction strengths within natural communities and how they change with community composition. Although topology of most real food webs is extremely complex, it is not at all clear how much of this complexity translates to strong dynamic linkages that influence aggregate biomass and community composition. Finally, there is a need for more detailed data on patterns of species loss from real ecosystems (community “disassembly” rules).

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Accepted 13 May 2002

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ISSN 0030-1299

What are the consequences of declining biodiversity for the functioning of ecosystems? Motivated by the accelerating global erosion of diversity, this question has spawned a new subfield of ecology and considerable controversy over the last decade (Loreau et al. 2001, Kinzig et al. 2002). Because plant traits strongly influence ecosystem processes such as primary production and nutrient fluxes (Chapin et al. 1997, Grime 1998), the identity and diversity of plants present in a community are expected to influence both the magnitude and variance of such processes (Tilman 1999). There is growing evidence from several systems that important ecosystem processes such as productivity and nutrient cycling can be significantly related to the species richness of plants (Kinzig et al. 2002), presumably because species richness serves as a proxy for trait diversity, although mechanistic interpretation of these phenomena remains a subject of debate (Loreau et al. 2001). If such diversity effects on ecological function are general phenomena, the implications are important for both basic ecology and conservation in the face of ongoing extinctions. Despite intense interest, however, the great majority of empirical research on diversity-function links has focused at the base of terrestrial food webs, primarily grasslands, and to a lesser degree, on aquatic microbial microcosms (Schlöpfer and Schmid 1999). There are obvious logistical and theoretical reasons for this. Nonetheless, the important questions of whether and how biodiversity might be related to ecosystem functional processes at higher trophic levels and in other ecosystem types have received surprisingly little attention.

Meanwhile, a separate research tradition has documented pervasive influences of predators and herbivores in a wide range of communities and ecosystems. Although they have rarely been considered explicitly in this context, such consumer-mediated processes are inextricably linked to the issue of how biodiversity influences ecosystem function (Allison et al. 1995). This is because, among other reasons, extinction is often strongly biased by trophic level and because the strength and penetrance of top-down control in ecosystems are widely believed to depend on diversity. Here I suggest that effects of changing biodiversity on ecosystem processes in many systems are equally, and sometimes more, likely to be mediated at the level of consumers than at the level of plants. In the context of complete communities with multiple trophic levels, these diversity effects will be realized through trophic interactions and their indirect effects on other ecosystem processes (Naeem 2002). As a step toward better incorporating trophic processes into the science of functional diversity, I offer several hypotheses and ask whether the limited, mostly indirect evidence available supports them.

Animals are important

Consumers strongly influence community structure and ecosystem processes in a variety of habitats, often changing plant biomass, community composition, physical vegetation structure, primary and secondary production, and decomposition rates (Lubchenco and Gaines 1981, Sih et al. 1985, McNaughton et al. 1988, Huntly 1991, 1995, Menge 1995, Chapin et al. 1997, Pace et al. 1999, Terborgh et al. 1999, Duffy and Hay 2001). A substantial proportion of these effects are indirect, i.e. mediated through more than one trophic link (Wootton 1994, Menge 1995) or via engineering effects on biotic habitat (Jones et al. 1994, Bruno and Bertness 2001). Strong indirect effects of consumers often propagate downward and laterally along links in the food web, causing substantial changes in abundance of organisms elsewhere in the web (Sih et al. 1985, Menge 1995). In marine food webs, for example, both controlled experiments (Menge 1995) and indirect inferences from fisheries data (Botsford et al. 1997, Pinnegar et al. 2000) and historical data (Dayton et al. 1998, Jackson et al. 2001) indicate that strong top-down forces are (or were) common and often have far-reaching indirect effects on ecological structure and function. Particularly striking examples of such indirect effects involve community-wide trophic cascades, in which a predator's impact penetrates through one or more intervening trophic levels to influence aggregate abundance of plants (Paine 1980, Carpenter et al. 1985). Although the concept was first articulated by terrestrial ecologists (Hairston et al. 1960), the best documented trophic cascades come from marine (Estes and Palmisano 1974, Estes and Duggins 1995, Estes et al. 1998) and freshwater (Carpenter et al. 1987, Power 1990, Brett and Goldman 1996) systems. Following Strong's (1992) contention that trophic cascades are "all wet", many ecologists have considered the apparently higher frequency of cascades in aquatic systems to be an important contrast with terrestrial systems (Persson 1999, Polis et al. 2000). Recent meta-analyses of trophic cascade experiments reach mixed conclusions on this issue, however (Schmitz et al. 2000, Halaj and Wise 2001). Trophic cascades may be less common on land (Halaj and Wise 2001, but see Schmitz et al. 2000), and there is considerable variance in their strength in both terrestrial and aquatic systems resulting from a variety of widely recognized processes such as omnivory, intraguild predation, and anticonsumer defenses. Nevertheless, strong cascades have been demonstrated or strongly implied in both types of ecosystems (Pace et al. 1999, Terborgh et al. 1999, 2001, Chase 2000, Schmitz et al. 2000). Yet there remain few experimental studies of terrestrial trophic cascades involving vertebrate consumers (Schmitz et al. 2000, Halaj and Wise 2001). The apparent paucity of strong top-down forcing in terrestrial systems is likely ex-

plained in part by anthropogenic reduction of large vertebrate consumers in many terrestrial ecosystems, the difficulty of experimentally manipulating such consumers, and the long time-scale of response of terrestrial vegetation (Estes 1995, Terborgh et al. 1999, Paine 2000).

What is meant by diversity and ecosystem function?

How do we expect diversity loss to affect functioning of ecosystems with multiple trophic levels? Interactions among organisms within food webs can be characterized qualitatively by topology of links (who eats whom) and quantitatively by interaction strength. The latter has been defined in a number of ways (Laska and Wootton 1998), and the corresponding metrics behave differently depending on a consumer's abundance, functional response, and the interaction's proximity to equilibrium (Berlow et al. 1999). Thus, there is no ideal, universally useful concept of interaction strength. Because I am concerned here primarily with extinction – the long-term effects of removing an entire population of a species – I use interaction strength to mean the raw change in equilibrium abundance of a prey (or other) species caused by removing a consumer species entirely. This is essentially the “removal” concept of interaction strength used by Paine (1980, Laska and Wootton 1998) and the “raw difference” of Berlow et al. (1999).

To address the effects of diversity on trophic interactions, we first must be specific about what diversity means. The number and range of functionally important (i.e. strong) interactions represented within an assemblage have variously been termed heterogeneity (Hunter and Price 1992), differentiation (Strong 1992), or complexity (Polis and Strong 1996). In the context of food web interactions such heterogeneity can in principle be divided into two components (Persson 1999). “Vertical” heterogeneity is roughly equivalent to the number of trophic levels from which a consumer feeds and is thus a property of individuals or species. The “horizontal” component of heterogeneity refers to the functional diversity within a trophic level and is thus a property of the assemblage as a whole. Several reviews have addressed the possible roles of omnivory (vertical heterogeneity) in food-web interactions (Polis and Holt 1992, Diehl 1993, Persson 1999, Halaj and Wise 2001). Here I focus on the horizontal component of functional diversity, which corresponds to the concept of diversity employed in previous studies of plant diversity effects on ecosystem function (reviewed by Tilman 1999).

In practice, functional diversity is often difficult to define and quantify objectively. Historically, studies of plant functional diversity have classified plants infor-

mally into broad groups based on growth form, phenology, and/or physiology (Körner 1993, Hooper and Vitousek 1997, Tilman et al. 1997b), although more quantitative approaches are currently being explored (Díaz et al. 1999). Assignment of species to functional groups often differs depending on the functional trait of interest (Körner 1993). Thus, functional diversity is best defined in terms of a particular type of trait or response variable. In food webs, functional traits are manifested as trophic interactions. Within a guild of consumers, trophic interactions can be distinguished quantitatively by their relative strength (e.g. keystone vs diffuse predation, Allison et al. 1995), and qualitatively by the identity of species with whom they interact. Thus, in the context of consumer/prey interactions, functional diversity may be defined as the number of unique combinations of prey species that are significantly impacted by consumers in an assemblage. This can be illustrated most easily with a hypothetical example (Fig. 1). Consider a system with two trophic levels (plants, herbivores) and three plant species. Focusing on the response variable “herbivore impact on plant biomass”, several kinds of interactions can be identified in this system in terms of which plant species are impacted (Fig. 1): herbivore 1 impacts plant species 1 and 2, herbivore 6 impacts all three plants, and herbivore 7 impacts only plant 3. Each of these consumers affects a unique combination of species. In contrast, herbivores 1, 2, and 3 all impact the same pair of plant species, thus they all share the same kind of interaction. Herbivores 4 and 5 have negligible impacts, thus (ignoring for the moment the issue of spatial and temporal variance in effects) their links can be considered “noise” in the interaction web.

The relationship between species diversity, or qualitative food-web topology, and functional diversity is accordingly not straightforward. Mechanistically, low functional diversity within a trophic level (consider herbivores, specifically) can be realized in any of several ways. First and most simply is *low species richness* per se (Fig. 1a). With a single consumer species, only one kind of interaction as defined above is possible. Second, where multiple species are present within a trophic level, functional diversity remains low if they are *functionally equivalent* in terms of both topological links (who they eat) and population-level interaction strengths (the toll they take on prey) (Fig. 1b). Such functional equivalence allows compensation by remaining species after one species is removed, and thus buffers against single-species removals (Fig. 2). This is seen, for example, among some tropical rocky intertidal predators (Menge et al. 1986) and among some benthic crustaceans feeding on periphyton (Duffy et al. 2001). Finally, even where several species differ in the topology of their links to other organisms, functional diversity remains low if there is pronounced skew in interaction strength such that one or a few species are

functionally dominant in influencing the prey (Fig. 1c). This is the classic situation of a keystone predator. Strong skew in per capita interaction strength has been demonstrated in several consumer-prey systems (Paine 1992, Raffaelli and Hall 1995, Wootton 1997, Sala and Graham 2002). In each of the three scenarios illustrated (Fig. 1a–c), there is only one “kind” of strong (functionally significant) interaction, namely grazing on both plant species 1 and 2. In contrast, where consumers have strong impacts on different prey species (complementarity), there is more than one kind of strong interaction, and functional diversity is higher (Fig. 1d). Thus, the functional diversity of an assemblage often will not map closely to species diversity, or to the simple number of topological links in a food-web diagram, a point emphasized by Paine (1980).

In this paper I use “ecosystem function” as a general term that could include any process influencing aggregate (i.e. community-wide) energy and materials flows or standing biomass. Total primary production, secondary production, aggregate consumption rate, com-

munity respiration, nutrient uptake and regeneration are examples (Schläpfer and Schmid 1999). Effects of a given change in diversity are likely to differ considerably among different response variables. In focusing on such community- and ecosystem-level functional processes, I do not consider directly the extensively documented (e.g. Sih et al. 1985, Menge 1995) impacts of consumers on prey community structure except insofar as they have concomitant effects on functional processes. Effects of herbivore diversity on plant assemblage structure and succession were reviewed recently by Ritchie and Olf (1999).

Animal diversity effects will be different than plant diversity effects

Given that consumers strongly influence functional processes in many ecosystems, and that their risk of extinction is often relatively high, a general conceptual

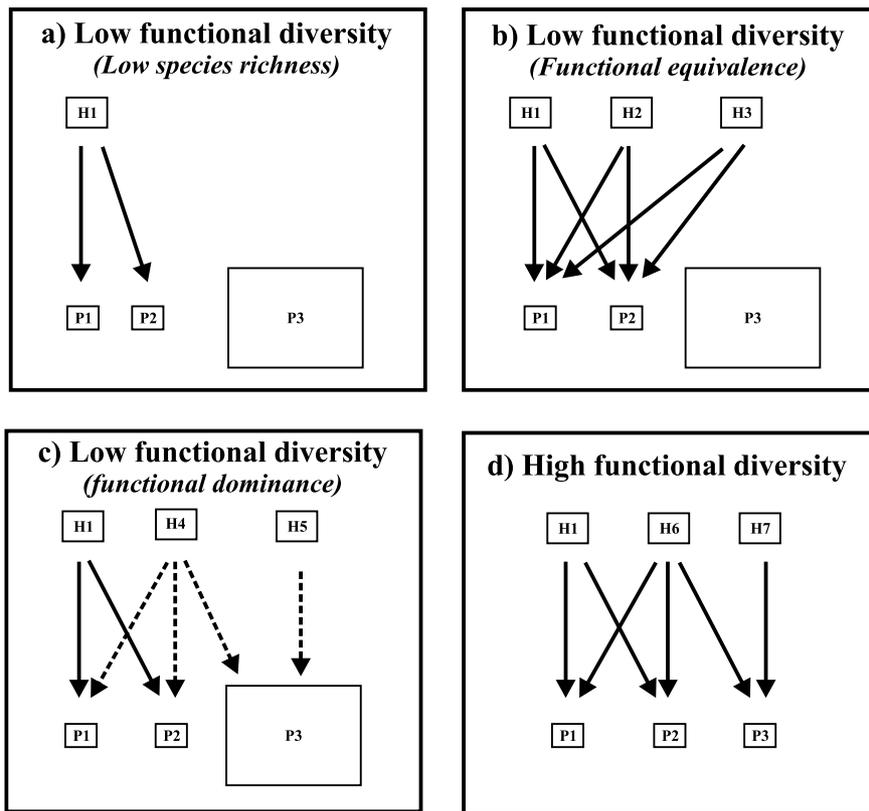


Fig. 1. Functional diversity in consumer-prey interactions. (a–c) Three possible mechanisms resulting in low functional diversity of consumers in a simple, two-level food web: (a) low consumer species richness. (b) Functional equivalence: all consumer species eat the same prey species at similar rates. (c) Functional dominance: one consumer species has a strong impact, whereas impacts of the others are negligible. In each of these three cases, there is only one “kind” of significant interaction, i.e. strong impact on plant species 1 and 2. (d) High functional diversity results from different consumer species having strong impacts on different prey species (complementarity). In this last case, complementarity among consumers results in greater overall grazing impact, i.e. lower total plant biomass. H1–7 are herbivore species, P1–3 are plant species. Size of each box is proportional to biomass. Solid arrows indicate strong interactions; broken arrows indicate weak (functionally insignificant) ones.

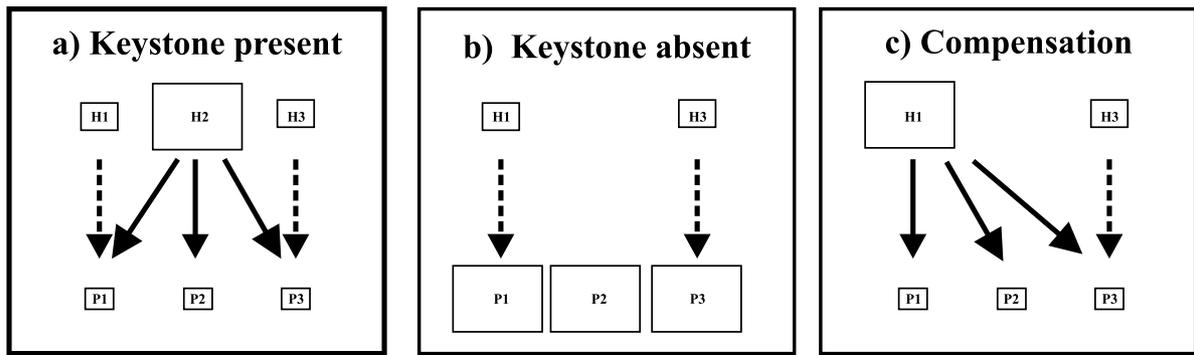


Fig. 2. Hypothesized influence of consumer compensation and diet switching on relationships between consumer diversity and consumer impact. (a, b) Keystone consumption, in which a single consumer strongly impacts aggregate prey biomass. (a) Presence of the keystone herbivore (H2) maintains low biomass of all three plant species. (b) Absence of compensation: removal of the keystone herbivore allows all three plant species to increase because intrinsic constraints on the remaining herbivore species (e.g. low grazing rates, interspecific interference competition) render them incapable of controlling the plants. (c) Compensation: removal of the formerly dominant consumer has no effect on plant biomass because one of the remaining consumers (H1) compensates by expanding its diet range and feeding rate. Symbols as in Fig. 1.

framework for predicting diversity effects on consumer-prey interactions is highly desirable. However, the effects of animal diversity on ecosystem functional processes (including cascading trophic interactions) are certain to be more complex (Polis and Strong 1996), and less easily generalized, than those of plants for several reasons.

Plants and animals differ in the diversity of their resources. Whereas plants share requirements for a limited suite of major, abiotic resources, heterotrophs exploit living, evolving, and highly diversified organisms or products thereof. Herbivores, for example, must obtain not only calories and nutrients from their prey, but must also contend with a variable and constantly changing suite of chemical, physical, and life history characteristics, many of which have evolved specifically to foil them (Hay and Fenical 1988). This distinction likely influences the intensity and nature of competition (relatively simple and common in plants, less so in herbivores) and its translation into expected effects of diversity on resource use. The specialized nature of many herbivore diets, compared with those of carnivores, means that general predictions for the influence of herbivores on ecosystem processes may be more difficult to make than those for either plants or carnivores. For example, carnivore effects may be relatively easily related to body size (Cohen et al. 1993, Jennings et al. 2001), whereas herbivore effects may be less so.

Plants and animals differ in the relationship between biomass and impact on ecosystem function. In terrestrial plant assemblages, both theory and empirical evidence support a “mass ratio hypothesis” in which the contribution of a plant species to ecosystem processes is closely related to its contribution to total vegetation biomass (Grime 1998). In contrast, the lack of concordance between a consumer’s biomass and its impact on community organization has emerged as a paradigm in

the form of the keystone predator concept (Paine 1966, 1980, Power et al. 1996). Sea otters, for example, comprise a minuscule fraction of total biomass in kelp beds, yet cascading effects of their removal produce a fundamental phase shift in structure (Estes and Duggins 1995, Estes et al. 1998) and function (Duggins et al. 1989) of northeastern Pacific coastal ecosystems. Top predators, usually present at low densities, can strongly affect the organization of many communities (Power et al. 1996, Pace et al. 1999) with concomitant changes in ecosystem functional processes. This difference between plant and animal effects emphasizes the need for a theory of diversity effects based on interaction strengths rather than abundance or biomass (Paine 1980, Hall and Raffaelli 1993, Laska and Wootton 1998).

Plants and animals differ in the complexity of their spatial relationships to competitors and resources. Plants are sessile and bound to a two-dimensional surface. Resources are supplied in a spatially consistent manner: light from above, nutrients from below, resulting in predictable and relatively easily modeled patterns of competition and resource use. Heterotrophs, in contrast, are generally mobile and their resources are structurally complex. Practical consequences of consumer mobility for field diversity experiments include the difficulty of maintaining specific treatment combinations of animals, as well as the “fencing effect” (Krebs et al. 1969) that prevents natural dispersal and population diffusion. As a result, testing the effects of animal diversity on ecosystem function will likely need to rely more than plant experiments have on natural experiments and patterns in unmanipulated systems (Estes 1995, Terborgh et al. 1999, 2001, Jackson et al. 2001) in addition to the elegant experimental designs so successful in previous research on plant diversity effects. The impacts of multiple consumer species on prey may also

be complicated by interference or other emergent effects of multiple co-occurring predators, introducing non-linearity into consumer-prey interactions (McCann et al. 1998, Sih et al. 1998, but see Schmitz and Sokol-Hessner 2002). These effects have received little attention and deserve more.

Defining the expectations

Thus, among the first challenges in assessing diversity effects within multi-trophic systems is defining the expectations. In this paper I first consider potential bias in extinction by trophic level: the first extinctions in an ecosystem often tend to affect the top of the food web, shifting the balance of ecosystem regulation toward stronger bottom-up control. In the remainder of the paper I focus on how declining diversity within a trophic level affects ecosystem processes. This question, applied specifically to primary production by plants, has occupied the vast majority of attention in previous research on links between diversity and ecosystem function (Tilman 1999, Schläpfer and Schmid 1999, Loreau et al. 2001). For plant assemblages, some sort of increasing function of primary productivity with plant diversity follows from mechanistic theory, given certain reasonable assumptions (Tilman et al. 1997a, Loreau 1998). Significant control by consumers introduces additional layers of complexity by extending the processes of interest from the two-level modules (abiotic resources, plants) on which most previous theory and empirical studies have focused to multi-level food webs with the concomitant proliferation of indirect effects (Menge 1995), feedbacks (Naeem and Li 1998, Norberg 2000), and the potential for influences propagating both upwards and downwards in the web (Polis and Strong 1996).

Trophic levels? Much of my consideration of consumer-prey interactions presupposes that trophic levels are sufficiently real to be useful constructs, which is not universally accepted (Polis 1991, Polis and Strong 1996, Persson 1999). Nevertheless, the existence and apparent commonness in some systems of trophic cascades (Pace et al. 1999, Pinnegar et al. 2000, Schmitz et al. 2000, Jackson et al. 2001) suggests that – despite the many potentially complicating factors – the trophic level concept adequately approximates trophic dynamics in many ecosystems or subsets thereof. Moreover, at least for well-studied marine intertidal systems, a comprehensive review of *strong* trophic interactions, as opposed to presence/absence of topological links in food webs, reveals that most consumers in these systems eat primarily either plants or animals but not both (Menge 1995). Similar, experimentally derived data from other systems are badly needed.

A focus on interaction strength. The apparently weaker relationship between biomass and community effect among animals, compared with plants, focuses attention on the importance of interaction strength in understanding consumer-prey interactions. Fundamental to establishing a general framework linking diversity to trophic processes are the questions of how interaction strengths are distributed in real communities and how they change with context, specifically the loss of potentially competing species at the same trophic level (Menge et al. 1994, Allison et al. 1995). For example, omnivory has often been suggested as a short-circuit to trophic cascades (Strong 1992, Polis and Strong 1996, Persson 1999) and may well be. Yet, while it is well established that many consumers feed from multiple trophic levels and that diet often changes during ontogeny (Polis and Holt 1992), it is less clear how such processes affect food webs and communities dynamically. The topology of strong interactions in a food web (i.e., the interaction web) often bears little resemblance to the pattern of qualitative links (the connectance web) or energetic pathways (the energy flow web) in traditional food webs and, thus, it is difficult or impossible to assess without experiments (Paine 1980). In terms of diversity effects on the trophic cascade, for example, three questions arise: (1) How does interaction strength differ among species within a level (Fig. 1)? (2) How sensitive are interaction strengths to context, e.g. abiotic factors or changes in community composition (Fig. 2)? And (3) how does the distribution of interaction strengths influence propagation of indirect effects through food webs? Many authors have considered the concentration of influence in one or a few species (Fig. 1a, c) to be key to the efficacy of trophic cascades. As Strong (1992) puts it, “cascades are restricted to fairly low-diversity places where great influence can issue from one or a few species” and “both the herbivores and the carnivores function as keystones”. The few empirical assessments available in fact suggest that interaction strength commonly is strongly skewed toward interactions of negligible effect, with a few species being disproportionately important (Paine 1980, 1992, Raffaelli and Hall 1995, Wootton 1997, but see Berlow 1999). Thus, functional diversity (as defined in Fig. 1) is likely to be often substantially lower than species diversity, which may make strong indirect interactions, including trophic cascades, more common than might be guessed from simple observations of species richness or food web linkage topology alone. This may explain emerging evidence that cascade-like dynamics can occur even in highly diverse ecosystems such as the open-ocean pelagic zone (Shiomoto et al. 1997) and coral reefs (Pinnegar et al. 2000).

Relative demographic rates. The nature of trophic interactions, and thus conclusions about how diversity affects them, will also depend on the relative rates at which consumer and prey assemblages are able to

change in density and composition, and on the time and space scales of observation. At one extreme, for example, studies of zooplankton grazing have focused on responses of fast-growing algal assemblages to a fixed density of grazers (Sommer et al. 2001). Such designs test the responses of a dynamic prey assemblage to a constant type and magnitude of top-down pressure from consumers. They are probably most relevant to systems where relatively large, mobile consumers forage widely, perceive the prey assemblage in a fine-grained manner, and have strong average impacts on prey. At the other extreme are field studies of insect assemblage responses to manipulation of plant diversity (Siemann et al. 1998, Knops et al. 1999, Koricheva et al. 2000, Symstad et al. 2000). This type of experiment measures responses of an open, dynamic consumer assemblage to an essentially fixed prey assemblage, i.e. bottom-up responses to type and quantity of resources. Such designs are most relevant to systems where consumers are small relative to prey, perceive the prey in a coarse-grained way, and have generally weak impacts on the prey assemblage.

Although the search for generalizations in such complexity is daunting (Polis and Strong 1996), several hypotheses arise that I believe are both logistically tractable, at least in judiciously chosen systems, and important to understanding real food webs. My discussion of these issues centers on four general questions: (1) How is extinction distributed among trophic levels? (2) How does prey diversity influence the strength of consumer impacts on aggregate biomass of the prey assemblage? (3) How does consumer diversity influence these consumer impacts? (4) How does diversity at intermediate trophic levels influence the penetrance of trophic cascades? Questions 2 and 3 assume modules (Paine 1980) in which a trophic level is effectively coupled only to the adjacent level, whereas the fourth assumes that influence may extend across trophic levels. To maintain brevity I do not consider most experiments testing effects of plant diversity on invertebrate assemblages (see last paragraph) since top-down effects appear weak in many such studies.

It's lonely at the top

The intense and growing interest in diversity effects on ecosystem function is largely motivated by conservation concerns. It is thus important to take account of patterns in the way diversity is lost in real ecosystems. Extinction is not random (Wilcove et al. 1998). For example, it is well documented (Pimm et al. 1995, Purvis et al. 2000) and intuitively obvious that rare species and those with small geographic ranges are especially at risk. But there are patterns in extinction vulnerability that suggest important consequences

for ecosystem function, notably the bias in extinction by trophic level. From a conservation perspective perhaps the most significant difference between higher-level consumers and plants is in average density and diversity. Basic thermodynamic constraints on metabolic efficiency yield the familiar trophic pyramids of many ecosystems, in which total numbers or biomass of organisms generally decrease with increasing trophic level (Elton 1927, Odum 1971). The typically larger average body size at higher trophic levels (with the important exception of the often much larger size of plants than of their invertebrate herbivores) accentuates this pattern (Cohen et al. 1993, Jennings et al. 2001). This trend of decreasing abundance with increasing trophic level suggests two important hypotheses in the context of biodiversity/function links.

Hypothesis 1. Extinction bias by trophic level results in weakening of top-down control as an early consequence of biodiversity loss. Lower average population size and density at higher trophic levels puts populations high in the food chain in more immediate danger of extinction from demographic and environmental stochasticity, all else being equal. Top predators also tend to be larger, longer-lived animals with inherently lower rates of population growth. Together, these characteristics should result in lower resilience to demographic perturbation and greater average risk of extinction in higher-level consumers, particularly vertebrates. The inherent demographic vulnerability of top predators is compounded by greater human harvesting and harassment pressure on large, conspicuous animals both on land (Woodroffe and Ginsberg 1998, Terborgh et al. 1999), and in the sea, where fisheries disproportionately target large animals near the top of the food chain (Botsford et al. 1997, Pauly et al. 1998, Jackson et al. 2001).

Empirical data offer some support for the prediction that higher trophic levels are more vulnerable to extinction. Microcosm experiments with aquatic protists subjected to environmental warming disproportionately lost herbivores and top predators relative to primary producers (Petchey et al. 1999). Phylogenetically controlled comparative studies confirm that high trophic level is a significant predictor of threatened status in mammalian carnivores and primates (Purvis et al. 2000). And monitoring of beetle populations in fragmented forests showed that predators were disproportionately represented among species that declined (Davies et al. 2000).

The community-wide consequences of such consumer extinctions depend on the strength and frequency of cascading trophic interactions, which remain controversial (Strong 1992, Pace et al. 1999, Polis et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001). Empirical data offer some support for the hypothesis that extinctions of top predators have cascading impacts lower in the food web, although data are limited and mostly

indirect. In the experimentally warmed aquatic microcosms just mentioned, extinction of consumers resulted in greater increases in producer biomass than expected from producer physiology, apparently because of reduced grazing (Petchey et al. 1999). At a much larger scale, the phase shift from kelp beds to coralline algal barrens after sea otters were hunted out in the north-east Pacific is a dramatic example of cascading impacts of predator extinction (Estes and Palmisano 1974, Estes and Duggins 1995). Similarly, in tropical forest fragments isolated by flooding, top predators were first to disappear, with concomitant large increases in density of smaller herbivorous vertebrates, and a reduction by half in density of small saplings (Terborgh et al. 2001). While the latter study is highly suggestive of top-down control, the potentially confounding role of restricted dispersal in concentrating herbivore populations (Krebs et al. 1969) cannot be discounted. Finally, fragmentation of native sage-scrub habitat in southern California led to loss of the top predator, coyotes, with consequent increases in density and activity of “mesopredators” (foxes, racoons, domestic cats), and local extinction of several scrub-nesting birds (Crooks and Soulé 1999). The probable enhancement of mesopredator densities by anthropogenic food sources in this system illustrates that trophic cascades may often depend on subsidy from other habitats (Polis and Strong 1996). Thus, on average, higher-level consumers are often at greater risk than plants, and their loss can have important indirect impacts on ecosystems. The frequency with which it does so depends on what factors control the degree of attenuation of top-down influence (McCann et al. 1998) and the extent to which herbivore populations are limited by food versus predation (Skoglund 1991).

Hypothesis 2. Functional redundancy is lower at higher trophic levels. Another expected consequence of smaller populations and longer generation times at high trophic levels is reduced average speciation rates, and thus lower average species richness of consumers, compared with plants (an important exception being insects). As a result, consumer diversity should more often encompass the low range of species richness, where functional redundancy is low and diversity effects on ecosystem function are predicted to be strongest (Vitousek and Hooper 1993, Tilman et al. 1997a, Schwartz et al. 2000).

There is good evidence for lower diversity at higher levels in most food webs. Well-studied food webs generally contain fewer species of predators than of plants (Havens 1992). Although densities and diversities of invertebrate herbivores are often comparable to (or, in the case of insects, greater than) those of plants, vertebrate herbivores are much less diverse. The lower natural diversity of consumers is reflected in the generally much smaller number of species considered in the few

experiments that have addressed consumer diversity effects, compared with studies of plant diversity effects (see below: Two-level modules: consumer diversity effects). That low diversity of top predators translates to low functional redundancy is implicit in the concept of keystone predators (Paine 1966, 1980), that is, predator species with uniquely strong impacts on community structure, which are known from a variety of systems (Power et al. 1996). An important exception to the pattern of low species richness at upper levels involves insect parasitoids, which are extraordinarily diverse (Godfray et al. 1999). The strength of top-down control by parasitoids is quite variable and often negligible, however (Hawkins 1992, Hawkins et al. 1999), raising the question of whether parasitoid diversity contradicts hypothesis 2 or simply contributes to the tangle of functionally insignificant trophic links that obscure the few strong interactions in a system (see next section).

Paradoxically, the implications of extinctions at upper trophic levels may already be mostly invisible to us since many of the large vertebrate consumers that evolved with modern vegetation on land have been extinguished – apparently by the ultimate top predator, humans – since the late Pleistocene/early Holocene (Alroy 2001). Most of those that remain, such as bison, wolves, mountain lions, and grizzly bears in North America, persist at such low densities that they are effectively ecologically extinct outside of a few national parks. Even today, the impacts of vertebrate consumers in terrestrial systems are poorly studied (Schmitz et al. 2000, Halaj and Wise 2001) and may be underestimated because of the logistical difficulty of manipulating them (Estes 1995, Terborgh et al. 1999, Paine 2000). Similarly, in marine systems, multiple lines of evidence suggest that coastal ecosystems were fundamentally different before humans fished out large consumers during the last centuries to millennia (Jackson et al. 2001). Interestingly, the most influential studies testing how plant diversity affects ecosystem processes have been conducted in North American and European grasslands where the most dramatic effects of diversity reduction – the effective extinction of top predators, and often large herbivores as well – have already taken place. Although the historical importance of top-down control in such systems is uncertain (Caughley 1970), it seems clear that it is now negligible. Several authors have cautioned that the random assembly of species used in diversity-function experiments does not reflect the (partially) deterministic patterns of species association typical of real ecosystems (Grime 1998, Sankaran and McNaughton 1999, Wardle 1999, Fridley 2001). The preceding argument emphasizes a similar determinism in diversity change, with potentially important consequences for ecosystem function, in complete multi-level communities. In short, the relationship between diversity and ecosystem function is inextricably linked to questions about how extinction is distributed within

food webs, and thus how changes in diversity affect trophic processes.

Two-level modules: prey diversity effects

The system-level consequences of consumer-prey interactions are likely to be affected by diversity at both consumer and prey levels. Interestingly, while there is a large literature on the influence of predation and herbivory on community diversity (Paine 1966, Menge and Sutherland 1976, 1987, Connell 1978, Lubchenco and Gaines 1981, Huston 1994), there has been comparatively little attention to influence flowing in the opposite direction. This is in marked contrast to the vigorous theoretical and empirical research on plant diversity effects on productivity cited above. Given that species within a trophic level often differ in linkage topology and interaction strengths with other species, some qualitative hypotheses can be made, as follows.

Hypothesis 3. Prey diversity should enhance resistance to consumption. Considering a two-level module of several consumer and prey species, consumer effects on aggregate prey biomass should be weakened by high prey diversity, all else being equal (Fig. 3b, c). This prediction stems from three assumptions: (1) variance among prey species in edibility and growth rate, (2) simple sampling probability: a more diverse prey assemblage should be more likely to include one or more species resistant to consumption, and (3) density compensation among competing prey species. Leibold (1996) modeled this situation formally, and showed that where there is a trade-off between competitive ability for resources and resistance to consumption, as appears true at least for freshwater algae (Agrawal 1998), increasing con-

sumer pressure will shift species composition of prey toward more resistant species, thus damping consumer impacts on aggregate prey biomass.

Although this predicted role of prey diversity in attenuating consumer impacts has been widely discussed (Leibold 1989, Strong 1992, Polis and Strong 1996, Persson 1999, Schmitz et al. 2000, Jackson et al. 2001), I am aware of only a single explicit, experimental test of the hypothesis. In a laboratory experiment, Steiner (2001) compared the impact of grazing cladocerans on accumulation of phytoplankton biomass under conditions of low prey diversity (a single, edible algal species) and high prey diversity (natural phytoplankton assemblages) in a laboratory experiment. In support of the hypothesis, consumer suppression of prey biomass was stronger in the single-species treatment than in the diverse natural assemblage. The diversity effect was especially marked under nutrient enrichment, where the grazed natural assemblage reached an order of magnitude higher biomass than the grazed single algal species. The higher resistance to consumption in the diverse algal assemblage was mediated by an increase in relative abundance of large grazer-resistant algal species. Strictly speaking, this experiment tested the effects of prey species composition rather than prey diversity (Huston 1997) since it was not possible to determine whether resistance of the natural assemblage was greater than that of each component species in monoculture. Nevertheless, the design addresses a significant question in that ungrazed systems are often dominated by rapidly growing, highly edible prey species. McNaughton (1985) reported a qualitatively similar result in a very different system, the large vertebrate grazers on the Serengeti grassland. Caging experiments showed that grassland plots of naturally higher diversity were more resistant, i.e. lost

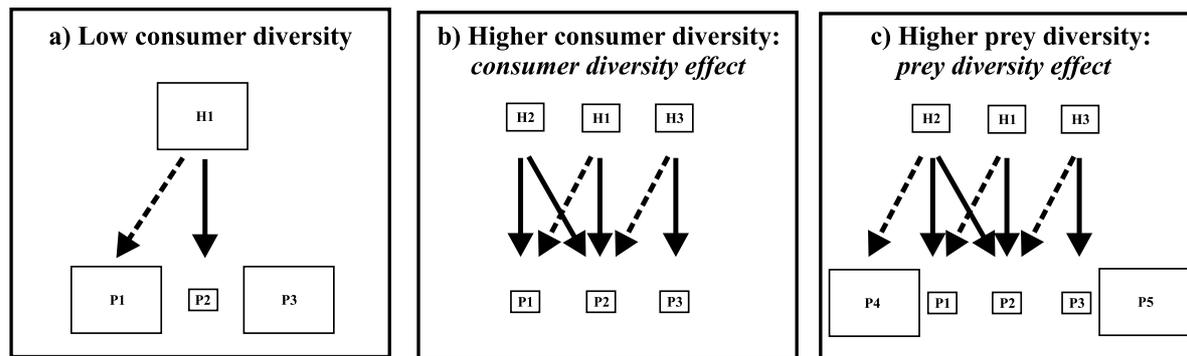


Fig. 3. Hypothesized influence of diversity on direct trophic effects in a two-level system. The upper and lower levels could represent, respectively, either herbivores (H) feeding on plants (P) as shown, or carnivores feeding on herbivores. The consumer diversity effect is the enhanced impact of consumers on prey biomass under (b) high consumer diversity, compared with (a) low consumer diversity. Total prey biomass is reduced under high consumer diversity because there is a greater chance that one or more of the consumers can effectively suppress each prey species present. The prey diversity effect is the reduction in impact of consumers on prey biomass under (c) high prey diversity, compared with (b) low prey diversity. Total prey biomass is greater under high prey diversity because there is a greater chance that one or more of the prey species will be resistant to suppression by all consumers present. Symbols as in Fig. 1.

less biomass, to (single-species) grazer herds than did plots with lower diversity. Because these plots varied naturally in diversity, with potentially confounding differences in other variables, the differences in resistance cannot rigorously be attributed to plant diversity. Nevertheless, the mechanism appears consistent with the hypothesis (Fig. 3b, c) as more diverse plots contained species resistant to grazing (McNaughton 1985). While not focused explicitly on the role of prey diversity, numerous other experimental studies also support a buffering role for prey diversity against consumer control, in showing that consumer pressure shifts dominance of the prey assemblage to resistant taxa. Blooms of noxious blue-green algae under sustained strong grazing pressure are a familiar example from lakes (Leibold et al. 1997). Similar dominance by unpalatable prey under strong grazing pressure has been documented in marine phytoplankton (Metaxas and Scheibling 1996) and especially in benthic seaweeds (Hay 1984b, Thacker et al. 2001). For probably similar reasons, cascading trophic interactions have weaker average effects on plants in diverse grasslands and woodlands than in low-diversity agroecosystems (Halaj and Wise 2001).

An intriguing possible counter-example to this trend has been documented by Mulder et al. (1999), who measured insect damage in experimental grassland plots varying in plant species richness. The subset of plant species visibly attacked by herbivores suffered greater damage in multi-species plots compared with the average level in monocultures. This resulted from a sampling effect, however: insect abundance (and thus grazing pressure) was determined primarily by presence of legumes, which were more frequent dominants in plots with high plant diversity. In contrast to the plankton (Steiner 2001) and Serengeti (McNaughton 1985) cases, damage to preferred plants in this study was not sufficient to allow resistant plants to achieve dominance, whether because of relatively weak herbivore impacts or insufficient duration of the experiment. Thus, it is unclear whether these results contradict the prediction.

Hypothesis 4. Diverse prey assemblages should be more stable in the face of consumption. The idea that diversity begets stability has a long and tumultuous history (MacArthur 1955, Elton 1958, May 1974, Goodman 1975, Pimm 1984, Cottingham et al. 2001). Mechanistically, high diversity may be expected to enhance an assemblage's resistance to disturbance via a sampling effect, that is, the greater probability that a more diverse assemblage will include one or more species resistant to the disturbance. Some empirical studies support this general effect, showing that more species-rich plant assemblages are less affected by drought (Tilman and Downing 1994, Mulder et al. 2001). By analogous reasoning, high diversity may be expected to

buffer a prey assemblage from the disturbance of predation.

I know of no direct test of this hypothesis, but it is supported indirectly by McNaughton's (1985) data for grazing ungulates on the Serengeti grasslands. Temporal variation in green plant biomass within unfenced (i.e. grazed) plots was negatively related to vegetation diversity and, in fact, vegetation diversity explained a larger proportion of the variance in green biomass than did rainfall variability. More diverse plots were also more resilient to grazing in that study, that is, they rebounded toward pre-grazing levels more quickly than did less diverse plots. Presumably, the more diverse plots were more likely to include species able to regrow quickly after grazing disturbance.

In summary, there is a fair amount of evidence that prey diversity enhances resistance to consumption. Most of this evidence is indirect, however, and all of the studies of which I am aware considered herbivores feeding on plants. More explicit experimental studies of prey diversity effects would be desirable, as would experiments addressing how diversity of animal prey affects resistance to predation.

Two-level modules: consumer diversity effects

Although decades of research have documented the impacts of consumers on prey populations and community structure (Sih et al. 1985, Menge 1995), few studies have explicitly addressed effects of consumer *diversity* on prey assemblages. The general mechanisms of complementarity and sampling proposed to explain plant diversity effects on productivity (Tilman et al. 1997a, Loreau 1998) can be applied to consumer-prey interactions to predict that a more diverse consumer assemblage should have stronger impacts on aggregate prey abundance than a depauperate one (Holt and Loreau 2002). However, consumer diversity effects will also be sensitive to phenomena specific to trophic processes, including plasticity of consumer diet breadth and interaction strength (Mikola and Setälä 1998). At one extreme (Fig. 2a, b), the diet range and interaction strengths of consumers may be intrinsically constrained (e.g. by diet specialization, territoriality, low metabolic rates) such that removal of a functionally dominant consumer has no effect on cooccurring consumer species, and the prey community responds strongly to the reduced consumer pressure. This is the classic situation of a keystone consumer (Paine 1966, Power et al. 1996). At the other extreme (Fig. 2c), removal of a formerly dominant consumer may release remaining consumers from competition, resulting in compensatory increases in density, (population-level) interaction strengths, and even diet breadth, such that there is no effect on prey biomass of removing the formerly dominant consumer (i.e. "diffuse predation", Menge et al. 1994).

Hypothesis 5. More diverse consumer assemblages should more strongly reduce aggregate prey biomass. All else being equal, a more diverse consumer assemblage should have greater impact on prey biomass because it is more likely to include one or more species capable of suppressing each of the prey species present (Holt and Loreau 2002; Fig. 3a, b). This hypothesis is a simple extension of the arguments based on niche complementarity and sampling proposed to explain why more diverse plant assemblages often achieve higher productivity at a given level of resource input (Tilman et al. 1997a). The strength of such consumer diversity effects should increase with the degree of differentiation among species in traits affecting feeding and trophic processes, such as consumer body size, feeding preferences, mobility, and so on. For example, there is some evidence for systematic differences in feeding ecology and impacts between large vertebrate and small invertebrate herbivores in both marine (Hay 1991) and terrestrial (Ritchie and Olff 1999) ecosystems, as well as for correlations between consumer and prey body sizes over several orders of magnitude (Cohen et al. 1993, Hansen et al. 1994).

This hypothesis is consistent with experimental and observational data which, while not addressing consumer diversity effects explicitly, show that different herbivores feed on different components of vegetation and that combinations of herbivores (or functional groups) can depress vegetation biomass more than single species or functional groups do. For example, experiments in a seaweed-dominated benthic community showed that the combination of large mobile vertebrates (grazing fishes) and small, less mobile invertebrates (amphipods) reduced total plant biomass to less than half the biomass present with either type of grazer alone (Duffy and Hay 2000). This was because fish grazing alone led to dominance by fish-resistant brown algae, whereas amphipod grazing alone resulted in dominance by red algae, which are non-preferred food for amphipods. Similarly, complementary feeding by a newt and a sunfish depressed abundance of anuran prey well below that of either predator alone (Kurzava and Morin 1998). Finally, in experiments with lake plankton, grazing by *Daphnia* alone or copepods alone led, respectively, to dominance by large- and small-celled algal species but neither grazer affected total algal biomass. In contrast, the two types of grazers together significantly depressed total algal biomass because of their complementary prey-size preferences (Sommer et al. 2001). The latter result could provide a very general mechanism for consumer diversity effects in systems where consumer and prey size are correlated.

Few studies have explicitly addressed effects of consumer diversity on prey. Of these, the most comprehensive is Naeem and Li's (1998) manipulation of food web structure and diversity in aquatic microbial microcosms. These authors found a strong and significant

reduction in algal biomass as species richness of protistan consumers increased from one through 7–9 species. Although this intriguing result is superficially consistent with hypothesis 5, it does not test the hypothesis directly for several reasons. First, because only a single primary producer species was present, the mechanistic basis for this result must differ from that outlined in Fig. 3a and b. Second, Naeem and Li's (1998) consumers included omnivores and a top predator as well as herbivores, such that algal biomass was controlled by a complex feedback interaction between grazing, predation, and changes in abundance of bacteria that influenced nutrient availability to the algae. Their results underscore that herbivores influence their prey not only by direct consumption but by regenerating nutrients and freeing up other resources such as space. Norberg (2000) also examined effects of planktonic consumer diversity, in this case four herbivorous cladoceran species, on algal biomass, productivity, and related ecosystem processes. The contrast between his results and those of Naeem and Li (1998) illustrates the important role of prey diversity in mediating ecosystem-level responses to changes in consumer diversity (Fig. 3). Although individual grazer species and combinations differed widely in their impacts, Norberg found no significant effect of grazer species richness on algal biomass. The absence of a grazer diversity effect resulted both from competition among the grazers, which essentially eliminated competitively inferior grazers from some multi-species treatments, and from compensatory shifts toward resistant algal species in heavily grazed treatments. Such prey compensation cannot operate where only a single prey species is present. Norberg's results did, however, support hypothesis 5 to the extent that particular combinations of species with complementary feeding preferences had greater grazing impacts than either species alone. A third experimental study measured effects of herbivorous crustaceans (three species in all possible combinations) on plant biomass accumulation in estuarine submerged vegetation (Duffy et al. 2001). As in Norberg's (2000) system, grazing impacts on plants were generally strong and differed among the three grazers, but there was no significant effect of grazer species richness on any response variable. The absence of a diversity effect in this case stemmed from the absence of complementarity: the most productive plant functional group, epiphytic algae, was similarly susceptible to all three grazers, whereas the foundation species, eelgrass, was eaten by only one. Thus, diets of two of the grazer species formed a subset of that of the third, and the latter's effects dominated the results.

Finally, McNaughton's (1985) study of grazing ungulates on the Serengeti provides two lines of indirect support for hypothesis 5. First, vegetation in areas grazed by multiple herbivore species lost an average of 82% of biomass whereas areas grazed by single-species

herds lost 32–74% of biomass depending on grazer species. This was because grazer species had complementary grazing preferences for different types of plants. Second, whereas the percentage of vegetation biomass eaten by single-species grazer herds was negatively related to vegetation diversity, grazing losses to multi-species herds were unrelated to vegetation diversity. That is, the grazing resistance of diverse vegetation toward individual grazer species was overcome by more diverse herbivore assemblages (as predicted in Fig. 3a, b).

Consumers may also influence ecosystem processes through the detritus pathway. Jonsson and Malmqvist (2000) measured the influence of three species of shredding aquatic insects on decomposition of leaf debris over 6.5 weeks in a laboratory assay. These authors found a strongly significant positive relationship between consumer species richness and decomposition rate. As in the protist grazing study (Naeem and Li 1998), however, the food in this experiment came from a single primary producer species. Thus, the mechanism outlined in Fig. 3a and b seems unlikely to apply. The authors suggested that facilitation among species or reduced inter- relative to intraspecific interference might explain their result.

On balance, then, the few studies available offer decidedly mixed support for hypothesis 5. They suggest that both diversity of the prey assemblage and the degree of complementarity in diet range among consumers have important influences on aggregate grazing impact. The data available are not ideal for testing the hypothesis, however. First, of the small number of studies that have manipulated consumer diversity experimentally, most have considered only two or three species. In experiments where diversity has been shown to correlate significantly with ecosystem processes, it generally explains a relatively small proportion of variance (McGrady-Steed et al. 1997, Naeem and Li 1998, Hector et al. 1999, Tilman et al. 2001), and it is clear from the variance around such regressions that a range in diversity of 2–3 species is likely to yield idiosyncratic results even where diversity does significantly affect a process over a wider range. Second, both of the experimental studies that documented significant effects of consumer diversity on prey biomass (Naeem and Li 1998, Jonsson and Malmqvist 2000) used only a single prey (or resource) species so hypothesis 5, which assumes multi-species prey assemblages, cannot be tested. Finally, it is noteworthy that most of these studies focused on consumers that are similar in body size and ecology and are taxonomically related. Although superficially similar consumers often show surprisingly different effects on prey and ecosystem processes (Norberg 2000, Duffy et al. 2001), it remains to be tested whether assemblages composed of more disparate functional groups impose generally greater grazing pressure on aggregate prey abundance.

Hypothesis 6. More diverse consumer assemblages should have more temporally consistent impacts on their prey. If abundances of species within an assemblage vary independently of one another, or in a complementary fashion due to competition, then the aggregate (summed) abundance of a multi-species assemblage will be less variable through time than will that of the average species, resulting in a negative correlation between species richness and temporal variance in aggregate abundance (Doak et al. 1998). Tilman et al. (1998) refer to this correlation as the “portfolio effect”. By extension, if a consumer’s impact is proportional to its abundance, then a more diverse consumer assemblage should show lower temporal variance in aggregate predation pressure by averaging out seasonal and interannual population fluctuations of its component species. Such variance-damping effects are likely to be among of the most general and robust consequences of high diversity for ecosystem processes because they emerge automatically as a statistical consequence of averaging fluctuations in unsynchronized populations. The phenomenon will be stronger where different populations have complementary phenologies (Micheli et al. 1999).

I am unaware of any direct test of this hypothesis. It is supported in several cases by indirect evidence, however. Aggregate abundance or biomass of multi-species assemblages is less variable than that of any component species in microbial microcosms (McGrady-Steed and Morin 2000), herbivorous zooplankton of North American lakes (Frost et al. 1995), and large vertebrate herbivores of East Africa (Prins and Douglas-Hamilton 1990). Although such abundance trends presumably translate into parallel trends in total consumption pressure, such studies have rarely if ever measured diversity effects on stability of consumption per se. The existence of functional redundancy among consumers (Menge et al. 1986, Duffy et al. 2001) also offers suggestive evidence for this hypothesis.

Multi-level food webs: diversity effects

As controversial as proposed effects of plant diversity on ecosystem function have been, predicting and testing diversity effects in more complete multi-level food webs is even more difficult. This is due both to the conceptual challenge of defining expectations in systems with a large number of trophic links and indirect effects (Polis and Strong 1996), as well as to the formidable logistical challenges of manipulating several trophic levels simultaneously. The latter issue explains why most experiments in this area have used laboratory microcosms of protists. To date, only a few studies have tested diversity effects in multi-level food webs. All of these have manipulated diversity simultaneously across multiple trophic levels and measured ecosystem responses in a

general search for ecosystem responses to changes in overall diversity. Since effects of consumer diversity or interactions with prey cannot be isolated from changes at other levels in these designs, they necessarily trade off mechanistic understanding for the goal of estimating the existence and form of biodiversity effects. The pioneering experiments of Naeem et al. (1994, 1995) established a nested series of diversity treatments in mesocosms with herbaceous vegetation and invertebrate consumers. They found significant positive correlations between diversity, total biomass, and CO₂ uptake. Although consumer impacts were not explicitly measured, so it is not possible to assess whether they played a role, the increase in plant biomass and CO₂ uptake with overall diversity suggests that the response variables measured were dominated by plant processes.

Two conceptually similar studies manipulated species richness of aquatic protists across 3–4 trophic levels in laboratory microcosms. Naeem and Li (1997) tested the “insurance hypothesis”, related to hypotheses 4 and 6 above, that diversity should reduce variance in ecosystem processes. Among microcosms subjected to a range in light and nutrient conditions, more diverse systems indeed showed lower variance in biomass of basal taxa (algae and bacteria). Consumers strongly reduced algal biomass in this experiment (Naeem and Li 1997), and a companion study demonstrated that algal suppression was greater under higher consumer diversity (Naeem and Li 1998). McGrady-Steed et al. (1997) similarly manipulated species richness of protistan producers, grazers, and predators, and measured CO₂ flux, organic matter decomposition, and success of an invading species. They found, as did Naeem and Li (1997) that more diverse microcosms had lower variance in an ecosystem process, in this case CO₂ flux. Interestingly, microcosms switched from net autotrophic (negative CO₂ flux) to net heterotrophic (net CO₂ consumption) with increasing diversity, confirming that consumer control was stronger at higher diversity (McGrady-Steed et al. 1997).

Finally, the most recent and comprehensive test of diversity effects in a multi-level food web manipulated both species richness and composition across well-defined plant, grazer, and predator trophic levels in freshwater mesocosms that simulated fishless ponds (Downing and Leibold 2002). This study demonstrated that a five-fold increase in diversity, from 3 to 15 manipulated species, significantly enhanced ecosystem-level productivity and respiration by approximately 8% each (estimated from their figures), although variation in species composition within richness levels produced considerably stronger changes in ecosystem-level metabolism.

Hypothesis 7. Prey diversity should reduce penetrance of trophic cascades. Although expectations for diversity effects in multi-level food webs are difficult to specify a

priori, at least one specific prediction has received much attention. Of several factors that appear important in mediating the strength and penetrance of cascading consumer control on ecosystems, biodiversity and food web complexity have repeatedly been cited as among the most important (Strong 1992, Polis and Strong 1996, Persson 1999, Polis et al. 2000, Schmitz et al. 2000). If high prey diversity reduces the impact of a consumer, it follows that it will also reduce the top-down influence of that consumer on levels of the prey’s resource. In other words, prey diversity will short-circuit the trophic cascade (Strong 1992, Polis and Strong 1996). Consider specifically the influence of diversity at intermediate trophic levels (Fig. 4). Where herbivore species are few and vulnerable to predators (Fig. 4a, b), addition of a carnivore can suppress herbivory and thus the carnivore’s influence can cascade down to increase aggregate plant biomass. In contrast, where herbivore diversity is high (Fig. 4c, d), the biomass of herbivore taxa lost to predation can be compensated by less susceptible herbivore taxa as they are released from competition with the formerly dominant herbivores (Leibold 1996). As a result, total grazing pressure on plants is little affected and plant biomass remains low despite addition of a carnivore. In general, high diversity within any but the top trophic level should reduce the impact of higher-level consumers and thus the penetrance of their effects to plants, short-circuiting the trophic cascade (Strong 1992). The corollary is that trophic cascades should become more pronounced as realized functional diversity (Fig. 1) of herbivores and plants is reduced.

Whereas the proposed role of diversity in foiling trophic cascades is approaching the status of a paradigm in ecology (Strong 1992, Polis and Strong 1996, Persson 1999), I have been unable to locate any explicit, experimental study that adequately tests this hypothesis. Perhaps the closest is that of Mikola and Setälä (1998), who studied a three trophic-level soil food web including microbes (bacteria and fungi), microbe-grazing nematodes, and a predatory nematode, in laboratory bottle experiments. These authors were primarily interested in whether and how consumer (grazer) species richness influenced community respiration and aggregate consumer biomass. Because previous work showed that these grazers did not significantly affect producer (bacteria and fungi) biomass, effects on cascading trophic interactions were considered a priori to be negligible. Mikola and Setälä (1998) established treatments in which diversity at the intermediate level varied from two species (in three different combinations) to six species. Ecosystem responses (trophic level biomass and respiration) were idiosyncratically related to changing consumer species composition and diversity: grazer species combinations differed in biomass accumulation, but there was no effect of grazer species richness per se on any variable. Predator biomass also

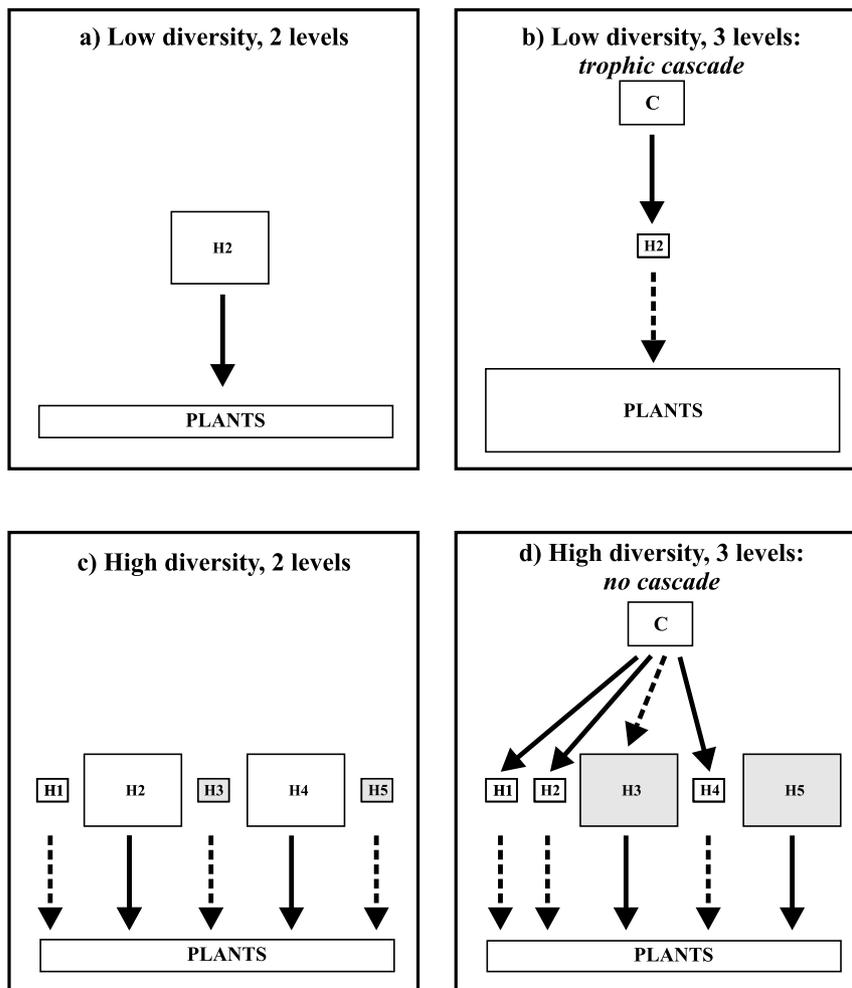


Fig. 4. Hypothesized influence of diversity at an intermediate trophic level on indirect trophic effects, i.e. the trophic cascade, in a three-level system. For simplicity, a single, functionally uniform carnivore and plant trophic level are considered. Top: under low herbivore diversity, (a) strong grazing results in low plant biomass, whereas (b) addition of a carnivore suppresses grazing and indirectly increases plant biomass, i.e. there is a strong trophic cascade. Bottom: under high herbivore diversity, (c) grazing suppresses plant biomass, and (d) addition of a carnivore has no indirect effect on plant biomass because formerly rare predator-resistant herbivore species (shaded) are released from competition, and their grazing compensates for loss of the formerly dominant herbivores. Symbols as in Fig. 1.

differed among treatments but was not clearly related to prey diversity.

The only statistically evaluated approach to testing hypothesis 7 of which I'm aware comes from the meta-analysis of Schmitz et al. (2000), who were able to demonstrate in a sample of 14 studies that indirect effects of terrestrial invertebrate carnivores on herbivore damage to plants were significantly weaker in experiments with more, versus fewer, than four herbivore species. Thus, the hypothesis was supported. Nevertheless, the paucity of explicit, experimental tests of how consumer biodiversity affects ecosystem processes represents an important obstacle to progress in this area.

Several more indirect lines of evidence, mostly from exploited marine systems, do support a role for diversity in reducing penetrance of top predator effects on deeper levels of the food web. What these data lack in rigorous experimental control is partially compensated by the much greater temporal and spatial scale of observations. One example comes from comparing the

classic sea otter-sea urchin-kelp cascade in Alaska (Estes and Duggins 1995, Estes et al. 1998) with the similar but more diverse kelp bed food web of southern California (Dayton et al. 1998). Although fur traders (apex predators in this case) decimated sea otter populations in both regions by the early 19th century, population explosions of sea urchins, and concomitant loss of kelp beds to grazing, occurred initially only in the low-diversity food web of Alaska, where otters act as keystone predators on urchins. In southern California, by contrast, kelps were not adversely affected until spiny lobsters and sheephead – also predators of urchins – began to be heavily exploited by humans in the 1950s (Dayton et al. 1998). Retrospective analysis of trends in marine food web structure following anthropogenic environmental changes, mostly involving fishing, also support a role for diversity in buffering ecosystems from top-down forces. On Caribbean coral reefs, decades of overharvesting of herbivorous (and other) fishes did not obviously influence reef algal biomass initially, apparently because sea urchin grazing compen-

sated for the reduced fish grazing (Hay 1984a, Hughes 1994, Jackson et al. 2001). Subsequently, however, disease decimated the sea urchin populations and algal biomass exploded (Carpenter 1990). The strong bloom of macroalgae on these reefs happened only after both major functional groups of herbivores, fishes and sea urchins, were greatly reduced. Similarly, experimental reduction of zooplanktivorous rainbow trout in Castle Lake, California did not result in the trophic cascade documented in more northerly lakes because other zooplanktivores increased in abundance, compensating for the missing trout and actually increasing predation pressure on zooplankton (Elser et al. 1995). In a review of fishing-related ecosystem shifts, Jackson et al. (2001), p. 636) conclude that "Ecological diversity and redundancy within trophic levels is probably the most important reason for the delay or time lag between the onset of fishing and the subsequent threshold response." Finally, it is possible that the lower frequency of trophic cascades in marine (Micheli 1999) compared with freshwater systems (Brett and Goldman 1996) is related to the generally higher diversity of plankton in the ocean. Despite the convergence of these various lines of evidence, it is striking that the potential damping role of diversity on trophic cascades remains untested experimentally.

I have focused on trophic cascades because their predictions are relatively straightforward and they have been well studied. It is worth emphasizing, however, that they are only one of many types of indirect effects in food webs (Menge 1995) and the others are not so easily predicted. From a conservation perspective, the important point is that the continuing extinctions of species occurring worldwide are likely to impact not only the species that interact directly with them but increasingly with other, more distantly connected species as well (Jackson et al. 2001). The sobering implication of such indirect interactions is that the community- and ecosystem-level impacts of species losses may become both stronger and harder to predict as biodiversity declines.

Issues and questions for future research

The bottom-up influences of plant species composition and diversity on ecosystem processes have been a subject of intense research and debate in the last decade. Most empirical research has come from ecosystems in which historically dominant consumers have been essentially eliminated (e.g. North American and European grasslands), so that consumers are consequently insignificant. Although such trophic skew may now be typical of most terrestrial ecosystems, they may give a biased view both of their pristine forebears and of those remaining systems where top-down control remains

strong (Paine 2002). The main point I wish to make is that effects of biodiversity erosion on ecosystem processes in systems with strong top-down forces, including many marine, freshwater, and probably terrestrial systems, are equally and sometimes more likely to be manifested through the action of consumers than at the level of primary producers (Petchey et al. 1999). This is because diversity of higher-level consumers is generally lower than that of plants, human harvesting pressure is more intense on higher-level consumers, and community impacts of consumers are less closely related to their relative biomass. Thus, perturbations at the upper levels of the food web are especially likely to ripple down through the rest of the system. For these same reasons, changes in consumer diversity are likely to have more idiosyncratic effects on ecosystem processes than are changes in plant diversity.

Many individual herbivore and predator species have well-documented impacts on prey biomass, community structure, and on carbon and nutrient fluxes (see above). Despite the concordance of various indirect lines of evidence, however, there remain few experimental tests of how diversity at consumer or prey levels affects any trophic or other ecosystem process, and none that explicitly tests the much-discussed influence of consumer diversity on strength of trophic cascades. The few existing studies mostly consider only two or three consumer species, which is insufficient to detect a diversity effect reliably even if one exists. There is clearly a need for direct experimental tests of the hypotheses I discuss above, as well as for systematic study of the distributions and context-specificities of interaction strengths in real communities, and patterns by which diversity is lost from real ecosystems, what might be called community disassembly rules. For example, whether declining diversity enhances trophic cascades, as might be expected (hypothesis 7), will depend critically on which prey species remain as diversity erodes. Because top predators are more mobile and sparsely distributed than most plants, understanding the possible impacts of consumer diversity on ecosystem function will also require creative exploitation of opportunities provided by, for example, habitat fragmentation (Crooks and Soulé 1999, Terborgh et al. 2001) and protected areas (Pinnegar et al. 2000).

In particular, there is a pressing need for careful experimental study of how predators (especially large vertebrates) influence the structure and function of naturally diverse communities. The vigorous debate over the importance of trophic cascades continues in significant part because of the paucity of appropriate data to resolve it. It is quite possible, as several authors have argued, that plant chemical defenses, omnivory, intra-guild predation, and other widely cited aspects of food-web heterogeneity and reticulation generally foil trophic cascades. But despite theoretical support for such effects (Leibold 1996) and frequent claims for their

importance, there are precious few rigorous experimental data available to evaluate them. Such data are critical to resolving this issue because there are a number of quite reasonable counterarguments (and some supporting data, Agrawal 1998) for why trophic cascades may emerge even in superficially complex systems. The principal of these was made many years ago (Paine 1980), that is, that qualitative food-web links tell us little about the number or topology of strong trophic interactions that significantly influence other populations, and thus community structure, aggregate biomass, and ecosystem-level response variables. The topology of most real food webs is extraordinarily complex and reticulate (Polis and Strong 1996). But how many of these links have a significant impact on either donor or recipient? A major challenge in assessing diversity effects on trophic interactions will involve pruning the often dense undergrowth of functionally negligible feeding links to reveal the strong limbs of the underlying interaction web.

Finally, in considering the relationships between functional and taxonomic diversity – the functional group problem, if you will – and its influence on food web structure and function, we should not underestimate the importance of subtle differences among species that manifest only under altered conditions or over long time periods. Such effects of individual species, and the emergent effects of biodiversity that emanate from them (Tilman and Downing 1994, Frost et al. 1995, Grime 1998, Mulder et al. 2001), are not easily captured in short-term experiments under tightly controlled conditions. Experimental field manipulations of consumer species that have been maintained over decades, and through large interannual variations in weather and abiotic forcing, show that subtle differences among species often have pronounced impacts on the system that show up only intermittently or after extended periods of time (Brown et al. 2001). Assessing the importance of such “cryptic” effects will be difficult, and argues for a precautionary approach to biodiversity conservation.

Acknowledgements – I thank John Bruno, Kristin France, Rom Lipcius, Rochelle Seitz, Amy Symstad, Liz Canvel, and participants in the spring 2002 Biodiversity seminar at VIMS for helpful discussion and comments on earlier versions of the MS. I am particularly indebted to Don Strong for a thorough review that inspired me to confront complexity more directly and to sharpen my arguments. Thanks to the NSF (OCE 95-21184, OCE 00-96226) for support during the gestation of this paper. This is VIMS contribution # Z473.

References

Agrawal, A. A. 1998. Algal defense, grazers, and their interactions in aquatic trophic cascades. – *Acta Oecologia* 19: 331–337.
 Allison, G. W., Menge, B. A., Lubchenco, J. and Navarrete, S. A. 1995. Predictability and uncertainty in community regu-

lation: consequences of reduced consumer diversity in coastal rocky ecosystems. – In: Mooney, H. A., Cushman, J. H., Medina, E. et al. (eds), *Functional roles of biodiversity: a global perspective*. John Wiley and Sons, pp. 371–392.
 Alroy, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal extinction. – *Science* 292: 1893–1896.
 Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. – *Nature* 398: 330–334.
 Berlow, E. L., Navarrete, S. A., Briggs, C. J. et al. 1999. Quantifying variation in the strengths of species interactions. – *Ecology* 80: 2206–2224.
 Botsford, L. W., Castilla, J. C. and Peterson, C. H. 1997. The management of fisheries and marine ecosystems. – *Science* 277: 509–515.
 Brett, M. T. and Goldman, C. R. 1996. A meta-analysis of the freshwater trophic cascade. – *Proc. Natl. Acad. Sci. USA* 93: 7723–7726.
 Brown, J. H., Whitham, T. G., Morgan, S. K. et al. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. – *Science* 293: 643–650.
 Bruno, J. F. and Bertness, M. D. 2001. Habitat modification and facilitation in benthic marine communities. – In: Bertness, M. D., Gaines, S. D. and Hay, M. E. (eds), *Marine Community Ecology*. Sinauer, pp. 201–218.
 Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. – *Mar. Biol.* 104: 67–77.
 Carpenter, S. R., Kitchell, J. F. and Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. – *BioScience* 35: 634–639.
 Carpenter, S. R., Kitchell, J. F., Hodgson, J. R. et al. 1987. Regulation of lake primary productivity by food web structure. – *Ecology* 68: 1863–1876.
 Caughley, G. 1970. Eruption of ungulate populations. With emphasis on Himalayan Thar in New Zealand. – *Ecology* 51: 53–72.
 Chapin, F. S. III, Walker, B. H., Hobbs, R. J. et al. 1997. Biotic control over the functioning of ecosystems. – *Science* 277: 500–504.
 Chase, J. M. 2000. Are there real differences among aquatic and terrestrial food webs? – *Trends Ecol. Evol.* 15: 408–412.
 Cohen, J. E., Pimm, S. L., Yodzis, P. and Saldaña, J. 1993. Body sizes of animal predators and animal prey in food webs. – *J. Anim. Ecol.* 62: 67–78.
 Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – *Science* 199: 1302–1310.
 Cottingham, K. L., Brown, B. L. and Lennon, J. T. 2001. Biodiversity may regulate the temporal variability of ecological systems. – *Ecol. Lett.* 4: 72–85.
 Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. – *Nature* 400: 563–566.
 Davies, K. F., Margules, C. R. and Lawrence, J. F. 2000. Which traits of species predict population declines in experimental forest fragments? – *Ecology* 81: 1450–1461.
 Dayton, P. K., Tegner, M. J., Edwards, P. B. and Riser, K. L. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. – *Ecol. Appl.* 8: 309–322.
 Díaz, S., Cabida, M. and Casanoves, F. 1999. Functional implications of trait-environment linkages in plant communities. – In: Weiher, E. and Keddy, P. (eds), *Ecological assembly rules. Perspectives, advances, retreats*. Cambridge Univ. Press, pp. 338–362.
 Diehl, S. 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. – *Oikos* 68: 151–157.
 Doak, D. F., Bigger, D., Harding, E. K. et al. 1998. The statistical inevitability of stability-diversity relationships in community ecology. – *Am. Nat.* 151: 264–276.

- Downing, A. L. and Leibold, M. A. 2002. Ecosystem consequences of species richness and composition in pond food webs. – *Nature* 416: 837–840.
- Duffy, J. E. and Hay, M. E. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. – *Ecol. Monogr.* 70: 237–263.
- Duffy, J. E. and Hay, M. E. 2001. The ecology and evolution of marine consumer-prey interactions. – In: Bertness, M. D., Hay, M. E. and Gaines, S. D. (eds), *Marine community ecology*. Sinauer Associates, pp. 131–157.
- Duffy, J. E., Macdonald, K. S., Rhode, J. M. and Parker, J. D. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. – *Ecology* 82: 2417–2434.
- Duggins, D. O., Simenstad, C. A. and Estes, J. A. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. – *Science* 245: 170–173.
- Elser, J. J., Luecke, C., Brett, M. T. and Goldman, C. R. 1995. Effects of food web compensation after manipulation of rainbow trout in an oligotrophic lake. – *Ecology* 76: 52–69.
- Elton, C. 1927. *Animal ecology*. – Sidgwick and Jackson.
- Elton, C. S. 1958. The ecology of invasions by animals and plants. – Methuen.
- Estes, J. A. 1995. Top-level carnivores and ecosystem effects. – In: Jones, C. G. and Lawton, J. H. (eds), *Linking species and ecosystems*. Chapman and Hall, pp. 151–158.
- Estes, J. A. and Palmisano, J. F. 1974. Sea otters: their role in structuring nearshore communities. – *Science* 185: 1058–1060.
- Estes, J. A. and Duggins, D. O. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community paradigm. – *Ecol. Monogr.* 65: 75–100.
- Estes, J. A., Tinker, M. T., Williams, T. M. and Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. – *Science* 282: 473–476.
- Fridley, J. D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? – *Oikos* 93: 514–526.
- Frost, T. M., Carpenter, S. R., Ives, A. R. and Kratz, T. K. 1995. Species compensation and complementarity in ecosystem function. – In: Jones, C. G. and Lawton, J. H. (eds), *Linking species and ecosystems*. Chapman and Hall, pp. 224–239.
- Godfray, H. C. J., Lewis, O. O. and Memmott, J. 1999. Studying insect diversity in the tropics. – *Phil. Trans. R. Soc. Lond. B* 354: 1811–1824.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. – *Q. Rev. Biol.* 50: 237–266.
- Grime, J. P. 1998. Essay review: benefits of plant diversity to ecosystems: immediate filter and founder effects. – *J. Ecol.* 86: 902–910.
- Hairton, N. G., Smith, F. E. and Slobodkin, L. G. 1960. Community structure, population control, and competition. – *Am. Nat.* 94: 421–425.
- Halaj, J. and Wise, D. H. 2001. Terrestrial trophic cascades: how much do they trickle? – *Am. Nat.* 157: 262–281.
- Hall, S. J. and Raffaelli, D. G. 1993. Food Webs: theory and reality. – In: Begon, M. and Fitter, A. H. (eds), *Advances in ecological research*. Academic Press, pp. 187–239.
- Hansen, B., Bjørnsen, P. K. and Hansen, P. J. 1994. The size ratio between planktonic predators and their prey. – *Limnol. Oceanogr.* 39: 395–403.
- Havens, K. 1992. Scale and structure in natural food webs. – *Science* 257: 1107–1110.
- Hawkins, B. A. 1992. Parasitoid-host food webs and donor control. – *Oikos* 65: 159–162.
- Hawkins, B. A., Mills, N. J., Jervis, M. A. and Price, P. W. 1999. Is the biological control of insects a natural phenomenon? – *Oikos* 86: 493–506.
- Hay, M. E. 1984a. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? – *Ecology* 65: 446–454.
- Hay, M. E. 1984b. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? – *Oecologia* 64: 396–407.
- Hay, M. E. 1991. Marine-terrestrial contrasts in the ecology of plant chemical defenses against herbivores. – *Trends Ecol. Evol.* 6: 362–365.
- Hay, M. E. and Fenical, W. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. – *Annu. Rev. Ecol. Syst.* 19: 111–145.
- Hector, A., Schmid, B., Beierkuhnlein, C. et al. 1999. Plant diversity and productivity experiments in European grasslands. – *Science* 286: 1123–1127.
- Holt, R. D. and Loreau, M. 2002. Biodiversity and ecosystem functioning: the role of trophic interactions and the importance of system openness. – In: Kinzig, A. P., Pacala, S. W. and Tilman, D. (eds), *The functional consequences of biodiversity*. Empirical progress and theoretical expectations. Princeton Univ. Press, pp. 246–262.
- Hooper, D. U. and Vitousek, P. M. 1997. The effects of plant composition and diversity on ecosystem processes. – *Science* 277: 1302–1305.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a coral reef. – *Science* 266: 1547–1551.
- Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. – *Ecology* 73: 724–732.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. – *Annu. Rev. Ecol. Syst.* 22: 477–503.
- Huntly, N. 1995. How important are consumer species to ecosystem functioning? – In: Jones, C. G. and Lawton, J. H. (eds), *Linking species and ecosystems*. Chapman and Hall, pp. 72–83.
- Huston, M. A. 1994. Biological diversity. The coexistence of species on changing landscapes. – Cambridge Univ. Press.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Jackson, J. B. C. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. – *Science* 293: 629–638.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C. and Boon, T. W. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. – *J. Anim. Ecol.* 70: 934–944.
- Jones, C. G., Lawton, J. J. and Shachak, M. 1994. Organisms as ecosystem engineers. – *Oikos* 69: 373–386.
- Jonsson, M. and Malmqvist, B. 2000. Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. – *Oikos* 89: 519–523.
- Kinzig, A. P., Pacala, S. W. and Tilman, D. (eds) 2002. *The functional consequences of biodiversity*. Empirical progress and theoretical expectations. – Princeton Univ. Press.
- Knops, J. M. H., Tilman, D., Haddad, N. M. et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. – *Ecol. Lett.* 2: 286–293.
- Koricheva, J., Mulder, C. P. H., Schmid, B. et al. 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. – *Oecologia* 125: 271–282.
- Körner, C. 1993. Scaling from species to vegetation: the usefulness of functional groups. – In: Schulze, E.-D. and Mooney, H. A. (eds), *Biodiversity and ecosystem function*. Springer, pp. 117–140.
- Krebs, C. J., Keller, B. L. and Tamarin, B. H. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. – *Ecology* 50: 587–607.
- Kurzava, L. M. and Morin, P. J. 1998. Tests of functional equivalence: complementary roles of salamanders and fish in community organization. – *Ecology* 79: 477–489.

- Laska, M. S. and Wootton, J. T. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. – *Ecology* 79: 461–476.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. – *Am. Nat.* 134: 922–949.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. – *Am. Nat.* 147: 784–812.
- Leibold, M. A., Chase, J. M., Shurin, J. B. and Downing, A. L. 1997. Species turnover and the regulation of trophic structure. – *Annu. Rev. Ecol. Syst.* 28: 467–494.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. – *Proc. Natl. Acad. Sci. USA* 95: 5632–5636.
- Loreau, M., Naeem, S., Inchausti, P. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – *Science* 294: 804–808.
- Lubchenco, J. and Gaines, S. D. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. – *Annu. Rev. Ecol. Syst.* 12: 405–437.
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. – *Ecology* 36: 533–536.
- May, R. M. 1974. Stability and complexity in model ecosystems. – Princeton Univ. Press.
- McCann, K., Hastings, A. and Strong, D. R. 1998. Trophic cascades and trophic trickles in pelagic food webs. – *Proc. R. Soc. London B* 265: 205–209.
- McGrady-Steed, J. and Morin, P. J. 2000. Biodiversity, density compensation, and the dynamics of populations and functional groups. – *Ecology* 81: 361–373.
- McGrady-Steed, J., Harris, P. M. and Morin, P. J. 1997. Biodiversity regulates ecosystem predictability. – *Nature* 390: 162–165.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: The Serengeti. – *Ecol. Monogr.* 55: 259–294.
- McNaughton, S. J., Ruess, R. W. and Seagle, S. W. 1988. Large mammals and process dynamics in African ecosystems. – *BioScience* 38: 794–800.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. – *Ecol. Monogr.* 65: 21–74.
- Menge, B. A. and Sutherland, J. P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. – *Am. Nat.* 110: 351–369.
- Menge, B. A. and Sutherland, J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. – *Am. Nat.* 130: 730–757.
- Menge, B. A., Lubchenco, J., Ashkenas, L. R. and Ramsey, F. 1986. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. – *J. Exp. Mar. Biol. Ecol.* 100: 225–269.
- Menge, B. A., Berlow, E. L., Blanchette, C. A. et al. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. – *Ecol. Monogr.* 64: 249–286.
- Metaxas, A. and Scheibling, R. E. 1996. Top-down and bottom-up regulation of phytoplankton assemblages in tide-pools. – *Mar. Ecol. Prog. Ser.* 145: 161–177.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. – *Science* 285: 1396–1398.
- Micheli, F., Cottingham, K. L., Bascompte, J. et al. 1999. The dual nature of community variability. – *Oikos* 85: 161–169.
- Mikola, J. and Setälä, H. 1998. Relating species diversity to ecosystem functioning: mechanistic backgrounds and experimental approach with a decomposer food web. – *Oikos* 83: 180–194.
- Mulder, C. P. H., Koricheva, J., Huss-Danell, K. et al. 1999. Insects affect relationships between plant species richness and ecosystem processes. – *Ecol. Lett.* 2: 237–246.
- Mulder, C. P. H., Uliassi, D. D. and Doak, D. F. 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. – *Proc. Natl. Acad. Sci. USA* 98: 6704–6708.
- Naeem, S. 2002. Autotrophic-heterotrophic interactions and their impacts on biodiversity and ecosystem functioning. – In: Kinzig, A. P., Pacala, S. W. and Tilman, D. (eds), *The functional consequences of biodiversity*. Empirical progress and theoretical expectations. Princeton Univ. Press, pp. 96–119.
- Naeem, S. and Li, S. 1997. Biodiversity enhances ecosystem reliability. – *Nature* 390: 507–509.
- Naeem, S. and Li, S. 1998. Consumer species richness and autotrophic biomass. – *Ecology* 79: 2603–2615.
- Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – *Nature* 368: 734–737.
- Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. – *Phil. Trans. R. Soc. London B* 347: 249–262.
- Norberg, J. 2000. Resource-niche complementarity and autotrophic compensation determines ecosystem-level responses to increased cladoceran species richness. – *Oecologia* 122: 264–272.
- Odum, E. P. 1971. *Fundamentals of ecology*, 3rd edition. – Saunders.
- Pace, M. L., Cole, J. J., Carpenter, S. R. and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. – *Trends Ecol. Evol.* 14: 483–488.
- Paine, R. T. 1966. Food web complexity and species diversity. – *Am. Nat.* 100: 65–75.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. – *J. Anim. Ecol.* 49: 667–685.
- Paine, R. T. 1992. Food-web analysis through field measurements of per capita interaction strength. – *Nature* 355: 73–75.
- Paine, R. T. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities – how different are the structuring processes? – *J. Mammal.* 81: 637–648.
- Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. – *Science* 296: 736–739.
- Pauly, D., Christensen, V., Dalsgaard, J. et al. 1998. Fishing down marine food webs. – *Science* 279: 860–863.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. – *Oikos* 85: 385–397.
- Petchey, O. L., McPhearson, P. T., Casey, T. M. and Morin, P. J. 1999. Environmental warming alters food-web structure and ecosystem function. – *Nature* 402: 69–72.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. – *Nature* 307: 321–326.
- Pimm, S. L., Russell, G. J., Gittleman, J. L. and Brooks, T. M. 1995. The future of biodiversity. – *Science* 26: 347–350.
- Pinnegar, J. K., Polunin, N. V. C., Francour, P. et al. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. – *Environ. Conserv.* 27: 179–200.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. – *Am. Nat.* 138: 123–155.
- Polis, G. A. and Holt, R. D. 1992. Intraguild predation: the dynamics of complex trophic interactions. – *Trends Ecol. Evol.* 7: 151–154.
- Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. – *Am. Nat.* 147: 813–846.
- Polis, G. A., Sears, A. L. W., Huxel, G. R. et al. 2000. When is a trophic cascade a trophic cascade? – *Trends Ecol. Evol.* 15: 473–475.

- Power, M. E. 1990. Effects of fish in river food webs. – *Science* 250: 411–415.
- Power, M. E., Tilman, D., Estes, J. A. et al. 1996. Challenges in the quest for keystones. – *BioScience* 46: 609–620.
- Prins, H. H. T. and Douglas-Hamilton, I. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. – *Oecologia* 83: 392–400.
- Purvis, A., Gittleman, J. L., Cowlshaw, G. and Mace, G. M. 2000. Predicting extinction risk in declining species. – *Proc. R. Soc. Lond. B* 267: 1947–1952.
- Raffaelli, D. G. and Hall, S. J. 1995. Assessing the relative importance of trophic links in food webs. – In: Polis, G. and Winemiller, K. (eds), *Foodwebs: integration of patterns and dynamics*. Chapman and Hall, pp. 185–191.
- Ritchie, M. E. and Olff, H. 1999. Herbivore diversity and plant dynamics: compensatory and additive effects. – In: Olff, H., Brown, V. K. and Drent, R. H. (eds), *Herbivores: between plants and predators*. Blackwell, pp. 175–204.
- Sala, E. and Graham, M. H. 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. – *Proc. Natl. Acad. Sci. USA* 99: 3678–3683.
- Sankaran, M. and McNaughton, S. J. 1999. Determinants of biodiversity regulate compositional stability of communities. – *Nature* 401: 691–693.
- Schläpfer, F. and Schmid, B. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. – *Ecol. Appl.* 9: 893–912.
- Schmitz, O. J. and Sokol-Hessner, L. 2002. Linearity in the aggregate effects of multiple predators in a food web. – *Ecol. Lett.* 5: 168–172.
- Schmitz, O. J., Hambaek, P. A. and Beckerman, A. P. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. – *Am. Nat.* 155: 141–153.
- Schwartz, M. W., Brigham, C. A., Hoeksema, J. D. et al. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. – *Oecologia* 122: 297–305.
- Shiomoto, A., Tadakoro, K., Nagasawa, K. and Ishida, Y. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. – *Mar. Ecol. Prog. Ser.* 150: 75–85.
- Siemann, E., Tilman, D., Haarstad, J. and Ritchie, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. – *Am. Nat.* 152: 738–750.
- Sih, A., Crowley, P., McPeck, M. et al. 1985. Predation, competition, and prey communities: a review of field experiments. – *Annu. Rev. Ecol. Syst.* 16: 269–311.
- Sih, A., Englund, G. and Wooster, D. 1998. Emergent impacts of multiple predators on prey. – *Trends Ecol. Evol.* 13: 350–355.
- Skoglund, T. 1991. What are the effects of predators on large ungulate populations? – *Oikos* 61: 401–411.
- Sommer, U., Sommer, F., Santer, B. et al. 2001. Complementary impact of copepods and cladocerans on phytoplankton. – *Ecol. Lett.* 4: 545–550.
- Steiner, C. F. 2001. The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. – *Ecology* 82: 2495–2506.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. – *Ecology* 73: 747–754.
- Symstad, A. J., Siemann, E. and Haarstad, J. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. – *Oikos* 89: 243–253.
- Terborgh, J., Estes, J. A., Paquet, P. et al. 1999. The role of top carnivores in regulating terrestrial ecosystems. – In: Soulé, M. E. and Terborgh, J. (eds), *Continental conservation*. Island Press.
- Terborgh, J., Lopez, L., Nuñez, V. P. et al. 2001. Ecological meltdown in predator-free forest fragments. – *Science* 294: 1923–1926.
- Thacker, R. W., Ginsburg, D. W. and Paul, V. J. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. – *Coral Reefs* 19: 318–329.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – *Ecology* 80: 1455–1474.
- Tilman, D. and Downing, J. A. 1994. Biodiversity and stability in grasslands. – *Nature* 367: 363–365.
- Tilman, D., Lehman, C. L. and Thomson, K. T. 1997a. Plant diversity and ecosystem productivity: theoretical considerations. – *Proc. Natl. Acad. Sci. USA* 94: 1857–1861.
- Tilman, D., Knops, J., Wedin, D. et al. 1997b. The influence of functional diversity and composition on ecosystem processes. – *Science* 277: 1300–1302.
- Tilman, D., Lehman, C. L. and Bristow, C. E. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? – *Am. Nat.* 151: 277–282.
- Tilman, D., Reich, P. B., Knops, J. et al. 2001. Diversity and productivity in long-term grassland experiments. – *Science* 294: 843–845.
- Vitousek, P. M. and Hooper, D. U. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. – In: Schulze, E.-D. and Mooney, H. A. (eds), *Biodiversity and ecosystem function*. Springer-Verlag, pp. 3–14.
- Wardle, D. A. 1999. Is “sampling effect” a problem for experiments investigating biodiversity–ecosystem function relationships? – *Oikos* 87: 403–407.
- Wilcove, D. S., Rothstein, D., Dubow, J. et al. 1998. Quantifying threats to imperiled species in the United States. – *BioScience* 48: 607–615.
- Woodroffe, R. and Ginsberg, J. R. 1998. Edge effects and the extinction of populations inside protected areas. – *Science* 280: 2126–2128.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – *Annu. Rev. Ecol. Syst.* 25: 443–466.
- Wootton, J. T. 1997. Estimates and tests of per capita interactions strength: diet, abundance, and impact of intertidally foraging birds. – *Ecol. Monog.* 67: 45–64.