

this reflects more complete use of certain resources by the more species-rich assemblages. As a result, starthistle added substantial biomass to species-poor communities while mainly displacing resident biomass in species-rich communities. Invasibility can thus decline while per-unit invader impact on the resident community increases, underscoring the importance of measuring both.

This study helps bridge the gap between our understanding of general biodiversity-function relations and the role of extinction order in determining the consequences of biodiversity loss. Additional experiments are needed to assess the consequences of ordered species losses for other ecosystems and ecosystem functions, as well as to expand research designs to incorporate species losses occurring through time at larger spatial scales. If, as we found, important functional traits disappear more rapidly than expected by chance in other communities, the ecosystem consequences of real biodiversity losses—even of rare species—will often exceed expectations based on randomized diversity studies.

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Supporting Online Materials

www.sciencemag.org/cgi/content/full/306/5699/1175/DC1

Materials and Methods

Table S1

References

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Extinction and Ecosystem Function in the Marine Benthos

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Rapid changes in biodiversity are occurring globally, yet the ecological impacts of diversity loss are poorly understood. Here we use data from marine invertebrate communities to parameterize models that predict how extinctions will affect sediment bioturbation, a process vital to the persistence of aquatic communities. We show that species extinction is generally expected to reduce bioturbation, but the magnitude of reduction depends on how the functional traits of individual species covary with their risk of extinction. As a result, the particular cause of extinction and the order in which species are lost ultimately govern the ecosystem-level consequences of biodiversity loss.

Marine coastal ecosystems are among the most productive and diverse communities on Earth (1) and are of global importance to climate, nutrient budgets, and primary productivity (2). Yet, the contributions that coastal ecosystems make to these ecological processes are compromised by human-induced stresses, including overfishing, habitat destruction, and pollution (3–5). These stressors particularly impact benthic (bottom-living) invertebrate communities because many species are sedentary and cannot avoid disturbance. Thus, marine coastal ecosystems are likely to experience a large proportional change in bio-

diversity should present trends in human activity continue (6–8).

Given these prospects, researchers have recently asked how the loss of biodiversity might alter the functioning of marine coastal ecosystems. Like most studies to date, these experiments have manipulated diversity by assembling random subsets of species drawn from a common pool of taxa (9–11). This approach (12, 13) may be useful for understanding the theoretical consequences of diversity loss but is unrealistic in the sense that it assumes species can go extinct in any order. Extinction, however, is generally a nonran-

dom process (14) with risk determined by life-history traits such as rarity, body size, and sensitivity to environmental stressors like pollution (15–18). Interspecific differences in extinction risk have implications for the ensuing changes in trophic interactions and community structure (18, 19), such that the ecosystem-level consequences of random versus ordered extinctions are likely to be fundamentally different (14, 20–22).

Here we explore how various scenarios of extinction for marine benthic invertebrates are likely to influence bioturbation (the biogenic mixing of sediment)—a primary determinant of sediment oxygen concentrations which, in turn, influences the biomass of organisms, the rate of organic matter decomposition, and the regeneration of nutrients vital for primary productivity (23, 24).

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Using a comprehensive study of 139 benthic invertebrate species that inhabit Inner Galway Bay, Ireland (25), we parameterized models that predict how species extinction is likely to affect the biogenic mixing depth (BMD), an indicator of bioturbation that can be measured from sediment profile images (Fig. 1). To estimate species contributions to the BMD, we used an index of bioturbation

potential (BP_p , Equation S1) that accounts for each species' body size, abundance, mobility, and mode of sediment mixing. We used data from monthly samples (over 1 year) of the benthic community to empirically derive a relation (Equation S2) between the BMD and the bioturbation potential of the community (BP_c). Using this relation, we performed numerical simulations to explore how the BMD

is expected to change when species go extinct at random versus ordered by their sensitivities to environmental stress, body size, or population size (25). As the functional consequences of extinction are known to depend on the response of surviving species (19, 20, 26), we simulated two different types of community interactions (8). First, we used a model in which species do not interact with one another; thus, surviving species do not exhibit compensatory responses (changes in population size) after extinction. This scenario leads to complete loss of bioturbation performed by an extinct species and represents a "worst-case" scenario. Second, we used an interactive model of community assembly in which species' abundances are limited by competition with other members of their functional guild (i.e., species with similar bioturbation modes but not necessarily similar extinction risks). This represents a "best-case" scenario that assumes compensation is additive and substitutions of abundance maintain total community density [i.e., full numerical compensation (25)].

Our models predict that loss of species diversity leads to a decline in mean BMD, regardless of extinction scenario (Fig. 2). Note, however, that Fig. 2, A to H, depict strikingly different patterns, suggesting that changes in the BMD depend on extinction scenario. Indeed, the rate of change, the species richness at which the BMD first declines, the variance surrounding the relation (i.e., predictability of change), and the range of potential values all depend on how species go extinct (Table 1). These divergent patterns are best explained by examining the covariance between each species extinction risk and the biological traits that influence bioturbation (Fig. 3). To illustrate these patterns, we first focus on scenarios of extinction that involve no compensatory responses (i.e., the noninteractive model; Fig. 2, A, B, C, and D). Random extinction (Fig. 2A) produces a clear bifurcation of the BMD, with values determined by the presence (>4.0 cm) versus absence (<4.0 cm) of a single species—the burrowing brittlestar, *Amphiura filiformis*. The strong impact of *A. filiformis* on bioturbation is well documented (27). In this study, *A. filiformis* has a disproportionate impact (Fig. 3A) on bioturbation because it is consistently one of the most abundant species in Galway Bay (Fig. 3B) and has a high per capita effect that results from it being a large (Fig. 3C), highly mobile species. Consequently, changes in the BMD following extinction largely depend on whether *A. filiformis* is among the survivors.

When extinctions are ordered by species sensitivity to stress (Fig. 2B), estimated as the relative change in the abundance of species along a gradient of disturbance (25), the risk of extinction among species varies by a

Fig. 1. The biogenic mixing depth (BMD, white arrows) of sediments [(A), site 1; (B), site 2] in Inner Galway Bay, Ireland. BMD was related to the bioturbation potential of a community (BP_c), an index that accounts for each species' population size and life-history traits (body size, mobility, mode of bioturbation) to estimate the capacity of a community to mix sediments (25).

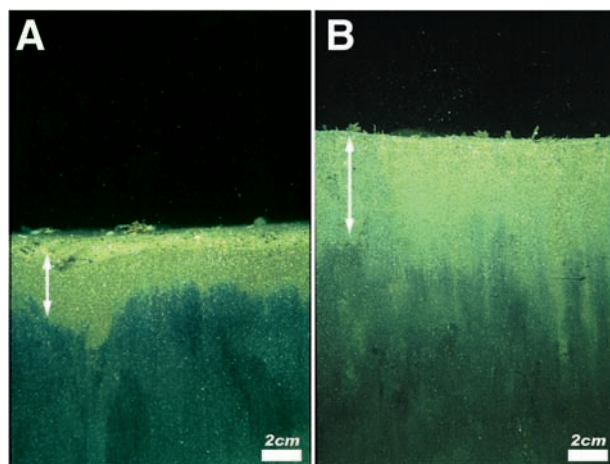
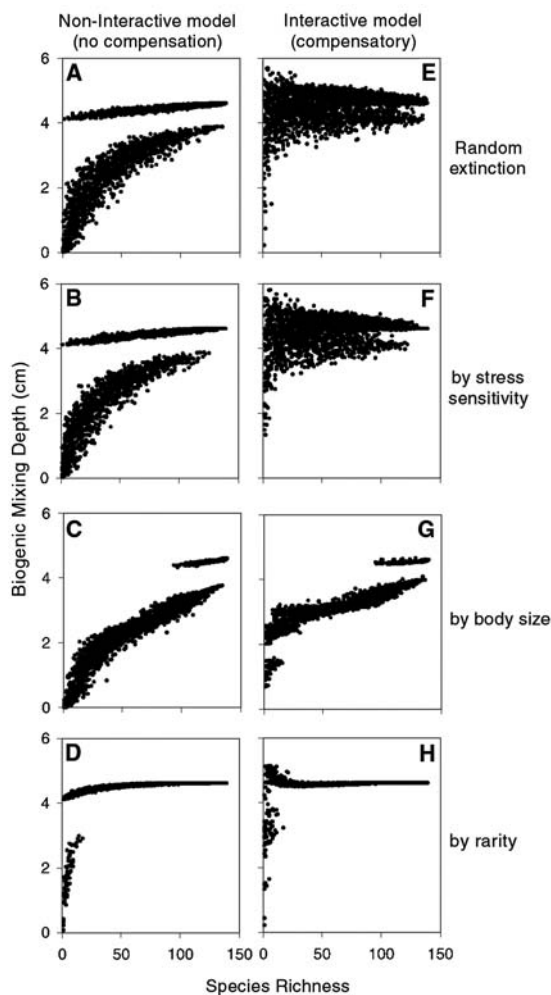


Fig. 2. Predicted changes in the BMD following benthic invertebrate extinctions. Each panel shows the results of 20 simulations per level of species richness, constrained by a probabilistic order of species extinction (indicated on the right). Simulations (A), (B), (C), and (D) are for a noninteractive model of community assembly assuming no numerical compensation by surviving species. Simulations (E), (F), (G), and (H) are for an interactive model that assumes full numerical compensation following extinction of competitors.



factor of 215; yet, stress sensitivity for *A. filiformis* (-0.99, Fig. 3D) is near the median value for the community as a whole (-0.98), which explains why changes in the BMD are comparable to the scenario of random extinction (compare Fig. 2, A and B). This conclusion is confirmed by statistical comparisons of the mean and range of values (minimum and maximum) of the BMD, which show an identical change with species loss for both scenarios; and a comparison of the variability in BMD, which reveals only a marginal difference between scenarios ($\alpha = 0.0125$; $P = 0.01$, Table 1).

For extinctions ordered by body size (Fig. 2C), probabilities of extinction were assumed to be proportional to mean species biomass to mimic the higher extinction risk generally faced by large-bodied organisms that often have small population sizes, have longer generation times, or are found at higher trophic levels (17, 28). Body size varied by a factor of >500,000 among species and was positively correlated with per capita effects on bioturbation ($r = 0.98$, $P < 0.01$) but not abundance ($r = -0.05$, $P = 0.56$, even excluding *A. filiformis*, $r = -0.08$, $P = 0.33$). In this scenario, larger species (high per capita effects) tended to be lost before smaller species (low per capita effects), leading to a faster decline in the mean BMD compared with random extinction (compare Fig. 2, A and C; Table 1). The range of values of the BMD (minimum and maximum) and total variation (CV) also changed with species richness more quickly than for random extinctions (Table 1). This was not due to the loss of entire functional guilds composed of large species because there was considerable overlap in species body size, and thus extinction risk, among functional guilds (25). Rather, patterns were generally a consequence of the early extinction of *A. filiformis*, the 19th largest species, which produced a step change in the BMD at a species richness of ≈ 100 .

Extinction risk is typically high for rare species, defined here as those with low local abundances, because small populations are more vulnerable to environmental and demographic stochasticity (17, 28). They also often have narrow geographic ranges and/or high specialization, further compounding extinction risk (28-30). When we assumed extinction probability was inversely proportional to species density, rare species were >6000 times more likely to be lost than the most common species. Yet, because small populations typically contribute little to bioturbation (Fig. 3B), extinctions of rare species had little impact on the BMD, and ecosystem functioning was maintained until the loss of more abundant species, such as *A. filiformis* (lower bifurcation, Fig. 2D). Hence, some scenarios of extinction do not lead to appre-

ciable loss of ecological function until a large proportion of species are lost.

Many studies suggest that when species go extinct from communities characterized by strong interactions, increases in the population size of species released from competition can compensate for loss of ecological function (20, 31, 32). Our models suggest that this is only true when the risk of extinction is not correlated with species functional traits. This is evident because compensatory responses only changed the probabilistic distribution of the BMD when species were lost at random (Fig. 2E) or in order of their sensitivity to stress (compare Fig. 2, A and E, and Fig. 2, B and F) (Table 1). However, when a species' risk of extinction covaried with its body size or abundance, compensatory responses did not alter the consequences of diversity loss (compare Fig. 2, C and G and Fig. 2, D and H) (Table 1). This is because when loss is ordered by body size, small species have little impact on bioturba-

tion and cannot offset functions performed by larger species. When species are lost in order of rarity, even full compensation has no notable effect on the BMD because the proportional change in bioturbation is small. Thus, compensatory responses of surviving species do not necessarily stabilize ecological processes when the traits required for maintaining function simultaneously increase extinction risk.

We have used numerical models parameterized by data from a marine benthic community to show that species extinction is generally expected to reduce the depth of bioturbated sediments. Such changes might be expected to alter the fluxes of energy and matter that are vital to the global persistence of marine communities (23), a conclusion that corresponds to evolutionary patterns in the fossil record showing a close association between the frequency of anoxia and the diversification of marine soft-bottom communities (33). We have also shown that crucial details (mean, range, and predictabil-

Fig. 3. The relation between per capita bioturbation, BP_p , and mean species abundance (A) reveals that at the population level (diagonal dashed lines, each an order of magnitude difference in bioturbation), most species contribute little to bioturbation (left of short-dashed line). Bioturbation is disproportionately affected by one large and highly active species, *Amphiura filiformis* (brittlestar, open circle). Population level bioturbation, BP_p , is proportional to species abundance (B) ($r = 0.83$, $P < 0.001$), body size (C) ($r = 0.39$, $P < 0.001$), and sensitivity to stress (D) ($r = -0.2$, $P < 0.05$). Arrows indicate order of extinctions.

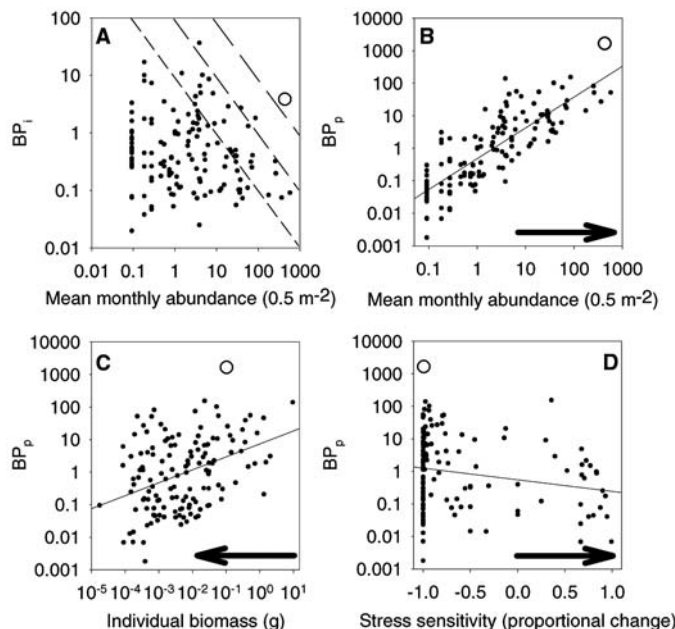


Table 1. Comparisons of how bioturbation changes with species loss for each extinction scenario (stress, size, rarity) relative to a random model of extinction, and between the interactive and noninteractive models of community assembly. The asterisk (*) denotes significant differences, $P < 0.0125$ [set conservatively to correct for the number of comparisons (25)]. CV, coefficient of variation.

	Mean	CV	Minimum	Maximum
<i>Comparison of random extinction to extinctions ordered by...</i>				
Sensitivity to stress	$\chi^2_4 = 0.73$	$F_{4, 1094} = 3.38^*$	$\chi^2_4 = 1.63$	$\chi^2_4 = 0.23$
Body size	$\chi^2_4 = 53.8^*$	$F_{4, 1094} = 42.8^*$	$\chi^2_4 = 15.1^*$	$\chi^2_4 = 15.1^*$
Rarity	$\chi^2_4 = 28.2^*$	$F_{4, 1094} = 250^*$	$\chi^2_4 = 97.6^*$	$\chi^2_4 = 3.8$
<i>Comparison of interactive to noninteractive model for extinctions that are...</i>				
Random	$\chi^2_2 = 35.07^*$	$F_{2, 274} = 629^*$	$\chi^2_2 = 30.94^*$	$\chi^2_2 = 10.37^*$
Ordered by sensitivity to stress	$\chi^2_2 = 25.76^*$	$F_{2, 274} = 307^*$	$\chi^2_2 = 20.94^*$	$\chi^2_2 = 10.19^*$
Ordered by body size	$\chi^2_2 = 7.42$	$F_{2, 274} = 166^*$	$\chi^2_2 = 10.71^*$	$\chi^2_2 = 5.56$
Ordered by rarity	$\chi^2_2 = 1.38$	$F_{2, 274} = 13.9^*$	$\chi^2_2 = 0.69$	$\chi^2_2 = 0.50$

ity of change) of how bioturbation changes following extinction depend on the order in which species are lost, because extinction risk is frequently correlated with life-history traits that determine the intensity of bioturbation. This finding is important because it argues that the particular cause of extinction ultimately governs the ecosystem-level consequences of biodiversity loss. Therefore, if we are to predict the ecological impacts of extinction and if we hope to protect coastal environments from human activities that disrupt the ecological functions species perform, we will need to better understand why species are at risk and how this risk covaries with their functional traits.

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Supporting Online Material

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 Materials and Methods
 Equations S1 and S2

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Bushmeat Hunting, Wildlife Declines, and Fish Supply in West Africa

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The multibillion-dollar trade in bushmeat is among the most immediate threats to the persistence of tropical vertebrates, but our understanding of its underlying drivers and effects on human welfare is limited by a lack of empirical data. We used 30 years of data from Ghana to link mammal declines to the bushmeat trade and to spatial and temporal changes in the availability of fish. We show that years of poor fish supply coincided with increased hunting in nature reserves and sharp declines in biomass of 41 wildlife species. Local market data provide evidence of a direct link between fish supply and subsequent bushmeat demand in villages and show bushmeat's role as a dietary staple in the region. Our results emphasize the urgent need to develop cheap protein alternatives to bushmeat and to improve fisheries management by foreign and domestic fleets to avert extinctions of tropical wildlife.

The trade in bushmeat for human consumption is a key contributor to local economies throughout the developing world (1, 2), but it is also among the greatest threats to the persistence of tropical wildlife (1–4). Efforts to manage the bushmeat trade are built on the premise that bushmeat consumption is driven by protein limitation. Thus, it is assumed that increases in livestock and agricultural production will reduce human reliance on wild sources of food (5–7). Although it makes intuitive and economic sense that consumption of wild meat would be linked to the availability of alternative sources of protein, there is little empirical evidence to support this assumption, particularly at large geo-

graphic scales (1, 5–7). Furthermore, contrary to predictions of the “protein limitation” hypothesis, unsustainable consumption of wildlife remains a problem even in many relatively prosperous countries (1). Identifying bushmeat's value as a dietary staple versus a nonessential good is vital for targeting conservation interventions and, equally important, for predicting the impacts of wildlife declines on human livelihoods.

We evaluated the protein limitation hypothesis by comparing annual rates of decline for 41 species of wild carnivores, primates, and herbivores (table S1) in six nature reserves in Ghana with supply of fish in the region from 1970 to 1998. As is the

case across the tropics, wild terrestrial mammals are used as a secondary source of animal protein in Ghana, and they comprise the chief commodities in a regional bushmeat trade estimated conservatively at 400,000 tons per year (8). Marine and freshwater fish are the primary source of animal protein consumed in West Africa, and the fisheries sector directly and indirectly accounts for up to one quarter of the workforce in the region (9, 10). From 1965 to 1998, the supply of harvested fish in Ghana (Fig. 1A) ranged from 230,000 to 480,000 tons annually and varied by as much as 24% between consecutive years (11). Here, we test a prediction of the protein limitation hypothesis that years with low fish supply will show larger declines in biomass of terrestrial mammals, suggesting a transfer of harvest pressure and consumption between these resources. We also test for evidence of a mechanism underpinning such a transfer by examining (i) rates of hunting in nature reserves, (ii) sales and price data from local markets, and (iii) spatial trends in correlations of fish supply and wildlife declines.

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