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## HABITAT LOSS, TROPHIC COLLAPSE, AND THE DECLINE OF ECOSYSTEM SERVICES

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**Abstract.** The provisioning of sustaining goods and services that we obtain from natural ecosystems is a strong economic justification for the conservation of biological diversity. Understanding the relationship between these goods and services and changes in the size, arrangement, and quality of natural habitats is a fundamental challenge of natural resource management. In this paper, we describe a new approach to assessing the implications of habitat loss for loss of ecosystem services by examining how the provision of different ecosystem services is dominated by species from different trophic levels. We then develop a mathematical model that illustrates how declines in habitat quality and quantity lead to sequential losses of trophic diversity. The model suggests that declines in the provisioning of services will initially be slow but will then accelerate as species from higher trophic levels are lost at faster rates. Comparison of these patterns with empirical examples of ecosystem collapse (and assembly) suggest similar patterns occur in natural systems impacted by anthropogenic change. In general, ecosystem goods and services provided by species in the upper trophic levels will be lost before those provided by species lower in the food chain. The decrease in terrestrial food chain length predicted by the model parallels that observed in the oceans following overexploitation. The large area requirements of higher trophic levels make them as susceptible to extinction as they are in marine systems where they are systematically exploited. Whereas the traditional species–area curve suggests that 50% of species are driven extinct by an order-of-magnitude decline in habitat abundance, this magnitude of loss may represent the loss of an entire trophic level and all the ecosystem services performed by the species on this trophic level.

**Key words:** biodiversity; conservation; ecosystem function; ecosystem services; food web; Little Rock Lake; species–area; species loss; trophic collapse.

### INTRODUCTION

The study of the effects of biodiversity on the functioning of ecosystems and their ability to provide goods and services has attracted much recent attention from theoreticians and experimentalists. Ecologists predict that decreases in biodiversity will lead to

reductions in ecosystem functioning and hence in the provisioning of services (Naeem et al. 1994, 1995, Daily 1997, Daily et al. 1997, 2000, Chapin et al. 2000, Loreau et al. 2001). The exact shape of this relationship depends on the ecosystem process and service as well as the order in which species are lost from, or potentially added to, the ecosystem (Mikkelsen 1993, Sala et al. 1996, Petchey et al. 1999, Petchey and Gaston 2002, Duffy 2003). A number of possible functional forms have been suggested for the relationships that couple biological diversity to the rate and resilience with which different types of ecosystem processes are undertaken (Sala et al. 1996, Tilman et al. 1996, Kinzig et al. 2001). Central to all of these is the argument that there is some asymptotic maximum rate at which the activity is undertaken that declines to zero as species diversity and abundance are

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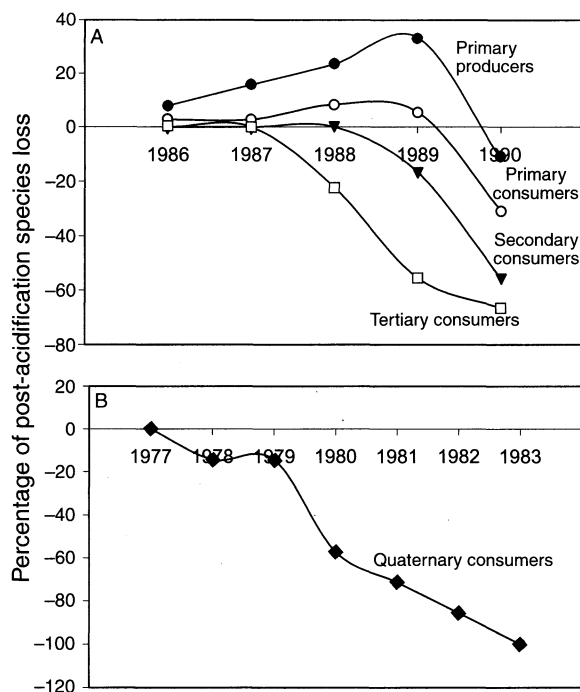


FIG. 1. Annual species loss (as a percentage of pre-acidification species number) in response to gradual experimental acidification in two north temperate lakes. (A) Four lower-trophic levels in Little Rock Lake, Wisconsin, USA: primary producers (initial  $N = 51$  phytoplankton species); primary consumers (initial  $N = 36$  primarily herbivorous zooplankton species); secondary consumers (initial  $N = 9$  omnivorous zooplankton species); and tertiary consumers (initial  $N = 9$  primarily carnivorous zooplankton species). (B) Quaternary consumers in Lake 223, Ontario, Canada (initial  $N = 7$  fish species). For (A), initial pH = 5.59, final pH = 4.75; for (B) initial pH = 6.49, final pH = 5.13. Complete fish data were unavailable for (A), and complete data for other taxa were unavailable for (B). For (B), the cessation of recruitment (absence of young-of-the-year) was treated as species extirpation. Additional experimental details are available for (A) in Brezonik et al. (1993) and for (B) in Schindler et al. (1985).

reduced (Mikkelsen 1993, Tilman et al. 1997, Loreau 1998, Crawley et al. 1999, Loreau et al. 2001). In cases where only one or a few species undertake the ecosystem function then decline may be rapid as the abundance of the species undertaking the activity declines (for example, population regulation of herbivores by top carnivores); ecosystem functions of this type are classified as brittle. In contrast, there will be other types of ecosystem function where competition between a diversity of species may create considerable redundancy, so that the loss of one species may be compensated for by increase in the abundance and activities of a competing species that occupies a similar niche (Naeem and Li 1997). In these cases, the relative rate at which the process declines will be relatively slow as species diversity and abundance decline. For example, we would argue that this is the case for nutrient cycling and water cleansing where a huge diversity of microbial species compete with each other while undertaking the function;

in these cases, the amount of nutrients and water processed may be almost linearly dependent upon the area of land under each stage of habitat conversion (Dobson 2005).

The earliest experiments to explicitly investigate the diversity-functioning relationship focused on above-ground primary production and plant species diversity. Large-scale manipulative experiments using grassland species in different regions of the world all showed a similar pattern, with the first species losses resulting in small decreases in primary production while further reductions in species diversity resulted in decreases in production (Tilman et al. 1996, 1997, Hector et al. 1999). In whole-lake experiments that examine specific stressors, acidification resulted in little loss of algal species, and no discernible changes in primary production or decomposition rates (Schindler et al. 1985). Empirical evidence of the effects of biodiversity loss on other services and for other ecosystem types is slowly becoming available (Kremen et al. 2002, Larsen et al. 2005), but more studies are needed on the sequence of the collapse or replacement of ecosystem services as habitats are disrupted or converted for other uses.

Examples from freshwater, terrestrial, and marine studies show that species at higher trophic levels are typically lost more rapidly than species from lower trophic levels with loss of habitat quality or quantity (Figs. 1–4). These and other examples suggest that some ecosystem services are dominated by specific trophic levels in a predictable way. A logical inference is that different ecosystem services respond differently to loss of habitat particularly if the spectrum of functional forms relating ecosystem services to biodiversity maps onto trophic levels (producers to consumers). Thus we might

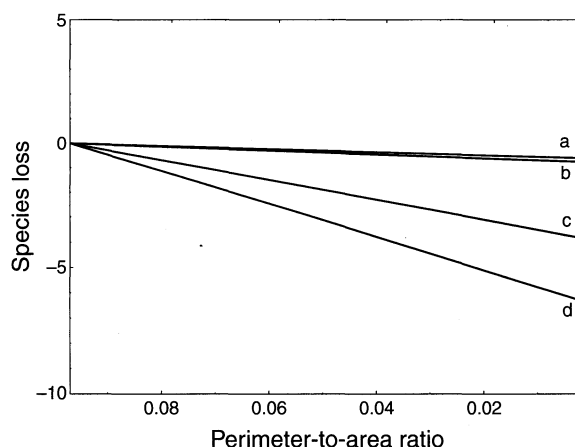


FIG. 2. Impact of landscape simplification (decreasing perimeter-to-area ratio) on the species loss (as percentage of pre-acidification species number) of herbaceous plants (line a) and carabid trophic groups (lines b–d) inhabiting wheat fields located in central Germany ( $n = 35$ ). Trophic groups of carabids include (b) mixophagous, (c) phytophagous, and (d) predaceous species. The regression coefficients are (c) 40.3 ( $P < 0.05$ ) and (d) 66.3 ( $P < 0.005$ ); the slopes of (a) and (b) are not significantly different from zero (Purtauf et al. 2005.).

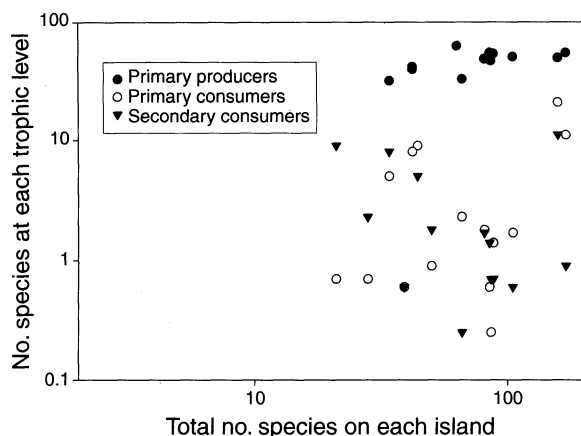


FIG. 3. Species loss and net species diversity (log-log scale) on different islands in Lago Guri (after Terborgh et al. 1997a, b, 2001). Ecological collapse is more advanced on smaller islands with lower net species diversity (x-axis). Although there is considerable scatter to the data, the rate of decline of plant species (solid circles) has a shallower slope than the rate of decline of primary consumers (open circles). The secondary consumers show no clear pattern, but Terborgh et al. (2001) record huge increases in ant abundance on the smaller islands in terminal stages of collapse, implying that predation on ants has essentially disappeared.

expect to see a predictable hierarchical loss of ecosystem services as habitats are eroded.

To further evaluate the relationships between habitat loss, trophic collapse, and ecosystem services, we have built a three component phenomenological model of biodiversity loss and decline of ecosystem services. Our principal aim is consider the consequences of biodiversity loss under the naïve assumption that there is a simple mapping between trophic diversity and the diversity of ecosystem services. The model explicitly ignores interactions between species on different trophic levels, thus there is no increase in prey abundance when predators are lost, these complications will be explored elsewhere (A. P. Dobson, *unpublished manuscript*). First, we assume the simplest possible relationship between decline in species diversity and reduction in habitat quantity; essentially we use species-area relationships to link habitat decline to biodiversity loss. Second, we propose a simple, but plausible, mapping of ecosystem services onto biodiversity, which explicitly assumes that specific ecosystem services are predominantly provided by specific trophic levels. We then model ecosystem collapse by assuming that higher trophic levels decline more rapidly than lower trophic levels.

We recognize that most ecosystem processes result from the interaction between trophic levels (particularly many key forms of population regulation; Naeem et al. 2000), but similarly many ecosystem processes and their associated services result predominantly from the activity of species located at specific trophic levels (Bunker et al. 2005). The most commonly observed empirical example would be the primary-production

response observed in grassland studies where losses of a few species are mostly compensated for by the remaining species until eventually further species losses result in a drastic decrease in ecosystem services (Schindler et al. 1985, Naeem et al. 1994, 1995, Frost et al. 1995, Crawley et al. 1999, Vinebrooke et al. 2003.). We suggest that this pattern of loss be classified as type A ecosystem services; these will be predominantly be those directly associated with primary production such as provisioning of fuel wood and fiber, or associated with total biomass or plant cover such as carbon storage, erosion control, and storm protection. In contrast, type E responses are the most brittle services; for these services, small changes in species biodiversity result in large changes in the provisioning of ecosystem services. These are services that depend predominantly on rare or fragile species. While many species located in the upper levels of trophic chains are likely to supply these more brittle services, we also acknowledge that keystone species at lower trophic levels may also have very brittle diversity-service relationships. Services provided by such species include recreation, ecotourism, and regulation of the abundance of the species on lower trophic levels on which they prey. We recognize that type A and type E responses are boundary conditions and that most of the biodiversity-ecosystem service relationships would fall between these two extremes. For example, an intermediate, "type C" response would show a linear decrease in service as each species is lost. Such services may depend on species from multiple trophic levels, each with unique characteristics such that their loss cannot be readily compensated for by the remaining species. In essence, the loss of each individual species results in the loss of a "unit" of ecosystem service. Examples of type C ecosystem services include the provisioning of fruits, pharmaceutical drugs, and genetic resources, supporting services

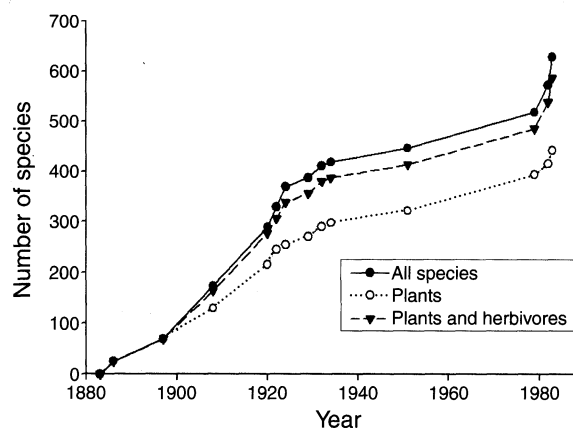


FIG. 4. Recovery of trophic diversity on Krakatau following the volcanic eruption that led to the total extinction of all life on the island (after Thornton 1996). The lowest line illustrates the number of plant species on the island, the middle line is the number of herbivore species, and the top line is the number of predatory species.

such as pollination (Kremen et al. 2002, Klein et al. 2003), nutrient cycling (Schwartz et al. 2000), and provision of habitat where individual species' characteristics play a unique ecological role as pollinators or seed dispersers (Kremen 2005).

We have used the list of ecosystem goods and services developed by the Millennium Ecosystem Assessment as the basis of our list of services provided by different natural and human-modified ecosystems (Table 1; Millennium Ecosystem Assessment 2003). We have then classified the response of ecosystem services to biodiversity change. Values in the table represent consensus that emerged from discussions after each author independently classified the services in each ecosystem. Some services were thought to be consistently resilient across all ecosystems services (primary production), while others were considerably more fragile in some ecosystems than in others (biological control). As we undertook this exercise, it became apparent that the sensitivity of ecosystem services to changes in biodiversity is strongly dependent on the trophic location of the dominant species providing the ecosystem service under consideration. Characteristics of each ecosystem type and the dominant service that they provide further modify the biodiversity-service relationship. For example, provisioning of food is the dominant service of cultivated lands, which is a service related to primary production, and shows a type A response. In contrast, in forest ecosystems, the provisioning of food is not the dominant service and is not directly related to primary productivity but rather to the presence of a broader spectrum of species (from fungi to plants and animals); it has a type C response, whereas the dominant service, provision of fiber, has a type A response. Sensitivity to biodiversity loss was minimal for services predominantly provided by decomposers and primary producers (type A) and maximal in the case of services provided by top predators (type E). The general patterns described in Table 1 identify two key assumptions for any model we might construct that predicts changes in ecosystem services as a result of increasing habitat losses: (1) species at different trophic levels perform different ecosystem services and (2) species at higher trophic levels will be lost more rapidly than those at lower trophic levels.

A number of examples of faunal collapse support our contention that species at higher trophic levels are lost more rapidly than those at lower trophic levels (Figs. 1–4; Wardle et al. 1997, Terborgh et al. 2001, Kremen 2005, Larsen et al. 2005). The classic studies of John Terborgh and colleagues on the islands of Lago Guri illustrate snapshots of the sequence of events that lead to ecosystem collapse (Terborgh et al. 1997a, b, 2001, Lambert et al. 2003); these are characterized by massive increase in herbivores when the predators at higher trophic levels go extinct. This in turn is followed by overexploitation of plant species, so that the vegetation becomes dominated by inedible and thorny species. This

in turn is matched by an increase in decomposing species, particularly leaf-cutter ants. In marine systems, fishing has explicitly focused on the removal of species from higher trophic levels this “fishing down of the food chain” has led to a shortening of the food chain. In contrast, in the Little Rock lake food web example (Locke 1996), acidification of the water supply has led to a change in food web structure that has seen a sequential loss of species from the top to successively lower levels of the food web. As a final example, we note that the long-term surveys of ecosystem recovery on Krakatau suggest that food webs and ecosystems will restructure themselves from the bottom up (Thornton et al. 1988, Thornton 1996); the island was first colonized by plants, then herbivores, and only after 50 years were there sufficient resources for predators to colonize.

As natural habitats are eroded in size, the net decline in species diversity has traditionally been described by a species–area relationship; here we will modify this approach and assume that because many species at higher trophic levels will have larger area requirements they will be lost at a faster rate than those at lower trophic levels (Holt et al. 1999). When habitat quality declines, as in the lake acidification example, the same pattern holds (Menge and Sutherland 1987). For example, in aquatic ecosystems, higher trophic levels decline disproportionately because they are physiologically more susceptible to environmental stress, have fewer resting stages to survive unfavorable periods, and are more dispersal limited (Menge and Sutherland 1987, Bilton et al. 2001, Vinebrooke et al. 2003). An increasing body of evidence suggests that species at higher trophic levels have steeper slopes in their species–area relationships (Holt et al. 1999), and that food chain length is a function of habitat size (Cohen and Newman 1991, Post et al. 2000, Post 2002). A combination of such theoretical and empirical studies suggest that declines in either habitat quantity (or quality) leads to decreases in the lengths of food chains and thus a more rapid loss of services provided by species at higher trophic levels.

#### MODELING THE DECLINE OF ECOSYSTEM SERVICES

These observations allow us to suggest that the collapse of ecosystem services will be determined by a hierarchical series of nested thresholds, or breakpoints, whose magnitude will occur at different levels of decline in overall species abundance. In order to model this effect, we assume that we can rank the species in a food web in a way such that the most resilient species are at the bottom of the food chain, while the least resilient are at the top of food chain. It may be that body size is a key determinant of both trophic position and resilience, however, there are important exceptions to this generality; some key herbivores such as elephants and whales are much larger than their predators, in contrast pathogens are tiny, but are key regulatory components at all trophic levels. Empirical studies supporting the relationship between body size, trophic level, and

TABLE 1. Qualitative assessment of the susceptibility of different ecosystem functions to species loss for a number of different ecosystems.

Ecosystem service	Ecosystem type									
	Urban	Cultivated	Drylands	Forests and woodlands	Coastal	Inland water systems	Island	Mountain	Polar	Marine
<b>Provisioning</b>										
Fresh water	A	E	A	A	NA	C	A	A	A	NA
Fiber	A	A	A	A	A	E	A	A	E	A
Fuel wood	A	E	A	A	E	NA	A	A	E	E
Food	A	A	A	C	A	E	A	A	E	E
Genetic resources	NA	E	C	C	E	C	C	C	C	C
Biochem and pharmaceuticals	NA	A	C	C	E	C	C	C	E	E
Ornamental resources	NA	A	E	E	E	E	E	E	C	E
<b>Regulating</b>										
Air quality	B	A	A	A	A	A	A	A	A	A
Climate regulation	C	A	A	A	A	A	A	A	A	A
Erosion control	C	A	A	A	E	E	A	A	A	NA
Storm protection	A	A	A	C	E	C	A	A	A	NA
Water purification and waste treatment	C	A	B	B	E	A	C	C	A	A
Regulation of human diseases	E	E	B	C	?	D	C	C	A	A
Detoxification	C	A	C	C	E	A	C	C	E	A
Biological control	D	E	D	D	E	E	C	C	A	E
<b>Cultural</b>										
Cultural diversity and identity	C	A	D	D	C	E	E	E	C	C
Recreation and ecotourism	D	A	D	D	C	E	E	E	C	C
<b>Supporting</b>										
Primary production	A	A	A	A	A	A	A	A	A	A
O <sub>2</sub> production	A	A	A	A	A	A	A	A	A	A
Soil formation and retention	A	A	A	A	E	A	A	A	A	NA
Pollination	C	E	C	C	A	NA	C	C	E	NA
Nutrient cycling	C	E	C	C	C	A	C	C	E	A
Provision of habitat	D	E	C	C	E	D	C	C	A	E

Notes: Type A ecosystem services are those for which losses of a few species are mostly compensated for by the remaining species. Types B–E are successively more susceptible to species loss, with Type E representing services that depend primarily on rare or fragile species (see *Introduction*). “NA” indicates not applicable; “?” indicates not known.

diversity have been achieved following intense and painstaking field studies of a limited number of food webs (Briand and Cohen 1987, Schoener 1989, Cohen et al. 2003). These studies provide a sufficient number of general insights for us to provide initial approximate estimates of the parameters that we need.

Our first step is to coarsely calibrate the relative hierarchical magnitude of the thresholds at which ecosystem services breakdown as diversity declines on each trophic level. To achieve this we need explicit estimates of the numbers of decomposers (*D*), autotrophs (*A*), primary consumers (*P*), and secondary consumers (*C*) in a variety of well-studied food webs. Alternatively, we can use ratio-based estimates of the relative numbers of each of these species (Briand and Cohen 1984, Cohen 1989, Schoener 1989). Here, we have opted to assume a constant ratio of species on successive trophic levels. We have set the ratio of species diversity on successive trophic levels at 4:3. Our main conclusions are robust to this naïve assumption of scale invariance. We then obtain an estimate of total species

diversity by summing the totals for each trophic level to obtain an estimate of the total number of species (here we explicitly acknowledge that our inability to sample exhaustively will lead us to underestimate total diversity, particularly at the lowest trophic levels).

We then need to set the “threshold” for decline of services provided by decomposers as a fraction of the total number of species. We will assume that the relationship between species diversity and function can be characterized by either an asymptotic or S-shaped function and that this function can be characterized by a level of diversity at which the function operates at 50% of its theoretical maximum. For any trophic level, we will assume that this threshold level of diversity is determined when the total number of species has been reduced to some fraction *p* of their original diversity. The fraction could take any value between zero and unity (as *p*  $\gg$  0, the services become more brittle at any trophic level), we will set this value to 0.1, and argue that this phenomenologically reflects the log-normal distribution of species abundance within each trophic level

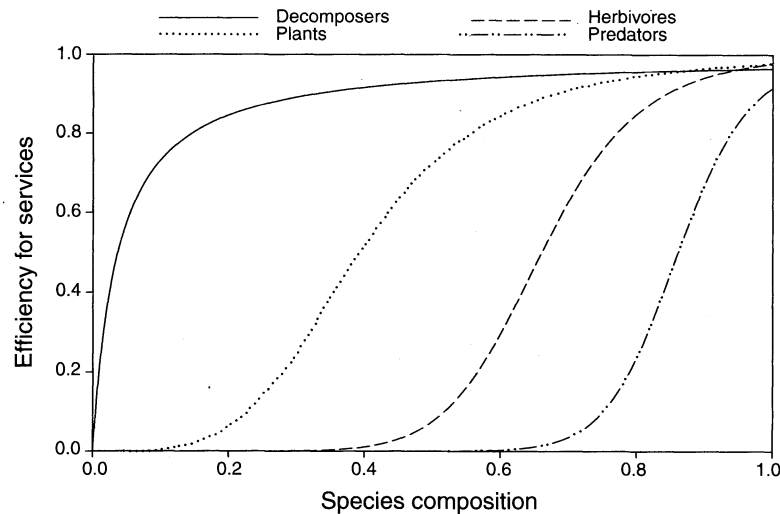


FIG. 5. Functional forms for the relationship between loss of biodiversity and loss of function. Each of the curves represents the decline in both number of species at each trophic level and the ecosystem services undertaken by species on different trophic levels as the total number of species in the community declines. The lowest line (alternating dots and dashes) is for predators and services on the top trophic level, the second lowest line is for herbivores, the dotted line is for plants, and the solid line is for decomposers. The threshold values occur when each trophic level passes through the value of species composition that corresponds to 50% of maximum efficiency for services undertaken at that trophic level.

(May 1975). This distribution of relative abundance makes a major contribution to the commonly observed phenomenon that greater than 90% of the ecosystem functioning is undertaken by less than 10% of the species (at any trophic level; Tilman et al. 1997, Loreau 1998, Petchey and Gaston 2002).

We can now sequentially set the breakpoints for each trophic level in a way that will give a hierarchical series of breakpoints with the lowest trophic levels being most resilient and the upper levels more brittle. Thus we set the threshold (50% efficiency) level for the lowest trophic level at  $p \times D$ . This assumes that when the net species abundance has declined so that only  $p \times D$  species are left in the community, then services performed by the lowest trophic level will have declined by 50%. The (50%) threshold for the next trophic level (autotrophs) is set for when species diversity is reduced to  $D + p \times A$  species. This assumes that processes at the second trophic level will decline at an earlier level of species loss than that at which the basal level declines. We use the same proportionality constant as at the lower level (although we could readily modify this to make upper trophic levels even more brittle; in the absence of more empirical data we will maintain our more parsimonious assumption of constant  $p$ ). The same logic allows us to set thresholds for primary and secondary consumers at  $D + A + p \times P$  and  $D + A + P + p \times C$ , respectively.

We now define a function that relates the rate at which ecosystem services are performed at each trophic level to the net number of species remaining in the community. Here we use a modified form of a function that was originally developed to characterize the strength with which density dependence in population

growth changes with increasing population density (Maynard Smith and Slatkin 1973, Bellows 1981). This simple function builds upon the hierarchical thresholds developed above and describes a general way in which ecosystem services decline with decreasing species diversity:

$$R_{\tau} = 1 - \left[ \frac{1}{1 + \left( \frac{S}{T_{\tau}} \right)^{\tau, \tau}} \right] \quad (1)$$

Here,  $R_{\tau}$  is the rate at which ecosystem services are performed by species on trophic level  $\tau$ ,  $S$  is the total number of species surviving in the degraded habitat, and  $T_{\tau}$  is the threshold level of diversity calculated above for trophic level  $\tau$ . Note that here we have intrinsically assumed that species are lost from each trophic level at a rate determined by  $R_{\tau}$ , we use the trophic-level parameter  $\tau$  to characterize the steepness with which services (and species) are lost as diversity declines, and we have arbitrarily set this function as a square of trophic level. The way with which this function characterizes declines in species diversity and ecosystem function at different trophic levels is illustrated in Fig. 5.

Standard species-area curves may be used to mimic the net loss of biodiversity as habitat is either lost or declines in quality (Simberloff 1988, Reid 1992). We note that the function  $N = cX^z$  (where  $N$  = species number,  $X$  = area,  $z$  = slope, and  $c$  = a constant), assumes that the community comes rapidly to equilibrium. A number of studies have shown that the slope of species-area curves tends to be steeper on local rather than continental scales and that slopes are also steeper

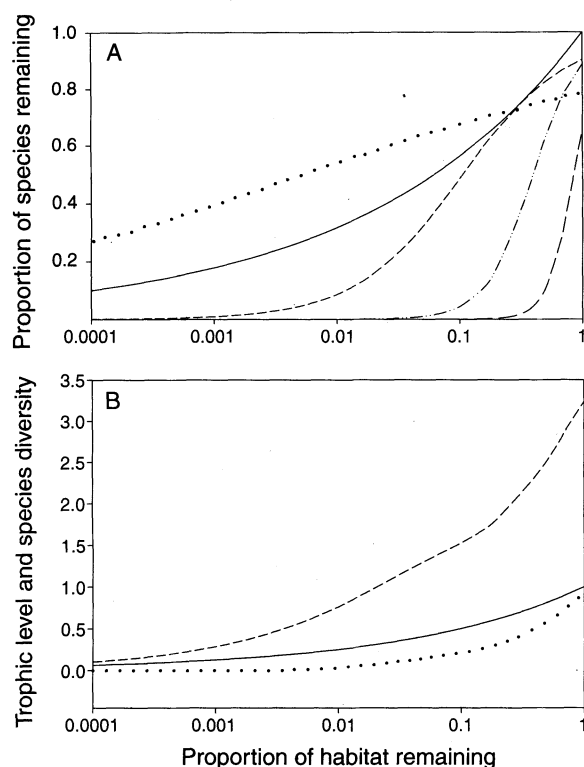


FIG. 6. (A) Decline in abundance of species from different trophic levels as habitat is lost at a constant annual rate. The solid black line illustrates the net loss of species as habitat declines, while the broken lines reflect loss of species and, hence, ecosystem services from sequentially lower trophic levels. The lowest dashed line represents top consumers, the alternating dotted-dashed line is primary consumers, the middle dashed line is plants (primary producers), and the dotted line is decomposers (bacteria and soil organisms). (B) Relationship between area of habitat remaining and length of food chain. The dashed line shows the maximum possible length of the food chain in the remaining habitat, the solid line shows the total proportion of original species still persisting, and the dotted line illustrates the average trophic position of the surviving species.

for real islands than for habitat islands (Scott et al. 1998). We will assume that loss of diversity on a local scale may be characterized by a slope  $z = 0.33$  (MacArthur and Wilson 1967, Connor and McCoy 1979, Simberloff 1992). This slope leads to a 50% decline in net species diversity for each order of magnitude decline in habitat area. It is then relatively straightforward to normalize the species area curve and express species loss as a proportional loss from each trophic level in response to proportional habitat loss. Eq. 1 can then be used to characterize the loss of ecosystem functioning from each trophic level as habitat is either lost or degrades in quality (Fig. 6). The model illustrates that although the overall loss of species as area declines is comparatively modest, because species at the highest trophic levels are lost most rapidly, the economic goods and services provided by these species will thus be lost at

a more rapid rate than those provided by species at lower trophic levels.

It is also possible to use Eq. 1 (and its underlying trophic thresholds) to calculate food chain length at different stages of habitat decline (Fig. 6B). This allows comparison with studies of marine and freshwater systems where decrease in food chain length in response to overexploitation is indicative of declines in "ecosystem size and quality" (Pauly et al. 1998, Post et al. 2000). An important observation here is that, although an order of magnitude loss in habitat only leads to a 50% reduction in species number, this represents a change in community structure equivalent to an average one trophic level decline in the average trophic position of the species persisting in the community. A second order of magnitude decline in habitat causes the loss of the top trophic level from the remaining community. This matches a result observed in heavily exploited marine fisheries (Pauly et al. 1998), where overexploitation causes a decline in average trophic positions. Our approach adds an important detail: trophic collapse would seem to be initiated by first a thinning of the species throughout the web (which would produce the observed decline in mean trophic position), followed by a more rapid shortening of the food web (the loss of top trophic levels). These results are robust to variation in the slope of the species-area curve and relatively robust to significant variations in the two other principal parameters of the model: ratio of species diversity on sequential trophic levels, and inequality in rates at which species drive ecosystem processes (characterized by  $p$ ). We would thus expect to see an initial sequential reduction in economic goods and services as natural systems are degraded, followed by a more rapid sequential collapse of goods and services. This implies that the sequence of ecosystem service loss is likely to be hierarchical and that the sequence of these declines may be predictable and potentially similar in different ecosystems (Table 1). Determining the relative position of the thresholds at which services breakdown and how interactions between species on different trophic levels affect these thresholds requires further urgent attention.

#### CONCLUSIONS

The model described here assumes no interaction between species at different trophic levels. It will therefore underestimate compensatory changes in abundance and diversity of species at intermediate levels as the upper levels are removed, thus important ecological interactions such as regulation of prey abundance by predators (meso-predator release) (Terborgh 1988, Terborgh et al. 1997b), and maintenance of soil structure by plants are ignored in this framework. We have also ignored the fact that many habitats are explicitly modified to create new habitats that directly supply key services to the human economy, particularly agriculture, but also lands for industry, homes, and



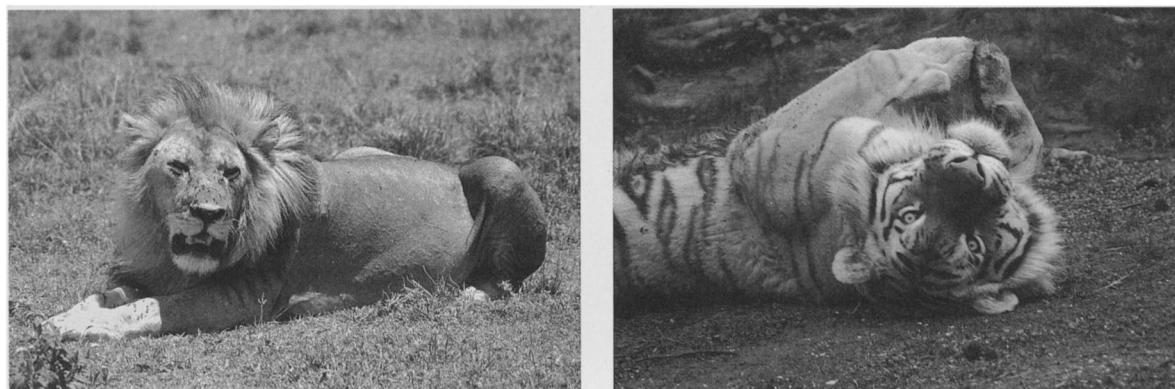


PLATE 1. Both lions and tigers provide ecosystem services as top predators. They also act as a major draw for ecotourists. If ecosystems and nature reserves can maintain healthy populations of top predators such as these, it is likely that they will also contain healthy communities and populations of the many species that perform a diversity of ecosystem services at lower trophic levels. Photo credit: A. P. Dobson.

recreation. Some models that explicitly explore changes in ecosystem services under habitat conversion are described in Dobson (Dobson 2005). Similarly, the model ignores the impact that alien species might have when they replace and compete with those left in a degraded community. This will be particularly important in agricultural areas, where large portions of the natural habitat are converted into monocultures (at the phototrophic level) that supply food as a major ecological service. The relevance of spatial pattern remains one of the central problems in using species area curves to estimate rates of loss of biodiversity (Simberloff 1988, Seabloom et al. 2002). Although habitat amount is of primary importance in determining the size and ultimately the persistence of populations, the spatial arrangement of persisting habitat patches becomes increasingly more important as habitat is lost (Flather and Bevers 2002). There is a rapid decline in connectivity once 30–50% of habitat is lost, which may have a significant impact on population dynamics and interactions between species (Cumming 2002, Flather and Bevers 2002). Consequently, accurate estimation of biodiversity loss has to take into account the potential for local extinctions as a consequence of habitat arrangement, not just as a function of net habitat remaining. The model framework we have developed could be adapted to consider all of these processes, although to a first approximation, modifying the magnitude of the threshold parameters ( $p_i$ ) may most readily capture the details of these more subtle processes.

None of this detracts from our principal conclusion; because different ecosystem services tend to be undertaken by species at different trophic levels and because trophic webs will tend first to thin and then collapse from top to bottom, we would expect to see a predictable hierarchical and sequential loss of the economic goods and services by natural ecosystems as they become eroded and degraded by anthropogenic

activities. This apparently simple, but important, insight has been overlooked in previous studies of ecosystem functioning. While there is significant conservation pressure at the present time to conserve top carnivores such as tigers, wolves, and fish (species that provide a heightened spiritual and recreational quality to ecosystems), there is limited economic incentive to conserve these species. In contrast, species such as nematodes, mites, earthworms, fungi, and bacteria undertake many of the economically crucial processes that cleanse air and water but receive limited conservation attention. At intermediate trophic levels, autotrophs (plants) provide not only structure and buffering against erosion, but also the energy and nutrients that are then passed up the food chain by primary and secondary consumers.

The empirical examples and phenomenological model described above suggest that the ecosystem services undertaken by species at high trophic levels will disappear before those undertaken by species at the bottom of the food chain. While the economic effects of this loss in services have so far been limited, the loss of species that benefit by simply serving aesthetic and recreational services (see Plate 1), serves as an important alarm bell for the subsequent loss of services to which human health and economic welfare are more tightly coupled. Ironically, because the volume of essential services provided by species at lower trophic levels is linearly dependent upon the size (and quality) of habitat remaining, the best way to maximize return on these essential services may be to ensure that the ecosystem remains viable for species with larger area requirements that have less readily quantified economic value.

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