

A latent threat to biodiversity: consequences of small-scale heterogeneity loss

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Abstract The threat of homogenisation to biodiversity is generally considered to occur at broad scales or in response to high-intensity impacts. Therefore, most biodiversity studies estimate local average or total species richness rather than local heterogeneity. Here we consider the potential for relative shifts between these different aspects of biodiversity at small spatial scales to be an early warning signal for biodiversity loss. In response to chronic, very low-level pollution, we observed a disjunctive response with gamma diversity (total species richness) and beta diversity (heterogeneity) decreasing while alpha diversity (average species richness) was still increasing. Homogenisation may, therefore, affect biodiversity through thresholds that alter the relationship between the average species richness and its heterogeneity, leading to the potential for regime shifts. Our stressor also had a strong negative effect on rare species, meaning that the purported importance of rare species as “insurance” in the face of environmental change may be overstated.

Keywords Alpha · Beta · Biodiversity · Contaminants · Estuary · Gamma · Heterogeneity · Macrofauna · Predictions · Species-accumulation

Introduction

In response to the growing threat of biodiversity loss in nearly every ecological system (Pimm et al. 1995) many ecologists are seeking better understanding of, and improved ability to predict, the consequences of anthropogenic disturbances (Loreau et al. 2001; Naeem 2002). As biodiversity is inextricably linked to habitat diversity (Huston 1994; Guégan et al. 1998; Ricklefs and Lovette 1999; Hewitt et al. 2005; Thrush et al. 2006), habitat homogenisation is expected to be a major threat to biodiversity. Habitat homogenisation particularly endangers the rare, often habitat-specific, species that represent a large

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proportion of species richness (Gaston 1994). Homogenisation is generally considered to occur as a result of broad-scale, high-intensity impacts that remove habitats (e.g., conversion of forests to pasture) or alter them (e.g., sedimentation in estuaries resulting in extended mud flats). Therefore, most biodiversity studies do not focus on estimating local heterogeneity in diversity, instead only estimating average or total diversity.

Biodiversity is a multidimensional concept (Purvis and Hector 2000) and encompasses many scales of variation in biological organisation (from genes-to ecosystems). Despite the broad nature of this term, species diversity is one of the more commonly used attributes. Even the simplest of its measures, species richness, has three aspects, generally referred to as γ (total number of species), α (average number of species) and β (variability, heterogeneity or species turnover (Loreau 2000)). Although γ -diversity usually refers to a region and α -diversity to the scale of the sampling unit in any particular study, there is no explicit spatial scale for any of these variables. Different ecological theories also frequently emphasise different aspects of biodiversity at different scales, e.g., eutrophication and habitat homogenisation affecting γ -diversity (Velland et al. 2007), biodiversity-ecological functioning experiments focussing on α -diversity (Tilman et al. 1996; Emmerson et al. 2001; Solan et al. 2004; Hooper et al. 2005).

The relationship between stress (whether driven by physical disturbance or contaminants) and ecological responses are not necessarily monotonic, especially when stress is imposed unevenly across landscapes. At low levels of stress, asynchronous dynamics of individual patches should produce heterogeneity, with mosaics of patches of differing successional ages emerging, increasing overall species richness (Connell 1978; Huston 1979). This leads to the potential for relative shifts in average, total and heterogeneity of the number of species found at small spatial scales to be an early warning signal for biodiversity loss as a result of low levels of anthropogenic stress.

Here we investigate the relationships between α -, β - and γ -diversity along a relatively weak gradient of heavy metal contamination (copper, lead and zinc), where even the most contaminated site was well below levels assumed to have no effects (see methods). Macrofaunal communities found below the mean tide mark in intertidal sandflats were used as they are generally species rich and contain multiple trophic levels.

Methods

Intertidal sandy sites were selected along a known contamination gradient (concentration of heavy metals produced by urbanisation) within a large harbour (Waitemata, New Zealand). Previous studies at 95 sampling stations along this same contaminant gradient established strong community and single species responses to contaminants (Thrush et al. 2008b; Hewitt et al. 2009). The four sites selected for the current study occupied the lower half of this gradient (low contamination), and represented a single substrate type (fine sand). Positioning of the sites was carefully chosen to prevent correlation with other possible gradients (e.g., inundation times, wave exposure and distance to channels). The four sites varied from domination by a patchy mix of suspension- and deposit-feeding bivalves and large tube-dwelling polychaetes (the least contaminated), through domination by two bivalve species with patches of varying densities of these and shell hash, to domination by a mix of species, mainly deposit feeders and often small.

At each site, 48 macrofaunal cores (13 cm diam. \times 15 cm deep) were collected along two parallel transects (80 m length, approximately 20 m apart). Core positions were randomly allocated every 3–4 m within a 1 m strip either side of the transect lines. Between

transects, smaller cores of surface sediment (2.5 cm diam. \times 2 cm deep) were collected approximately every 15 m for contaminant analysis and to confirm that sediment grain size at the sites was similar.

Macrofaunal cores were sieved across a 0.5 mm mesh screen prior to identification and enumeration to as low a taxonomic resolution as possible (predominantly species level). Species accumulation curves were derived for each site using the jackknife technique available in Estimate S (Colwell 2006). γ -diversity for each site was determined as that predicted to be achieved by the species accumulation curve at 100 samples. Note that 100 samples was chosen as the degree of separation between the curves had largely stabilised by this point. β diversity was defined as the difference between gamma diversity and average species richness (within-site heterogeneity Lande 1996; Crist et al. 2003; Gering et al. 2003; Klimek et al. 2008). This definition, rather than γ/α (Whittaker 1960; Legendre et al. 2005; Ricotta 2008), was used as the latter more accurately represents species turnover rather than within-site heterogeneity. Species evenness, Shannon–Weiner and Simpson’s Index were calculated using Primer *E* (Clarke and Gorley 2006). Rare species (those occurring in only 1 or 2 of the 40 replicates at a site) were identified at each site. Those species that were rare at the least contaminated site were examined at each of the other sites to determine whether they continued to be rare, disappeared, or became more common.

Contaminants in the harbour were mainly those associated with storm-water inputs, which are indicated by heavy metal concentrations (i.e., copper, lead and zinc). Other contaminants (e.g., arsenic, mercury) have previously been measured at the four locations, but concentrations found to be low with minimal variation. Concentrations of total recoverable copper, lead and zinc were determined at each site using strong acid digestion of the <0.5 mm sediment fraction in aqua regia (HCl/HNO₃) at 100–110°C. As within-site variance was low, averages were then calculated for each site to be used in future analyses. Maxima of 7.1, 18.0 and 56 mg kg⁻¹ for copper, lead and zinc respectively were obtained for the sites (Table 1), values well below sediment quality guideline values considered to be rarely associated with biological affects (18.7, 30.2 and 124 mg kg⁻¹ for total copper, lead and zinc respectively (MacDonald et al. 1996)). As the effects of these three metals had previously been demonstrated to be multiplicative for some species in this harbour (Thrush et al. 2008b), a combined contamination index (CI) was derived using the equation for the first PCA axis derived from average copper, lead and zinc concentrations across 84 sites in Waitemata Harbour, as given in Hewitt et al. (2009). That is

$$CI = 0.619(\ln(x_{Cu}) - 2.426) + 0.536(\ln(x_{Zn}) - 4.383) + 0.574(\ln(x_{Pb}) - 2.897)$$

where x_{Cu} , x_{Zn} , x_{Pb} are concentrations of copper, zinc and lead, respectively, at the site. This PCA axis explained 94% of the variability.

Table 1 Total contamination index at each site together with measured sediment concentrations of copper, lead and zinc (mg kg⁻¹)

Contamination index	Copper (mg kg ⁻¹)	Lead (mg kg ⁻¹)	Zinc (mg kg ⁻¹)
1.5	3.2	4.1	14
2.6	4.1	9.9	34
3.8	4.8	15	52
4.0	7.1	11	56

Results

Obvious differences in species accumulation curves were observed between sites, with the least contaminated site exhibiting a log–log relationship, and the other three sites exhibiting linear–log relationships (Fig. 1). As a result, predicted γ -diversity for each site showed a clear negative relationship with the contaminant gradient (Fig. 2a, Pearson's $R = -0.97$, $P < 0.0001$).

Interestingly, while there was a clear negative relationship for γ -diversity with stress, no such relationships were observed for the more typically used expressions of biodiversity in impact assessments e.g., average species richness (α -diversity), evenness, Shannon–Weiner H' or Simpson's diversity indices (Fig. 2). α -diversity exhibited a unimodal curve; initially increasing with increasing contamination then decreasing as contamination continued to increase (Fig. 2b). These different relationships with stress between γ - and α -diversity resulted in high β -diversity at less contaminated sites and a strong negative linear relationship with the contaminant gradient (Fig. 2a, Pearson's $R = -0.99$, $P < 0.0001$). No relationships were obvious for evenness, Shannon–Weiner H' or Simpson's diversity indices (Fig. 2c).

The percentage of rare species at sites declined with increasing contamination from 42% to a low of 18% at the most contaminated site (Fig. 2d, Pearson's $R = -0.98$, $P < 0.0001$). However, declining percentages of rare species could be caused by either species disappearing or becoming more common due to turnover along the gradient. Investigation of the identity of which species were rare at each site revealed that only 9 of the 22 rare species found at the least contaminated site became more common at the next site along the contaminant gradient, most (11) disappeared and three continued to be rare (Table 2). The species disappearing included large, tube building or suspension-feeding polychaetes (7) as well as three small crustaceans and a small grazing gastropod. A similar percentage of species that were rare at the second most contaminated site were not found at the third most contaminated site (2 species of crabs, 3 of the larger isopods, 1 nemertean and a small deposit feeding polychaete), but fewer became common (29% cf. 41%). The

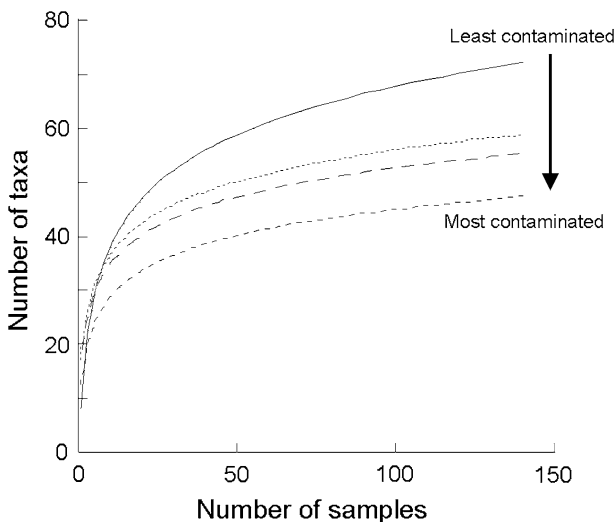


Fig. 1 Species accumulation curves calculated for the four sites

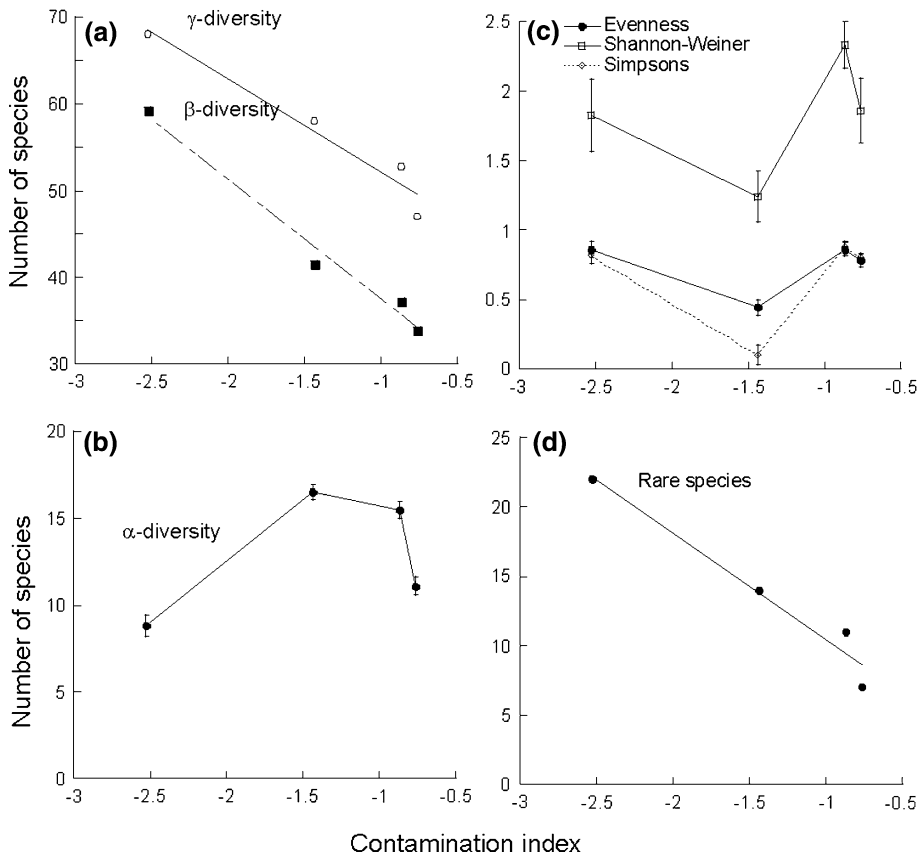


Fig. 2 Response of different aspects of biodiversity to the contaminant gradient. **a** γ -diversity, **b** α -diversity, **c** average evenness, Shannon–Weiner H' and Simpson's diversity indices and **d** number of rare species

Table 2 Effect of the contaminant gradient on rare species

Contamination index	Rare species	Not found at next site	Common at next site	Rare at next site
1.5	22	11	9	3
2.6	14	7	4	3
3.8	11	8	3	0
4.0	7			

For each site, the number of rare species found is given together with whether they were not found, were common or were rare at the next most contaminated site

majority of the species that were rare at the third most contaminated site were not found at the most contaminated site (72%). Thus, the decline in rare species actually signalled a loss of most of those species, with very few displaying robustness to the contamination gradient.

Discussion

Studies on the response of biodiversity to stress/disturbance generally focus on species richness following a unimodal response to increasing stress (e.g., Connell 1978; Hacker and Gaines 1997), and do not incorporate effects on β -diversity. However, patch theory suggests that massive stress events should override patch dynamics by re-setting all patches to the same (early) successional state (Connell and Slatyer 1977; Pearson and Rosenberg 1978; Denslow 1980), while at lower levels of stress, asynchronous dynamics of individual patches should produce heterogeneity (Connell 1978; Huston 1979). While we observed indications of a unimodal response of average species richness, we did not observe an initial increase in β - and γ -diversity, both of which were decreasing while α -diversity was still increasing. α -diversity did not begin to decrease until the ratio of γ to β was greater than 1.46.

The implications of habitat heterogeneity and habitat selectivity to biodiversity preservation are accepted (Olson et al. 2001; Hoekstra et al. 2005) and the protection of habitats and connectivity between them is a focus of many conservation networks. However, Dornelas et al. (2006) recently demonstrated that similar habitats adjacent to each other can have markedly different communities, thereby decreasing the scale at which we should consider heterogeneity to be important to biodiversity. Similarly, our results suggest that, even within a soft-sediment habitat apparently homogeneous at the 100 m scale, enough heterogeneity in species distributions can exist such that homogenisation of these can still pose a threat to gamma diversity.

Such changes to within-site β -diversity have important implications for assessing the potential for a regime shift. It has recently been suggested that regime shifts are indicated by increasing temporal variation (Carpenter and Brock 2006). Our results suggest that ecological shifts and functional impairment associated with anthropogenic stressors may be signalled at an early stage by decreasing spatial heterogeneity in biodiversity as numbers of rare species and habitat formers decrease and more of the community is represented by less vulnerable, more robust species, resulting from a strong link between spatial and temporal community dynamics (Thrush et al. 2008a). These less vulnerable species become more common, increasing α -diversity at the same time that the overall γ -diversity and heterogeneity declines (Fig. 3). Finally a threshold is reached at which α -diversity also reduces and a depauperate, homogeneous community of small, robust species begins to develop.

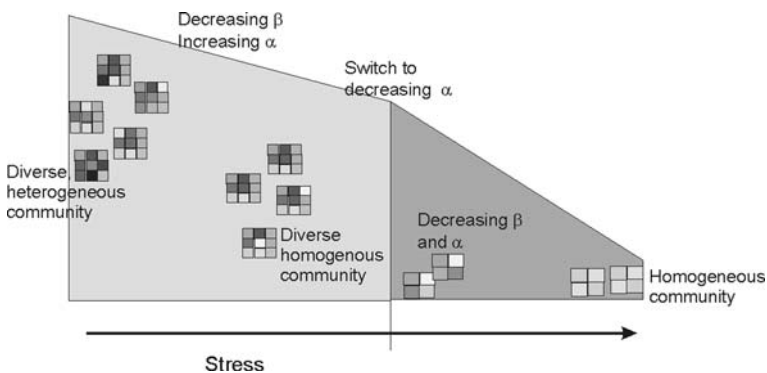


Fig. 3 Conceptual diagram of the effect of anthropogenic stressors on community heterogeneity and biodiversity

The interplay observed between α -, β - and γ -diversity has a major implication for resilience. Rare species have been implicated as providing insurance and functional resilience against change (Walker 1992; Lawton and Brown 1993; Naeem and Li 1997; Yachi and Loreau 1999). The percentage of rare species (those found in only one or two samples) we observed at our least contaminated site (42%) was similar to other figures reported for marine systems (Schlacher et al. 1998; Shin and Ellingsen 2004; Ellingsen et al. 2007). Moreover, our rare species appeared more sensitive to our stressor than many of the more common species as the percentage of rare species dropped to 18% at the most contaminated site, similar to findings by Hewitt et al. (2009), and most of the rare species found at the least contaminated site did not become more common over the contaminant gradient. This suggests that communities with a high proportion of rare species may prove less resilient, as indicated by early studies of species abundance distributions under stress (e.g., Whittaker 1975; Gray and Mirza 1979). In this case the stressor is likely to have an increasing effect, rapidly approaching a threshold, over which a regime shift occurs. As many rare species are large and often functionally important (Loreau et al. 2001; Thrush and Dayton 2002), their response to stressors is crucial for functional resilience. Our empirical results therefore give new impetus to the need to include the response of γ - and β -diversity and rare species into theoretical models predicting resilience and regime shifts and to empirical studies trying to understand the role of rare species in different systems.

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