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IDEAS AND PERSPECTIVES

Biodiversity loss, trophic skew and ecosystem functioning

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Abstract

Experiments testing biodiversity effects on ecosystem functioning have been criticized on the basis that their random-assembly designs do not reflect deterministic species loss in nature. Because previous studies, and their critics, have focused primarily on plants, however, it is underappreciated that the most consistent such determinism involves biased extinction of large consumers, skewing trophic structure and substantially changing conclusions about ecosystem impacts that assume changing plant diversity alone. Both demography and anthropogenic threats render large vertebrate consumers more vulnerable to extinction, on average, than plants. Importantly, species loss appears biased toward strong interactors among animals but weak interactors among plants. Accordingly, available evidence suggests that loss of a few predator species often has impacts comparable in magnitude to those stemming from a large reduction in plant diversity. Thus, the dominant impacts of biodiversity change on ecosystem functioning appear to be trophically mediated, with important implications for conservation.

Keywords
Biodiversity, conservation, ecosystem functioning, extinction, trophic structure.

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INTRODUCTION

The influence of changing biodiversity on ecosystem functioning has been a central and rapidly growing theme in ecology during the last decade. Research in this area is motivated in significant part by the practical issue, cited within the first paragraph of most publications on the subject, of understanding how declining diversity influences ecosystem services on which humans depend. The most influential empirical research on biodiversity-ecosystem functioning (BD-EF) linkages has been the series of experiments manipulating diversity in grasslands (reviewed by Tilman *et al.* 2002) and in aquatic microbial microcosms (reviewed by Petchey *et al.* 2002). Typically these have tested how ecosystem-wide biomass accumulation or metabolic rates change along gradients of species richness achieved by randomly assembling experimental communities from a pool of species. The grassland experiments have manipulated plant species richness, and sometimes also functional group richness. The microbial experiments more often have manipulated several trophic levels simultaneously, but usually with proportional changes at each level. Several such experiments have demonstrated significant positive correlations between species richness and plant biomass accumulation or metabolic rates (reviewed by Schmid *et al.* 2002b), and these relationships have garnered wide attention.

Research on BD-EF has stimulated a new and highly productive intercourse between population, community, ecosystem, and conservation ecology (Kinzig *et al.* 2002; Loreau *et al.* 2002). Yet it has also proven controversial. A persistent criticism of experimental BD-EF research involves the perceived artificiality of the random community assembly (or disassembly) used to create most experimental diversity gradients. Several authors have emphasized that natural and anthropogenic diversity gradients show clearly non-random patterns in the order and characteristics of species lost (Grime 1998; Wardle 1999; Huston *et al.* 2000; Srivastava 2002; Díaz *et al.* 2003). Such extinction bias raises questions about how useful inferences from randomly assembled experimental communities will be for informing conservation efforts.

Even the strongest critics of BD-EF experiments have generally followed the authors thereof in focusing on processes within trophic levels. Accordingly, recent reviews of experimental design in BD-EF experiments include detailed dissections of the roles of competition, facilitation, and sampling within plant assemblages but have little or nothing to say about trophic interactions (Schmid *et al.* 2002a; Díaz *et al.* 2003). A review entitled 'Evaluating the relative strengths of biotic vs. abiotic controls on ecosystem processes' (Huston & McBride 2002) does not even mention consumers at all! Indeed, with very few exceptions (e.g. Holt & Loreau 2002), trophic interactions have not been incorporated into the framework of BD-EF theory in any systematic way (Duffy 2002). This narrow focus contrasts markedly with the extensively documented impacts of consumers on ecological structure and functioning in a wide range of ecosystems. The poor integration of trophic interactions into BD-EF stems in part from the daunting complexity of trophic interactions (Raffaelli *et al.* 2002). For example, changes in diversity at one trophic level can produce cascading changes in diversity at other levels (e.g. Dyer & Letorneau 2003). Yet one pattern seems relatively clear, consistent, and central to the effects of changing biodiversity on ecosystem functioning. This is the disproportionate impact of anthropogenic extinctions on large consumers, and consequent change in trophic structure, which I refer to as trophic skew. Surprisingly, this phenomenon seems poorly appreciated. Here I explore the evidence for trophic skew in extinction and its consequences for ecosystem functioning. I identify some apparent patterns that may be considered hypotheses for more rigorous future study.

TROPHIC-LEVEL BIAS IN EXTINCTION

The sequence of species loss from a community under human pressure (i.e. community disassembly) is not random but depends on traits of organisms. General principles of population biology and empirical evidence confirm that extinction risk in both plants and animals is exacerbated by rarity, small population size, small geographical range size, slow population growth, and specialized ecological habits (Pimm *et al.* 1988; Lawton 1995; Didham *et al.* 1998; Purvis *et al.* 2000; and references therein). Beyond these commonalities, however, important distinctions between plants and animals affect their risk of anthropogenic extinction, which in turn influence impacts of those extinctions on ecosystem functioning. In general, the most important threats to plants are various forms of habitat destruction. These threats are non-selective in the sense that extinction is a consequence of reducing the habitat as a whole, rather than of activities directly targeted at the plants themselves (selective logging being a possible exception), and potentially affects all species present. All else being equal, therefore, habitat destruction should be especially detrimental to endemic species and those living at low population densities, which will generally make up a small proportion of total vegetation biomass. According to the mass-ratio effect (Grime 1998), these species will generally have a relatively minor influence on ecosystem processes (but see Lyons & Schwartz 2001), compared with dominant species, which by definition comprise a large proportion of total vegetation biomass. The implication is that plant extinction is biased toward species of weak ecological effects, meaning that loss of the most vulnerable species generally will have little impact on either community structure or ecosystem processes (here I refer to the *species-level* interaction strength, i.e. the influence on the system of removing the entire population of the focal species, Paine 1980; Laska & Wootton 1998). Life history may complicate this conclusion, however. Models that include a competition-colonization trade-off initially made the counterintuitive prediction that dominant plant species should actually suffer greater extinction than competitively inferior (thus, rarer) species because the former are poor dispersers and cannot maintain viable metapopulations in fragmented landscapes (Tilman *et al.* 1994). Subsequent models have demonstrated that the predicted extinction bias toward dominant competitors depends critically on model assumptions, including the configuration of habitat patches, strength of competition, and rigidity of the competition-colonization trade-off (Loehle & Li 1996; Klausmeier 2001). Importantly, under certain reasonable values of these parameters, extinction bias shifts from superior (common) to inferior (rare) competitors. Therefore, because the extinction sensitivity of rare and low-density plants is empirically well documented, whereas that of dominant competitors is less certain, and because plant effects on ecosystem processes tend to be roughly proportional to their biomass, I suggest that plant extinction is often biased toward species of low functional importance to the ecosystem.

Habitat fragmentation presumably also threatens animals through the loss of plants that provide their food or substratum. However, two distinct processes tend to make large animal consumers especially vulnerable to extinction. First, because many of the aforementioned demographical risk factors are characteristic of animals high in the food web, top predators should be especially vulnerable to habitat destruction (Pimm *et al.* 1988; Lawton 1995). Experiments in both model systems and the field confirm that top predators are differentially lost under habitat alteration or fragmentation (Didham *et al.* 1998; Gilbert *et al.* 1998; Petchey *et al.* 1999). The second risk factor for large vertebrate consumers generally, both predators and herbivores, is human hunting. Compared with plants, vertebrate consumers are far more affected by selective threats in the form of targeted hunting and persecution. The most consistent correlate of animal vulnerability to both habitat destruction and hunting appears to be large body size. The bias in vulnerability toward larger animals and higher trophic levels has been documented repeatedly in a wide range of terrestrial (Diamond 1982; Redford 1992; Didham *et al.* 1998; Purvis *et al.* 2000; Alroy 2001; Cardillo & Bromham 2001) and aquatic (Pauly *et al.* 1998; Jackson *et al.* 2001; Myers & Worm 2003) ecosystems. Moreover, while rarity is always a risk factor, commonness does not necessarily confer protection from hunting and harassment of animals. This is supported dramatically by the mass extinctions of formerly abundant Pleistocene megafauna, which closely followed human arrival on continents and islands throughout the world, and by the decline or extinction of the bison, great auk, and passenger pigeon more recently (Diamond 1982; Alroy 2001). The comparatively low vulnerability of large plants is illustrated by the fact that disappearance of a single widespread tree species at the end of the Pleistocene was considered so unusual as to be published in Science (Jackson & Weng 1999). Similarly, in the sea, relentless fishing pressure throughout the oceans has systematically depleted top predators, and then shifted to the next most valuable (usually the next largest) animals, a phenomenon dubbed 'fishing down the food web' (Pauly *et al.* 1998). The parallel phenomenon on land is less obvious only because it was completed on most continents long before humans became aware of what was being lost, an example of the 'sliding baseline' phenomenon (Dayton *et al.* 1998). Of equal significance as their high vulnerability, large vertebrate consumers often have pervasive impacts on ecosystem structure and functioning through predation, selective grazing, seed predation, seed dispersal, nutrient regeneration, disturbance, and bioengineering activities (Owen-Smith 1987; Redford 1992; Terborgh *et al.* 1999; Jackson *et al.* 2001; and references therein). That is, large consumers tend to have high functional importance in the sense that their removal results in large changes in community organization and ecosystem properties. Thus, based on the mostly indirect data available, I suggest that, in contrast to plants, animal extinction is biased toward species of high functional importance to the ecosystem.

In summary, patterns of extinction have a strongly deterministic component, and the determinants of extinction risk differ importantly between plants and animals. Thus, the first species lost or rendered ecologically extinct from an ecosystem are almost invariably large vertebrate consumers. Moreover, this trophic bias in extinction is aggravated by the lower species richness of large vertebrates than of plants in most systems, which results in less redundancy and less potential for functional compensation for lost species at higher trophic levels. As a result, the earliest and most predictable effect of humans on ecosystems is skew in trophic structure, that is, a vertical compaction and blunting of the trophic pyramid because of proportionally greater losses of higher-level species.

TROPHIC SKEW AND ECOSYSTEM FUNCTIONING

How does the resulting trophic skew affect ecosystem functioning? Rigorous analysis of this question is complicated by the pre-historic timing of many important extinctions, paucity of good baseline data, often poor quantification of impacts, and the commonness of confounding factors. In an ecological science that demands high standards of experimental rigour these constraints have likely contributed to the lack of recognition of large consumer impacts on ecosystems. Yet numerous indirect lines of evidence clearly point to strong influences of large vertebrates on ecosystems (Terborgh *et al.* 1999; Paine 2000). We can, however, seek evidence from controlled experiments as well. This approach also is imperfect as ecosystem-level consequences of changing plant and animal diversity have very rarely been examined in the same study, and experimental studies are all of relatively small scale and short duration. Indeed, the only published study that factorially manipulated plant diversity and animal consumers (Mulder *et al.* 1999) found that removal of insects with insecticide almost doubled plant biomass accumulation, and removed the significant enhancement of plant biomass accumulation by plant species richness in unsprayed plots. Thus, overall, removal of insect herbivores had a stronger effect than a sixfold change in plant diversity. In a somewhat similar example, Naeem *et al.* (2000) demonstrated that inclusion of decomposers (bacteria) in aquatic microcosms eliminated the dependence of algal biomass on algal species richness.

In a first attempt to compare effects of plant and animal species loss on ecosystem-level properties, I focused on the most commonly studied ecosystem property, net aboveground plant biomass accumulation, a proxy for the primary production that sustains all ecosystems. I examined literature data for both plant-diversity and consumer-removal experiments and expressed them in the common currency of effect size, defined here as the log ratio of the property in the presence vs. absence of altered diversity. This metric of effect size is symmetric about zero and can take either negative or positive values. For example, a positive effect of top predator removal could result if grazers facilitate plant biomass accumulation, and predators suppress this facilitation, or if the system approximates a linear food chain with four levels (e.g. Power 1990; Estes *et al.* 1998). Data were extracted from graphs and tables in published sources. For plant removals I used the list of experimental biodiversity manipulations compiled by Schmid *et al.* (2002b), except that I considered the eight regional experiments reported by Hector *et al.* (1999) as separate studies. For animal consumers there are few experimental data on effects of changing species richness *per se* (Duffy 2002), in part reflecting the smaller number of functionally significant consumer species than of plants in most ecosystems. Nonetheless, we can estimate how top predator extinction might affect ecosystem functioning from experimental tests of trophic cascades. Thus, as summary estimates of the impacts of predator reductions on plant biomass I used the mean effect sizes tabulated for various ecosystem types in the meta-analysis of trophic cascade experiments by Shurin *et al.* (2002).

The relative impacts of experimentally removing plant species vs. top predator species are shown in Table 1. The median effect [log (degraded/'intact')] of removing a large fraction of plant species, averaged across all 18 studies was −0.62 (95% CI = −0.286 to −0.986, obtained by bootstrapping). This corresponds to a median 46% reduction in plant biomass over the range of plant species richness considered. By comparison, the mean effect on plant biomass of removing predators ranged from −0.12 to −1.53 depending on type of system, corresponding to an 11–78% reduction in plant biomass. These limited experimental data suggest that removal of carnivore species often has impacts on total plant biomass comparable with, or greater than, those of removing a large fraction of plant species.

The comparison in Table 1 clearly is preliminary and subject to several confounding factors. First, the plant diversity experiments examined the effects of removing a fraction of species within a trophic level, whereas the consumer experiments usually removed an entire trophic level. Clearly, removing an entire trophic level will generally have a larger ecological impact than removing part of its species richness as the latter potentially allows for functional

Table 1 Relative impacts on total standing plant biomass of manipulating plant vs. carnivore species

Reference	Ecosystem	Diversity levels	Effect size
(a) Plant diversity manipulations			
Naeem & Li (1997)	Aquatic microbes	1, 3	−1.10
Symstad *et al.* (1998)	Grassland	8, 12	−1.09
Symstad *et al.* (1998)	Grassland	1, 10	−0.48
Naeem *et al.* (1996)	Ruderal	1, 16	−0.37
Smith & Allcock (1985)	Grassland (high N)	1, 2	−0.21
Smith & Allcock (1985)	Grassland (low N)	1, 2	−0.55
Tilman *et al.* (1996)	Grassland	1, 24	−0.55
Hooper & Vitousek (1997)	Grassland	–	0.00
Tilman *et al.* (1997)	Grassland	1, 16	−0.88
Hector *et al.* (1999)	Grassland (Germany)	1, 16	−0.79
Hector *et al.* (1999)	Grassland (Portugal)	2, 14	−1.02
Hector *et al.* (1999)	Grassland (Switzerland)	1, 32	−0.84
Hector *et al.* (1999)	Grassland (Greece)	–	0.00
Hector *et al.* (1999)	Grassland (Ireland)	–	0.00
Hector *et al.* (1999)	Grassland (Sweden)	2, 12	−0.92
Hector *et al.* (1999)	Grassland (Sheffield)	1, 8	−0.68
Hector *et al.* (1999)	Grassland (Silwood)	–	0.00
Spehn *et al.* (2000)	Grassland	1, 8	−1.00
Median			−0.62
95% CI upper			−0.29
95% CI lower			−0.90

Reference	Ecosystem	*n*	Effect size
(b) Predator manipulations			
Shurin *et al.* (2002)	Terrestrial	18	−0.12
Shurin *et al.* (2002)	Lentic benthos	12	−0.83
Shurin *et al.* (2002)	Stream benthos	33	−0.60
Shurin *et al.* (2002)	Marine benthos	8	−1.53
Shurin *et al.* (2002)	Lentic plankton	22	−0.77
Shurin *et al.* (2002)	Marine plankton	9	−0.17

Effect size = ln (degraded/control) where 'degraded' is the treatment from which plant species (a) or predators (b) were removed. 'Diversity levels' lists the species richness at which minimum and maximum plant biomass were recorded, respectively. Data and references in (a) are from the review of Schmid *et al.* (2002b). 95% CI in (a) were obtained by bootstrapping.

compensation among the remaining species (e.g. Jonsson & Malmqvist 2003). This concern may be less serious than it seems, however, because (1) the range in plant richness in most experiments approaches the extremes found at the plot scale at a given site; (2) the top trophic level in most systems consists of a small number of vertebrate species – indeed, more than half of the experiments included in the meta-analysis of Shurin *et al.* (2002) manipulated only a single species of predator; and (3) human activity commonly depletes the entire top trophic level in a variety of systems. Thus, as I have argued above, removal (or ecological extinction) of the top trophic level from an ecosystem is probably at least as common as a large reduction in native plant diversity.

A more serious problem with the comparison in Table 1 is that the plant experiments come overwhelmingly from terrestrial grasslands, whereas the consumer experiments are from a wide range of mostly aquatic ecosystems. If we restrict the comparison to terrestrial systems we obtain a mean effect of plant diversity reduction of -0.55 ($n = 17$), compared with a mean effect of terrestrial predator removal of -0.12 ($n = 18$). The latter value did not differ significantly from zero (Shurin *et al.* 2002). At face value this suggests that reduction of predators has weaker effects than reductions of plant diversity in terrestrial systems. This may be true, and is consistent with arguments that community-wide trophic cascades are rare on land (e.g. Strong 1992; Polis 1999). On the other hand, few experiments have examined reductions of large vertebrates, which are precisely the animals that are most vulnerable and expected to have strongest ecosystem effects (Terborgh 1988). Supporting this, Shurin *et al.* (2002) found that, across ecosystem types, vertebrate predators (usually relatively small vertebrates) in their sample had about twice as large a cascading effect on plant biomass as did invertebrate predators. Importantly, terrestrial experiments were less likely than those in other systems to use vertebrate predators. Thus, existing meta-analyses, based necessarily on published studies of experimentally cooperative animals, very likely underestimate the effects of removing the large grazers and predators that humans affect first and most severely.

I have focused here on total plant biomass because this is the ecosystem response variable most frequently measured and because trophic cascade hypotheses make explicit predictions about it. However, predators or grazers can also cause dramatic shifts in vegetation composition without appreciably changing total plant biomass (Terborgh 1988; Strong 1992; Polis 1999). This is one reason, along with hunting of vertebrate herbivores, why much of the world remains green after top predators are hunted out. Such changes in vegetation composition may be equally important to ecosystem services as changes in total plant biomass. Most experiments are neither open enough nor of long enough duration to incorporate the species turnover that can eventually compensate for large changes in consumer or competitor abundance (Leibold *et al.* 1997). Thus, while experiments may overestimate consumer effects on aggregate properties like total plant biomass, they may equally underestimate potential consumer-mediated shifts in community composition resulting from species turnover.

Finally, it should be reiterated that my arguments apply primarily to vertebrate consumers. Invertebrate predators and parasitoids are much more diverse, and their functional or community importance less well understood on average, than those of vertebrates. For such diverse, invertebrate-dominated food webs, manipulations of consumer diversity using the combinatorial approach common in plant diversity experiments would be informative (see, e.g. Duffy *et al.* 2003). More generally, experiments that manipulate consumer diversity, rather than simply presence or absence of a trophic level, remain an important frontier for studies linking biodiversity to ecosystem functioning (Duffy 2002).

IMPLICATIONS FOR ECOLOGY AND CONSERVATION

The several uncertainties in the available experimental data, and their imperfect simulation of open systems dominated by large vertebrates, emphasize that the conclusions I draw are preliminary. Nevertheless, these caveats are unlikely to change the central points that (1) large consumers are the first species to go under anthropogenic influence, and (2) because of their relatively low diversity, low functional redundancy, and high interaction strengths, loss of large consumers tends to have impacts on ecosystem properties of comparable or greater magnitude to those of eroding plant diversity. What are the practical implications of these patterns? The principal one is that changing biodiversity in natural ecosystems is likely to have much more complicated impacts on ecosystem functioning than predicted from changes in plant diversity alone. As diversity is lost from a system, the decline in plant biomass predicted from plant-only experiments may be either exacerbated, if simultaneous loss of predators releases grazers from suppression, or reversed if large vertebrate herbivores are lost along with the plants. Impacts may also depend on the number of effective trophic levels (Hairston *et al.* 1960; Power 1990; Estes *et al.* 1998). Thus, an important challenge for future research is documenting how diversity – at both species and functional group levels – is lost across trophic levels in nature.

Why worry about such effects if large vertebrates are already gone from most ecosystems? There are several answers. First, although greatly reduced in numbers and influence, and thus ‘ecologically extinct’, large animals still persist in many ecosystems and efforts are underway to conserve and restore them. Understanding impacts of these consumers is critical to predicting ecosystem-level consequences of restoration efforts that would increase their numbers. Second, for forests specifically, long generation times of dominant plants lead to long lag times in vegetation responses to consumer depletion, and a deceptive impression that consumers have little impact on system properties; this phenomenon can lull us into a false sense of security about the status of forests (Terborgh 1988; Redford 1992). Third, recognizing the large effects of individual consumer species helps put in perspective the frequently catastrophic impacts of introduced consumers. Perusal of the literature suggests that the strongest documented effects of changing biodiversity on ecosystem functioning often involve not deletions from native diversity but *additions* of non-native plant or animal species. While there are numerous documented accounts of extinction resulting from introduced predators (i.e. between-trophic level processes, Goldschmidt *et al.* 1993; Findlay *et al.* 2000), there are few if any clear cases of extinction caused by introduced competitors (i.e. within-trophic level processes, Rosenzweig 2001). Even invasiveness of competitors often depends on skewed trophic structure insofar as their success is facilitated by reduced pressure from consumers, parasites, and pathogens in the new environment (Mitchell & Power 2003; Torchin *et al.* 2003).

Experiments exploring BD-EF linkages have much to offer both basic ecology and conservation science. As the intense interest in BD-EF linkages stems largely from concern that ongoing biodiversity loss may negatively impact ecosystem properties beneficial to humans, it seems reasonable to expect such studies to begin incorporating the dominant trends in biodiversity loss worldwide. As argued above, the most conspicuous and consistent such trend is trophic skew. Studies of BD-EF linkages will more effectively inform conservation as they incorporate the reality that changing trophic interactions are an inextricable – and quite possibly dominant – component of the mechanisms mediating changes in ecosystem functioning as diversity erodes in the face of human influence.

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