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Ecosystem functioning in a disturbance-recovery context: Contribution of macrofauna to primary production and nutrient release on intertidal sandflats

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ABSTRACT

Although many ecologists have described relationships between biodiversity and ecosystem functioning, changes in functioning after disturbance and during recovery are not well documented. Diversity–functioning theory predicts a decline in functioning with decreased diversity (e.g., following disturbance) and a gradual increase in functioning coincident with biotic recovery. We tested this theory empirically by measuring primary production and nutrient release (indices of sandflat functioning) at three sites at the beginning, middle and end of a year-long recovery period. Although microphytobenthos stock (sediment chlorophyll *a* content) recovered quickly, rates of gross photosynthetic oxygen production were reduced in disturbed plots, relative to controls, in 7 of 9 comparisons. Plots with high macrofaunal richness had enhanced ammonium efflux, and greater efflux of ammonium likely increased rates of primary production. The site with the highest bioturbation potential, which was dominated by large bivalves, exhibited the largest decline in functioning immediately after disturbance. This site also had the most persistent treatment–control differences during recovery, probably because the large bivalves remained at low abundance in treated plots throughout the year-long experiment.

1. Introduction

The loss of biodiversity is a worldwide environmental concern, with biodiversity having been shown to contribute to the maintenance of valued ecosystem services (Costanza et al., 1997; Wall, 2004). Many ecologists are now investigating the consequences of biodiversity loss by measuring key ecosystem functions across gradients of species richness and diversity (Kinzig et al., 2002; Loreau et al., 2002; Hooper et al., 2005). Recent research has included tests over wider gradients of species diversity (Spehn et al., 2005), expansion of studies from single to multiple trophic groups (Raffaelli et al., 2002; Petchey et al., 2004), appreciation of the influence of spatial scale (Levine, 2000; Cardinale et al., 2004), and recognition of the non-randomness of species loss in natural communities (Zavaleta and Hulvey, 2004; Solan et al., 2004). The weight of evidence from the majority of such studies suggests increased ecosystem functioning with increased levels of biodiversity.

Based on these diversity–functioning relationships, the consequences of biodiversity loss are implied by moving from right to left along the *x*-axes of bivariate regression plots. Surprisingly, however, there have been few direct studies of ecological functioning performed in conjunction with marked reductions in biodiversity, even though biodiversity is known to decline sharply, for example, after intense disturbance events. Furthermore, patterns of ecological succession and recovery following disturbance are well known for a variety of ecosystem types (Begon et al., 2006), providing a solid conceptual basis for studies of ecological functioning in a disturbance-recovery framework.

The early stages of recovery following a catastrophic disturbance are the most consistent across ecosystem types: diversity is at its minimum immediately following the disturbance. Although the process of recovery may begin immediately after the disturbance, it generally takes time for the biota to accumulate in the disturbed habitat. The speed and trajectory of recovery becomes harder to predict after the earliest phase, given the many factors contributing to disturbance-recovery dynamics (e.g., the type, intensity and scale of the disturbance; the life-histories of the plants and animals disturbed; the degree of isolation of the disturbed habitat; the composition of the colonist pool; the movements of wind and water that influence colonist supply; the degree of facilitation and inhibition among colonizing species; etc.). Nevertheless, after the post-disturbance minimum, biodiversity will generally increase for a period of time (Pearson and Rosenberg, 1978; Thrush et al., 2008; Van Colen et al., 2008; Montserrat et al. 2008). Consequently, a logical hypothesis is that ecological functioning will be low following disturbance, and that

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it will increase with the gradual accumulation of individuals and species (and/or densities of particular "key" species) as the habitat recovers (Elliott et al., 2007; Van Colen, 2009; Rossi et al., 2009).

Intertidal soft-sediment systems are well suited for a test of above hypothesis because (1) they are often inhabited by rich biotic communities, (2) it is feasible to create disturbances at an appropriate spatial scale in this habitat type, and (3) evidence of recovery can be observed during a one- to two-year experiment (Thrush et al., 2008; Van Colen, 2009). Regarding the diversity of a sandflat, several trophic and taxonomic groups are represented by the macrofaunal inhabitants alone (grazers, predators, deposit- and suspension-feeders; gastropods, bivalves, echinoderms, crustaceans, polychaetes, nemerteans, cnidarians, etc.). Additionally, microscopic primary producers living at the sediment surface (collectively known as microphytobenthos) co-occur with the macrofauna, serving as their food, and oxygenating the upper veneer of the sediment column in the daytime. Aerobic and anaerobic bacteria are the principal recyclers of organic matter in soft-sediment habitats, an activity that regenerates inorganic nutrients and fuels microphyte primary production. Although microbial communities are the ones that actually decompose organic matter and transform it back into inorganic nutrients, macrofaunal activities can greatly influence the speed of bacterially-mediated processes. Furthermore, by mixing and irrigating sediments, macrofauna can alter bentho-pelagic fluxes by orders of magnitude (i.e., simple diffusion vs. non-local transport). Thus the generalized soft-sediment system is an interconnected web of trophic and biogeochemical interactions (Herman et al., 1999; Norkko et al., 2001; Solan et al., 2004; Lohrer et al., 2004; Thrush et al., 2006; Hewitt et al., 2006; Montserrat et al. 2008; Rossi et al., 2009).

We submit that rate variables, such as fluxes of oxygen and nutrients across the sediment–water interface, are valid indicators of ecosystem functioning in soft-sediment systems (Lohrer et al., 2004; Thrush et al., 2006; Hewitt et al., 2006; Norling et al., 2007). Bacteria, microphytes, and macrofauna all influence oxygen and nutrient concentrations simultaneously, via direct and indirect pathways, and fluxes are the net result of various positive and negative interactions. From fluxes of oxygen, we can determine the system's overall respiratory demand, photosynthetic rate, and status as net autotrophic or heterotrophic. By estimating the flux and uptake of key nutrients, we can examine a bottom-up driver of primary productivity in the system. Based on the importance of macrofaunal bioturbation in soft-sediment habitats, we predict that significant declines in macrofaunal abundance and diversity will reduce the provisioning of nutrients and consequently the habitat's rate of primary productivity. However, the speed and trajectory of the system's functional recovery may be affected by differing rates of recovery of component organisms. For example, benthic diatoms and other microscopic primary producers likely recover faster than the larger macrofauna (Montserrat et al., 2008, Larson and Sundbäck, 2008). We explored these issues and interactions at three sites in a northern New Zealand estuary, where patches of intertidal sandflat were experimentally disturbed.

2. Methods

Experimental disturbance treatments were established in the same way, at the same time, at three intertidal sites in Mahurangi Harbour, North Island, New Zealand (36°29′ S, 174°42′ E). The three sites (BB, UNB and PIS) varied in sediment type, hydrodynamic regime and macrofaunal community structure (Thrush et al., 2008). BB and UNB were on opposite sides of the main harbour channel and PIS was in a separate arm of the estuary. UNB was the muddiest sandflat, with crab burrows (*Macrophthalmas hirtipes*) present every few metres. Cockle shells (*Austrovenus stutchburyi*) and associated shell hash were dominant at PIS. The BB site was characterised by homogenous firm sand with polychaetes and wedge shells (*Macomona liliana*).

At each site, alternate treatment and control plots (9 m^2, $n=3$), separated by about 5 m, were established at the mid-tide level. Treatment plots were defaunated (smothered) by covering the sediment surface with polythene plastic sheets, which were weighted down with concrete tiles (Thrush et al. 2008). Treatment plots were established on November 24th and the polythene was left to smother the sediment until January 12th (mid-summer). Detailed sampling of defaunated and control plots at each site began 1 day after the polythene was removed. Macro-invertebrates and sediment properties (granulometry, chlorophyll *a* and organic matter content) were assessed on 9 occasions between 13-January-2005 and 9-February-2006 (Thrush et al., 2008).

Additional benthic parameters (including oxygen and nutrient fluxes) were studied on 3 occasions to gauge the recovery trajectories of biogeochemical processes integral to sandflat functioning. The first of these detailed sampling events came 3 weeks after the treated plots were uncovered and exposed to oxygenated seawater (4-February-2005). Although it was possible for some macrofaunal recovery to occur during the first 3 weeks of the experiment, it was important to wait for redox gradients to re-establish before making initial biogeochemical measurements, particularly as sediment oxygen levels influence biogeochemical transformations and our method of defaunation involved oxygen deprivation (smothering). The same sets of measurements were made at the three study sites on two more occasions (7-June-2005 and 9-February-2006). Thus, balanced data sets were obtained at the beginning, middle and end of the recovery period, with the first and last dates coming one year apart during summer.

To measure fluxes of oxygen and nutrients across the sediment–water interface, we placed two benthic chambers–one light and one dark–in each of the six plots per site. The sediment area covered by each chamber was 0.016 m^2, with space for ~0.85 l of seawater above the sediment–water interface. Tubing was connected to the chambers to enable sampling during tidal immersion (tube length ~180 cm). In addition, we collected a sample of ambient bottom water each time the chambers were sampled ($n=1$ $site^{-1}$), and we assessed water column oxygen and nutrient dynamics at each site using light and dark bottles ($n=1$ $site^{-1}$, incubated *in situ*, concurrent with chamber deployments).

Fluxes of oxygen and nutrients were quantified by measuring changes in chamber water chemistry during incubation. Here, flux calculations were based on initial and final chamber water samples. On all three sampling dates, low neap tides occurred in the early morning and the incoming water began covering the experimental plots between 10:00 and 13:00 h. When the water depth at a site reached ~30 cm on the incoming tide, chambers were flushed with ambient seawater and placed on the seabed. To cleanse all tubes and sampling ports, approximately 150 ml of water was pulled through the chamber system and discarded before an initial sample of 60 ml was collected and saved. Collection times were recorded, and all 12 chambers per site were sampled in the span of about 15 min. Final samples were collected at higher tide, after incubations of 3–4 h during peak sunlight. Seawater present in the sampling tube (~20 ml) was discarded before a final 60 ml water sample was kept.

As soon as sampling was complete, levels of dissolved oxygen (DO) were measured with a YSI model 5730 BOD bottle probe. Water samples were filtered immediately thereafter (1.1 μm pore size Whatman GF/C glass fibre filter). All samples were kept in darkness and stored frozen until analysis. Analysis for ammonium nitrogen (NH_4^+–N), nitrate-plus-nitrate nitrogen (NO_3^-–N + NO_2^-–N, hereafter NO_X–N) and dissolved reactive phosphorus (DRP, mainly HPO_4^{2-}–P) was performed in the laboratory using standard methods for seawater (Grasshoff et al., 1999) on an AlphKem series 500 air-segmented continuous flow auto-analyser with detection limits of <0.1 μmol l^{-1} for N and P.