

PREDICTING THE EFFECTS OF HABITAT HOMOGENIZATION ON MARINE BIODIVERSITY

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Abstract. Seafloor habitats throughout the world's oceans are being homogenized by physical disturbance. Even though seafloor sediments are commonly considered to be simple and unstructured ecosystems, the negative impacts of habitat homogenization are widespread because resident organisms create much of their habitat's structure. We combine the insight gained from remote sensing of seafloor habitats with recently developed analytical techniques to estimate species richness and assess the potential for change with habitat homogenization. Using habitat-dependent species–area relationships we show that realistic scenarios of habitat homogenization predict biodiversity losses when biogenic habitats in soft sediments are homogenized. We develop a simple model that highlights the degree to which the reductions in the number of species and functional diversity are related to the distribution across habitats of habitat-specific and generalist species. Our results suggest that, by using habitat-dependent species–area relationships, we can better predict variation in biodiversity across seafloor landscapes and contribute to improved management and conservation.

Key words: biodiversity; habitat diversity; habitat homogenization; marine benthos; marine soft sediments; seafloor disturbance; species richness; trawling effects seafloor.

INTRODUCTION

Homogenization of landscapes due to human activity is a recognized broad-scale human impact in terrestrial ecosystems (Western 2001). However, there is increasing evidence that seafloor habitats are also being impacted and homogenized throughout the world's oceans (Thrush and Dayton 2002, Aronson et al. 2004, Thrush et al. 2004). Homogenization of the seafloor is caused by wholesale physical destruction or the selective removal of habitat-forming species. Marine soft sediments are likely to be particularly vulnerable to habitat homogenization because resident organisms create much of their habitat's structure through the provision of hard-substrates such as shells, by burrowing, digging, and bioturbating sediments, and by modifying surface topography and biogeochemistry (Thrush and Dayton 2002, Lohrer et al. 2004). Homogenization of habitat structure is suspected to be a major contributor to the sliding baselines that affect our ability to make ecological assessments of broad-scale changes in marine ecosystems (Dayton et al. 1998, Jackson 2001). Over most of the continental shelf and in some deeper ocean habitats, bottom trawling is the major direct human-disturbance agent that can reduce the density of large and emergent benthic organisms capable of enhancing habitat heterogeneity over large areas of the seafloor (Dayton et al. 1995, McConnaughey et al. 2000, Cryer et

al. 2002, Thrush and Dayton 2002). In coastal regions eutrophication leading to “dead zones” and high rates of terrestrial sediment run-off also remove habitat-structuring organisms over large areas of the seafloor (Karlson et al. 2002, Rabalais et al. 2002, Thrush et al. 2004).

That species richness (S) scales with area (A) (the Arrhenius power law, $S = cA^z$ [Arrhenius 1921]) is one of the clearest empirical laws in ecology (MacArthur and Wilson 1967). This relationship has frequently been used in terrestrial conservation to assess the effects on species richness of changes in the spatial extent of modified or conserved habitat (Rosenzweig 1999, May and Stumpf 2000). In the marine environment, species–area relations have been employed mainly at small, experimental scales and have not been expressly applied to conservation or management of soft-sediment habitats, despite the variety of impacts that threaten biodiversity in coastal/shelf sediments (Gray 1997, Neigel 2003).

Typically species–area relationships assume species richness in the area of interest does not exhibit any spatial pattern, thus their application in conservation implicitly assumes that habitat loss occurs in a random fashion, which can significantly underestimate the risk of species loss (Seabloom et al. 2002). It is important to differentiate between species–area relationships and species accumulation curves. *Species–area relationships* represent general descriptions of the number of species found in areas of different size, irrespective of the identity of individual species, whereas *species accumulation curves* represent the rate of accumulation of new species over a sampled area and thus depend on species

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identity (Ugland et al. 2003, 2005). In reality, both species–area relationships and species accumulation curves represent both a statistical sampling phenomenon and a surrogate that encompasses both habitat variation and the spatial processes that influence species richness (He and Legendre 2002). In marine soft sediments, spatial variation in species richness is common across a broad range of spatial scales, and habitat heterogeneity is generally considered an important driver of biodiversity (Conner and McCoy 1979, Tokeshi 1999, Levin et al. 2001, Ellingsen 2002). Integrating traditional core or grab sampling with acoustic and photographic imagery of the seafloor has demonstrated that habitat structure is not solely created by physical features such as sediment particle size but is intricately connected to the resident biota creating biogenic habitat structures ranging from complex biogenic reefs to landscapes of more sparsely distributed organisms (Thrush et al. 2001, Thrush and Dayton 2002, Zajac et al. 2003).

We propose that, across a broad range of spatial scales, habitat pattern will be a far more important descriptor of species richness than area alone. For example, when samples are collected from a homogeneous area, new species will be added to the species accumulation curve in a consistent or at least random fashion (Fig. 1a). This situation would also occur if the scale of habitat heterogeneity is small enough that every new sample is taken in a new habitat. However, when a number of distinct habitats occur within an area (Fig. 1b), species accumulation is likely to be dependent on the variation in species richness between habitats and the number of habitat-specific species. Similarly, when habitats contain different proportions of species with different functional attributes (e.g., size, feeding and mobility modes) habitat is likely to be a better proxy than area for estimating functional richness.

By combining new analytical techniques that define species–area relationships (Ugland et al. 2003) with data generated by multi-resolution sampling of seafloor communities (Hewitt et al. 2002, 2004), habitat-specific species–area relationships can be used to resolve scales of variability in species richness relative to habitat diversity, increasing the predictive ability of species–area models. In conjunction with the identification of habitat-specific and habitat-generalist species, these relationships can assess the magnitude of change in species richness, on the 1–100 km² scale, associated with habitat homogenization or habitat removal.

METHODS

Sampling

We collected samples to define species–habitat relationships at two different coastal locations with potentially different species pools and different habitat arrangements. Surveys were conducted in Kawau Bay (KB) (36.4° S, 174.8° E; February 1999), on the northeast coast of North Island, and in and around Tonga Island Marine Reserve (TIMR) (40.9° S, 173.8°

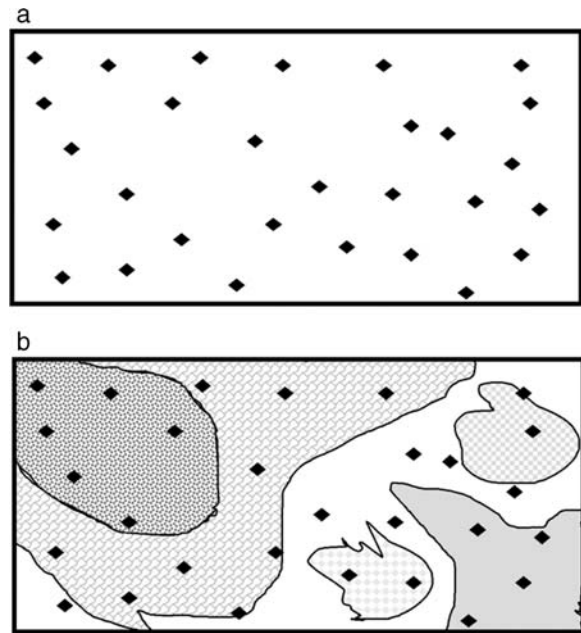


FIG. 1. (a) Homogeneous landscape from which samples are collected to estimate species richness. (b) A landscape composed of distinct habitats with different species richness.

E; September 2003), on the north coast of South Island of New Zealand. Both locations are not exposed to commercial bottom fishing, and contained a variety of soft-sediment habitats. Given the dispersal potential of soft-sediment macrofauna and the spatial scale of our sampling, most species would have the potential to move from one habitat to another within each location.

Initially, in both locations, broad-scale habitat description based on side-scan sonar, QTC acoustic habitat classification, and remote video imagery was used to identify a range of habitats for video and core sampling (see Hewitt et al. [2004]) for details of methods). Quantitative video images of the seafloor were then used to describe habitats based on both physical characteristics and the density of habitat-forming organisms (Table 1). Macrofaunal core samples and video images of the seabed were collected along paired 20 m transects haphazardly located within broad-scale habitat types. Cores were located along transects to maximize the within-site variability encompassed, with 2–5 cores collected per transect depending on the degree of within-site variability (see Thrush et al. 2001). A total of 10 sites with different habitats was sampled in each location with a total of 72 and 114 core samples from TIMR and KB, respectively. In TIMR core samples encompassed an extent of ~10 km and ranged in depth from 8 to 24 m, while at KB core samples encompassed an extent of 5 km and ranged from 6 to 22 m depth. Cores (10-cm diameter, 12 cm deep) and video images of the seabed around cores were collected by SCUBA divers. The TIMR sites were sampled 3–8 March 2002, while the KB sites were sampled 18–25 February 1999.

TABLE 1. Habitat categories and descriptions derived from video imaging of the seafloor in and around Tonga Island Marine Reserve (TIMR; north coast of South Island) and in Kawau Bay (KB; northeast coast of North Island), New Zealand.

TIMR habitat		KB habitat	
Category	Description	Category	Description
1	Sand structured by bivalves and gastropods	1	Homogeneous bare sand
2	Homogeneous sand with sparse epifauna	2	Coarse sand, dense algal turf
3	Sandy mud with rubble patches, fan worms, hermit crabs	3	Mud stabilized by worm tubes
4	Sandflats with high densities of mobile epifauna	4	Mud with dense <i>Atrina zelandica</i> beds
5	Mud with microphytobenthos and hermit crabs	5	Coarse sand, heavily bioturbated
		6	Complex biogenic sand with <i>Atrina</i> and sponges

After collection the core samples were sieved (500- μ m mesh), and then preserved in 70% isopropanol and 0.1% Rose Bengal in seawater. In the laboratory, macrofauna were sorted and differentiated to the species level (except for syllid, exogonid and *Peresiella/Heteromastus* polychaetes, phoxocephalid amphipods, and nemerteans). Species functional traits were defined according to their typical adult body size (small, <5 mm; medium, 5–20 mm; and large, >20 mm longest dimension). Feeding modes used were (1) predators/scavengers, (2) deposit feeders, (3) grazers, and (4) suspension feeders. Species were also categorized by depth into surface dwelling, top 2 cm, below 2 cm, and throughout the sediment column.

Species richness–habitat predictions

The analytical approach developed by Ugland et al. (2003) enabled us to develop habitat-specific species accumulation curves and link these using total-species curves to estimate species richness. The estimates from this technique were contrasted with those derived from simple randomization procedures (Colwell and Codrington 1994). These techniques were used rather than the rarefaction curves that are common in benthic studies. Rarefaction techniques perform poorly when species exhibit patchy distributions and when communities are strongly numerically dominated by one or two species (see Krebs 1989), both characteristics of macrofaunal communities that can be apparent in heterogeneous habitats.

The number of habitat-specific species was identified for each habitat defined from the video images (Table 1) and we tested whether the number of habitat-specific species and the number of species with different functional traits were distributed randomly across habitats and locations using χ^2 statistics. For the across-locations comparisons, the expected value was the average across locations and for the across-habitats comparisons the expected value was the average across habitats at each location.

Habitat-homogenization effects

Initially a simple comparison was conducted at each site between the predictions of species richness across all habitats based on a reduced number of habitats. Two of the more complex habitats were selected for removal

(habitats 1 and 3 in TIMR and 4 and 6 at KB, see Table 1). These habitats had long-lived surface-dwelling species that are expected to be susceptible to trawling or sedimentation impacts (Thrush and Dayton 2002, Thrush et al. 2004). The habitats were converted into already-existing simpler ones in our data sets, thus preserving the number of samples available.

However, the scale at which habitats are defined and the relative proportions of species specific to one or a number of habitats vs. habitat-generalist species are clearly important influences on species loss associated with habitat homogenization. To investigate the role of these processes we developed a simple model consisting of 10 habitats that contained both species that are specific to a single habitat and species that are common to all habitats. The species richness associated with increasing number of habitats was modeled as

$$S(k) = S_{\text{end}}(k) + S_{\text{com}}(k) \quad (1)$$

where S is species richness (normalized to 100 species) for each of k habitats, S_{end} is species richness due to endemic species, and S_{com} is species richness due to species common in all habitats and k ranges from 1 to 10. S_{end} is the expected number of habitat-specific species in a random selection of k habitats and, given that each habitat can occur equally often, is defined as

$$S_{\text{end}}(k) = H \frac{k}{10} \quad (2)$$

where H is the number of habitat-specific species found across k habitats.

S_{com} is calculated assuming a saturation curve for the number of observed common species (C) in a random selection of k habitats ($k = 1, \dots, 10$) of the form

$$S_{\text{com}}(k) = C(1 - e^{-\mu k}) \quad (3)$$

where μ is a constant (in our simulations $\mu = 0.4$).

Homogenization of an area was modeled as a reduction in the species richness resulting in a corresponding reduction in the variability in species composition. The species accumulation curves were calculated for a random sample of 1-to-10 habitats with increasing removal of species in communities with varying proportions of the number of habitat-specific species (i.e., 0, 0.2, 0.4, 0.6, 0.8, 1.0).

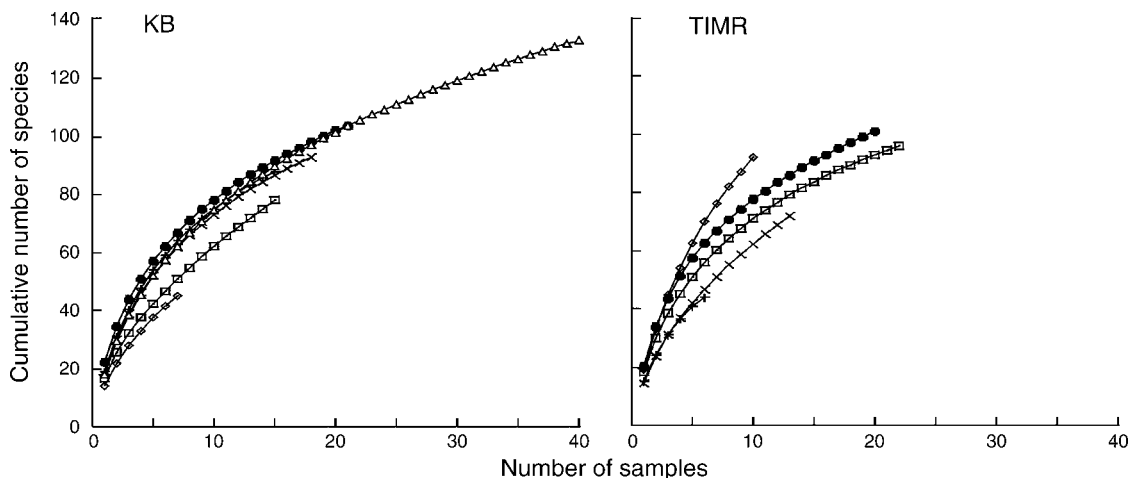


FIG. 2. Species accumulation curves for the six habitats in Kawau Bay (KB) and the five habitats in Tonga Island Marine Reserve (TIMR) reveal differences in species diversity with habitat type in the two locations.

RESULTS

Species richness-habitat predictions

We identified 194 macrofaunal taxa from Tonga Island Marine Reserve (TIMR) and 221 taxa from Kawau Bay (KB), New Zealand. Habitat-specific species accumulation curves for each location (Fig. 2) indicate important differences in the spatial variance of species richness between habitats. The broader spread of habitat-specific curves in TIMR imply large-scale habitat variability relative to the scale of sampling, while in KB the similarity in slope and proximity of habitat-specific curves implies small-scale variability relative to the scales of sampling (Ugland et al. 2005). Further evidence of the value of using habitat informa-

tion in estimates of species richness is provided by the comparison between the total-species curves and the simple randomized species-accumulation models. Although the differences between methods were slight at our sampling intensity, when extrapolated to the asymptote, the total-species curves estimated 47 and 40 more species, respectively, for TIMR and KB than the random models (Fig. 3).

Habitat-homogenization effects

In TIMR, the removal of two of the five habitats resulted in a total-species curve estimate of 133 species (61 species lost), while in KB the removal of two of the six habitats decreased richness from 222 species to 173

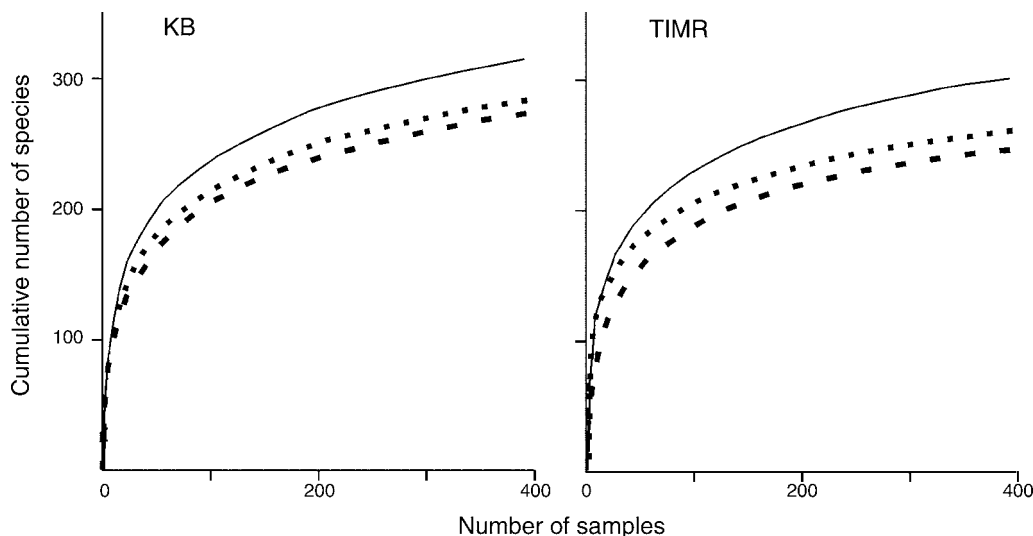


FIG. 3. Predicted species accumulation curves, for up to 400 samples, for Kawau Bay (KB) and Tonga Island Marine Reserve (TIMR) using total-species curves (solid line) and simple randomization procedures (dotted line) based on sampling all habitats. The dashed line represents the total-species curve derived by removing the two habitats most sensitive to disturbance; it reveals a distinct drop in the estimated species richness compared to that based on sampling all habitats.

TABLE 2. Percentage decreases in macrofaunal community functional attributes associated with habitat removal (habitats 1 and 3 in TIMR, and 4 and 6 at KB; Table 1).

Functional attribute	Attribute decrease (%)	
	TIMR	KB
Large species	43	35
Medium species	25	18
Small species	21	13
Epifauna	26	22
Surface dwelling (<20 mm deep)	36	30
Deep dwelling (>20 mm deep)	42	13
Found throughout sediment column (0–120 mm)	23	15
Predator/scavengers	22	21
Deposit feeders	24	24
Grazers	60	0
Suspension feeders	36	18
Highly mobile adults	21	23
Restricted-mobility adults	33	19
Sedentary adults	29	20

(49 species lost) at our sampling intensity (Fig. 3). The differential response between the two locations reflects differences in the scale of variation in species richness relative to habitat as illustrated by Fig. 2. In TIMR, 31 and 25 species were specific to habitats 1 and 3, respectively, while for KB, 18 and 22 species were specific to habitats 4 and 6, respectively (Table 1). Habitat-specific species were not distributed randomly across habitats at either location and KB had significantly fewer habitat specialists than TIMR (χ^2 statistics for within and between locations $P < 0.05$). Only 12 out of 194 species were common across all habitats in TIMR, while 9 out of 221 species were common in KB. Removal of habitats also resulted in a significant drop in the proportion of species with different functional attributes in both locations (χ^2 for each location $P <$

0.05). Habitat removal demonstrated a consistent loss of large individuals, epifauna, surface dwellers, and deposit feeders for each location (Table 2). However, TIMR tended to show larger proportional decreases compared to KB.

Our model of the relative importance of habitat-specific species vs. habitat-generalist species demonstrated variation in both the rate of species accumulation associated with the proportion of species common across all habitats and the impact of habitat homogenization on species richness (Fig. 4). It also demonstrates that these two processes interact, with decreasing proportions of habitat generalists increasing the effect of habitat homogenization on species richness. These model results are especially significant given that only ~5% of species were common across all habitats in either KB or TIMR, providing further evidence that many benthic marine species are not widely distributed (Ellingsen 2002).

DISCUSSION

Our empirical and model results highlight the fact that using habitat information to inform species–area relationships can improve our understanding of biodiversity and the application of species–area relationships in conservation or habitat management. Given the scale of anthropogenic disturbance to marine sediments, our approach helps focus conservation and management on the role of seafloor organisms in influencing their habitat’s structure and provides a useful tool to help investigate and manage the use of seafloor habitats. Generally, habitat management rather than species management is the most viable option for seafloor conservation and biodiversity management. Multi-scale integrated sampling strategies that can resolve important

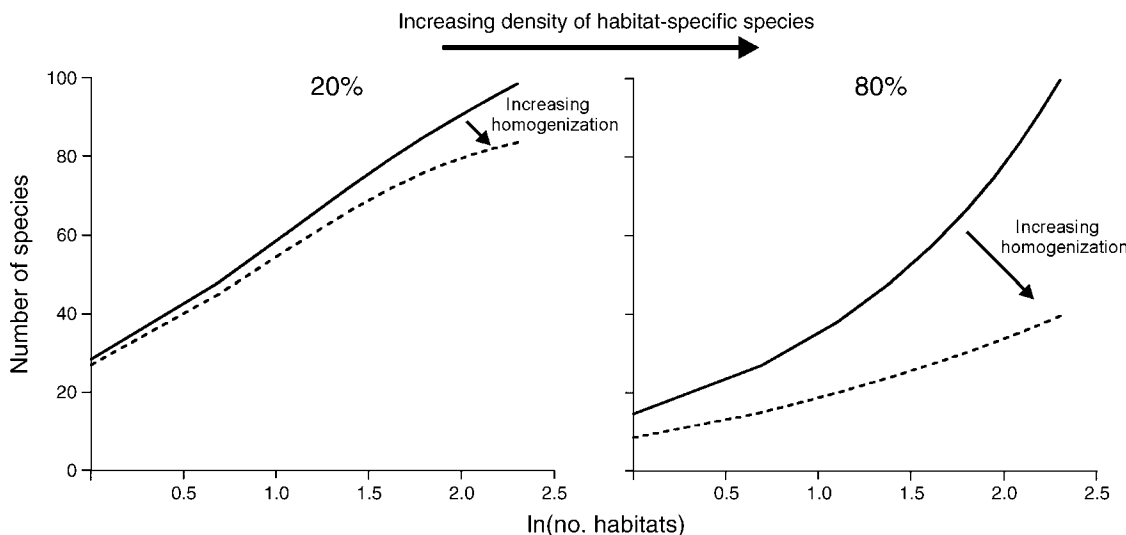


FIG. 4. Total-species curves derived from sampling modeled assemblages with 80% and 20% of species common across all habitats. While the model predicts both the rate of species accumulation and overall richness, the magnitude of the effect is dependent on the proportion of habitat-specific species.

but often fine-grained habitat structure (Zajac et al. 2003, Hewitt et al. 2004, 2005) and provide information to develop habitat-specific species–area relationships for seafloor environments is thus critical to seafloor habitat management.

Our results substantiate the importance of fine-scale biogenic, structurally complex habitats for functional diversity and species richness. The changes in the diversity of functional attributes observed in our habitat-homogenization scenarios represent important shifts likely to affect ecosystem processes. Macrofauna play important roles in regulating ecosystem processes (e.g., nutrient regeneration, carbon sequestration, and the decomposing of organic matter); in particular, large individuals often disproportionately affect fluxes and suspension feeders play important roles coupling water column and benthic processes (Snelgrove 1998, Thrush and Dayton 2002, Lohrer et al. 2004). Previous studies in both Kawau Bay and Tonga Island Marine Reserve have demonstrated that fine-scale biogenic heterogeneity is an important influence on seafloor diversity (Thrush et al. 2001, Hewitt et al. 2005). The development of habitat-specific species–area relationships and the insights gained from our model of how habitat-specific and habitat-generalist species contribute to richness help to scale up the implications of these observational studies and suggest that the distribution of species across habitats and the level of habitat specificity are important factors for predicting changes in species and functional diversity. The influence of biogenic structure on habitat heterogeneity in soft sediments is not restricted to only small spatial scales; nevertheless, the role of habitat in affecting species richness must be nested into broader-scale patterns of variation in regional species pools (Witman et al. 2004). As pointed out by Witman et al. (2004) the issue is not that processes operating at one scale may overwhelm other process, but rather the need to develop a broad perspective to understand how processes can interact across scales to create emergent patterns in species richness. In our study we were able to demonstrate the importance of habitat diversity in influencing species richness under different environmental constraints in different biogeographic regions.

A number of mechanisms have been postulated to explain species–area relationships although there remains no clear theoretical underpinning of these patterns (McGuinness 1984, May and Stumpf 2000). Despite their phenomenological nature, species–area relationships can still usefully be applied to help inform environmental issues. Accounting for habitat heterogeneity when estimating species richness, using total-species curves (Ugland et al. 2005), both gave higher estimates of richness and provided more ecologically interpretable patterns than the simple randomization procedures commonly used in terrestrial conservation. Moreover, a better accounting of habitat variation will help to explain why traditional species–area relation-

ships typically only account for 50% of the variation in species richness (Conner and McCoy 1979, Kerr et al. 2001) and help to isolate sampling effects from underlying processes. In particular, an understanding of the scaling of habitat variation relative to species richness is a prerequisite to linking habitat, not area per se, to richness, irrespective of whether the processes underlying species–area relationships relate to the relative abundance of species or self-similarity (Harte et al. 1999, Plotkin et al. 2000).

The total-species curve technique allowed us to investigate scenarios of habitat homogenization in diverse seafloor habitats. Another approach to consider the effects of habitat loss on species richness is the incorporation of geographic ranges in species–area relationships (Ney-Nifle and Mangel 2000). While both approaches emphasize the significance of habitat degradation and homogenization for biodiversity, our more empirically driven approach makes fewer assumptions and its explicit focus on definable habitats allows estimation of the effects of the removal of specific habitats. Furthermore, landscape connectivity may not depend so strongly on dispersal (mobility) for habitat generalists as for habitat specialists (Plotnick and Gardner 1993, With and Crist 1995), suggesting that models based around dispersal/geographic ranges may break down at local- to-regional scales where habitat specialists are common. Examination of biogenic habitats in TIMR demonstrated differences in the abundances of surface deposit-feeding bivalves, grazing gastropods and large predatory polychaetes as well as the highly mobile hermit crabs, cumaceans and amphipods, suggesting that the proportion of mobile species was mediated by small-scale habitat preferences (Hewitt et al. 2005).

Our approach offers a simple way of developing scenarios of habitat change and their implication for both local and regional biodiversity—a much-needed application of ecology to the management of seafloor habitats subjected to a wide range of anthropogenic disturbance regimes. Such analyses facilitate an advance from a simplistic focus on “biodiversity hotspots” to a more integrated understanding of variation in species richness and functional diversity across seafloor landscapes.

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