

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).

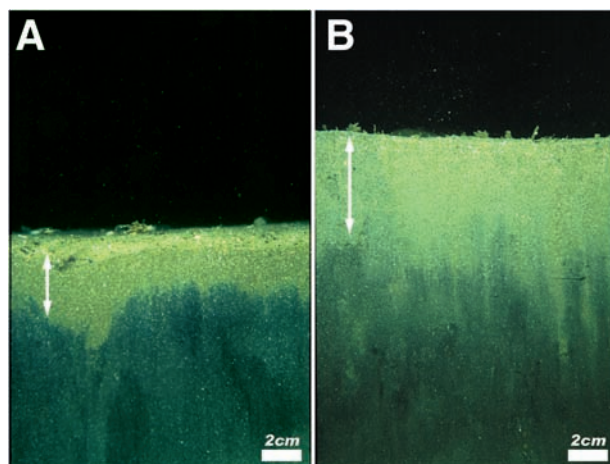
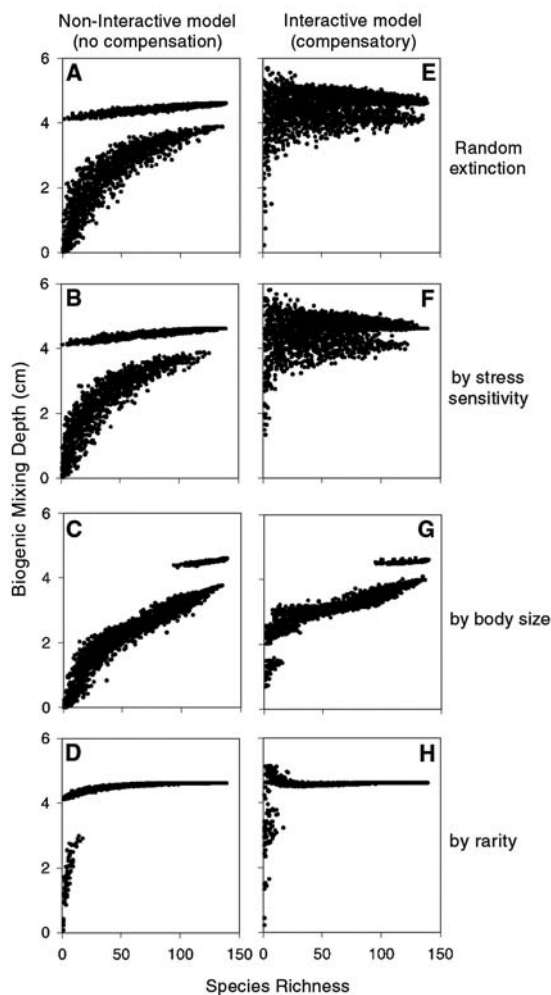


Fig. 2. Predicted changes in the BMD following benthic invertebrate extinctions. Each panel shows the results of 20 simulations per level of species richness, constrained by a probabilistic order of species extinction (indicated on the right). Simulations (A), (B), (C), and (D) are for a noninteractive 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.

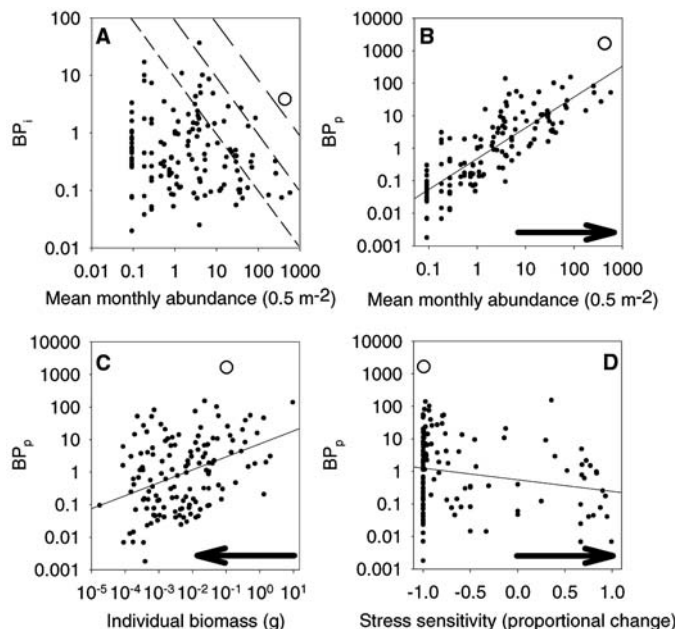


Table 1. Comparisons of how bioturbation changes with species loss for each extinction scenario (stress, size, rarity) relative to a random model of extinction, and between the interactive and noninteractive models of community assembly. The asterisk (*) denotes significant differences, $P < 0.0125$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

www.sciencemag.org/cgi/content/full/306/5699/1177/DC1
 Materials and Methods
 Equations S1 and S2

23 July 2004; accepted 23 September 2004

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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SUPPORTING ONLINE MATERIAL

MATERIALS AND METHODS

Study sites & data collection

Data were collected from two sites located in Inner Galway Bay on the central west coast of Ireland as part of an extensive monitoring program (*S1*, *S2*). Site 1 (Leverets; 9m water depth, 53° 15.50'N, 09° 2.02'W) is ~0.75 nautical miles SE of Galway City docks and is perturbed by freshwater discharge from the River Corrib, untreated domestic sewage from the city (36-41,000 m³ d⁻¹, *S3*) and frequent bouts of storm driven tidal surge. Site 2 (Margaretta; 22m water depth, 53° 13.50'N, 09° 6.50'W) is ~3.35 nautical miles SW of Site 1 and has been identified as a 'pristine' area of scientific interest by a European Community programme (*S4*). Local prevailing currents form a gyre (*S5*) in Inner Galway Bay that results in both sites recruiting from the same regional species pool (147 species, 56% common to both stations; *S1*, *S2*, *S6*); yet, Site 1 forms a low diversity (91 taxa) admixture of Site 2 (139 taxa). The 8 taxa unique to Site 1 were not included in our analyses because the gradient of perturbation (and likelihood of extinction) is directional, increasing from Site 2 to Site 1.

Samples of macro-invertebrates ($n = 5$, 0.1m² van Veen grabs) were collected from each site approximately monthly over a one-year period (December 1996 – November 1997, $n = 11$). Species were identified to the lowest possible taxon (79% to species, 11% to genus, 6% to family, 4% to higher taxonomic levels) to determine the composition, abundance, biomass and functional types of the benthic community. Sampling efforts were coupled with photographic images of the sediment profile ($n=10$, SPI camera system; *S7*) so that we could use standard image analysis to directly measure the biogenic mixing depth (BMD) of the sediments. The BMD is a measure of bioturbation that can be estimated from the vertical colour change in the sediment profile (*S8*), delimited at the lower boundary as the interface between the oxidized (high reflectance) and reduced (low reflectance) sediment (Fig 1).

Characterizing bioturbation

We used an index ($S1, S2$), modified from widely used metrics of bioturbation ($S9-S12$), to characterize the per capita effect of each species on sediment mixing:

$$BP_i = \overline{B}_i^{-0.5} \times M_i \times R_i \quad (1)$$

This index accounts for three biological traits known to influence sediment bioturbation: (i) mean body size (\overline{B}_i , biomass in grams), (ii) propensity to move through the sedimentary matrix (mobility, M_i), and (iii) method of reworking sediments (reworking mode, R_i). \overline{B}_i was square root transformed so species impacts conformed to a linear scale ($S1, S2, S10-S12$). M_i was scored on a categorical scale that reflects increasing activity of the species (1 = in a fixed tube, 2 = limited movement, sessile, but not in tube, 3 = slow movement through sediment, 4 = free movement via burrow system, $S10$). R_i was also scored on a categorical scale to reflect increasing impacts on the sediment turnover (1 = epifauna that bioturbate at the sediment-water interface; 2 = surficial modifiers, whose activities are restricted to <1-2 cm of the sediment profile; 3 = head-down/head-up feeders that actively transport sediment to/from the sediment surface; 4 = biodiffusers whose activities result in a constant and random diffusive transport of particles over short distances; and 5 = regenerators that excavate holes, transferring sediment at depth to the surface). These functional types are well-established classifications in the marine literature and explicitly recognize that individual species have differing impacts on the BMD (for review, see $S9$). Per capita effects were multiplied by mean species abundances in monthly grab samples to determine the population-level bioturbation potential, BP_p , of a given species, $BP_p = BP_i \times A_i$. BP_p was summed across species in a sample to estimate the community-level bioturbation potential, BP_c .

The relationship between BP_c and the measured biogenic mixing depth (BMD) was fit empirically as:

$$BMD = \log\left(\frac{BMD/6}{1 - BMD/6}\right) = 4.55 + 0.719 \log BP_c \quad (2)$$

Equation 2 places an upper bound on the mixing depth at zero (the sediment-water interface) and a lower bound at 6-cm (the lowest depth that animals typically burrow in Galway Bay). BP_c was found to be a strong predictor of the BMD, explaining 69% of all variation over the sampling year. The robustness of equation 2 as a predictive model was evaluated using a cross-validation procedure (*SI3*) that compares the r^2 of the fitted data set to that of a jack-knifed distribution (CVr^2). The small difference between the CVr^2 value (= 0.61) and the original estimate ($r^2 = 0.69$) indicates that equation 2 is stable predictor of the BMD. We further compared the predictions of equation 2 to a partial regression model where BMD was taken to be a function of the partial regression coefficients of each species BP_p (i.e. bioturbation potential after accounting for the correlated impacts of species). We found that equation 2 and the partial regression model had identical explanatory power.

Modelling & statistical analysis

We modelled scenarios of extinction that match likely drivers of change in marine coastal ecosystems. For each scenario, we ran 20 simulations at each level of species richness (1 to 139 species) using equations 1 and 2 to predict the BMD of each community. The starting community consisted of all species ($n = 139$) and the corresponding BMD was assembled using the mean monthly abundances for each species. Subsets of the full assemblage were then chosen to represent communities of reduced richness with the probability of species extinction (exclusion from the subset) being either random ($1/n$), or assumed to be proportional to mean abundance (rare species first, lowest to highest

A_i), body size (large species first, largest to smallest B_i), or sensitivity to stress. For the stress model, the probability of extinction was taken to be the proportional change in abundance of a species from site 2 (a pristine site) to site 1 (a stressed site). This approach does not differentiate among the multiple stressors at site 1 (described above) and ignores the fact that species tolerances to specific stress regimes were not measured individually. Nevertheless, the scenario is useful for comparative purposes. For extinctions ordered by body size, it should be noted that results are not driven by the loss of entire functional guilds composed of large species as there is considerable overlap in the body size of species in different functional guilds (and thus, in the probability of extinction, Fig. S1). The only significant difference in body size (B_i) occurs between functional guilds 2 (surficial modifiers) and 4 (biodiffusers) (ANOVA followed by pair-wise contrasts using Fisher's Least Significant Differences, $p < 0.05$).

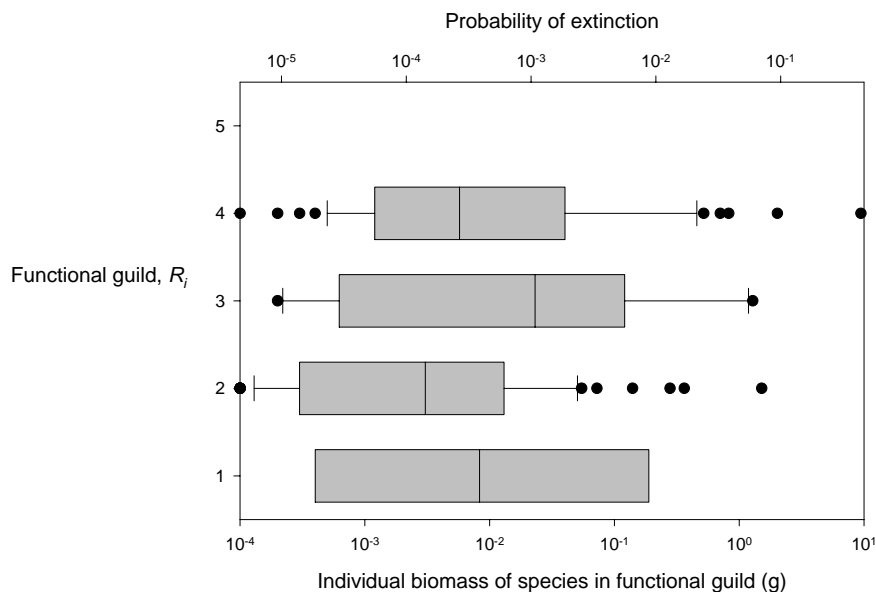


Figure S1. The mean individual biomass of species in each of the five functional guilds (R_i), and their probability of extinction.

For simulations incorporating compensation, compensating species were chosen at random from those surviving in the same functional guild, R_i (Equation S1), which mimics the likely scenario

of compensation among potential competitors. We focussed on full numeric, as opposed to biomass, compensation because (a) density is a more conserved property in the benthic communities of Galway Bay (coefficients of variation in monthly samples were 0.40/0.20 for community density and 0.41/0.77 for community biomass at sites 1 and 2, respectively) and (b) density compensation has generally been the focus of empirical and theoretical work to date, and thus, is useful for comparison (S14, S15).

Results of simulations could not be compared using standard statistical models because the pronounced affect of *A. filiformis* created patterns difficult to represent with known functions and error distributions. Therefore, we computed four metrics (mean, coefficient of variation, minimum, and maximum) that collectively describe the distribution of values of BMD at each level of species richness, and which did conform to known distributions (the mean, minimum, and maximum fit logistic functions of species richness with a binomial error structure, $r^2 = 89-94\%$, and the CV fit a logarithmic function with a Gaussian error structure, $r^2 = 85\%$). The full model includes one continuous variable, species richness, and two categorical variables (extinction type, compensation type) and all interactions. Differences between random and any other extinction type were evaluated by combining these two extinction types in the model. Differences between interactive and non-interactive scenarios were tested in separate models (explanatory variables: species richness, compensation type and interaction) for each extinction type. As the response variables are not independent, α was set conservatively at 0.0125. Analyses were performed using *R 1.9.0* (available from <http://www.r-project.org>).

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