Experimenting with ecosystem interaction networks in search of threshold potentials in real-world marine ecosystems

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Abstract. Thresholds profoundly affect our understanding and management of ecosystem dynamics, but we have yet to develop practical techniques to assess the risk that thresholds will be crossed. Combining ecological knowledge of critical system interdependencies with a large-scale experiment, we tested for breaks in the ecosystem interaction network to identify threshold potential in real-world ecosystem dynamics. Our experiment with the bivalves *Macomona liliana* and *Austrovenus stutchburyi* on marine sandflats in New Zealand demonstrated that reductions in incident sunlight changed the interaction network between sediment biogeochemical fluxes, productivity, and macrofauna. By demonstrating loss of positive feedbacks and changes in the architecture of the network, we provide mechanistic evidence that stressors lead to break points in dynamics, which theory predicts predispose a system to a critical transition.

Key words: Austrovenus stutchburyi; *bifurcations; bivalves; break points; ecosystem dynamics;* Macomona liliana; *Manukau Harbour, New Zealand; marine sandflats; thresholds; turbidity.*

INTRODUCTION

Many changes in ecological systems are abrupt, profoundly limiting our understanding of ecosystem dynamics, and our ability to predict changes and cope with the consequences (Carpenter et al. 2001, Scheffer et al. 2001). Concern about crossing regional- and global-scale thresholds underscores the need to better define the risk of tipping an ecosystem into ecologically and socioeconomically unfavorable states (Brook et al. 2013). Theories of how critical transitions lead to threshold change in ecological systems have progressed rapidly, but empirical support is patchy and often focused on specific systems, restricting generality (Kéfi et al. 2013).

A number of techniques have been developed to identify the statistical properties of time series or spatial patterns that precede thresholds (Dakos et al. 2012, Scheffer et al. 2012). These techniques represent a valid way of ranking different systems in terms of their predisposition to approaching and crossing thresholds, but for real-world ecosystems, this requires significant investment in high-frequency monitoring that is generally uncommon (Hewitt and Thrush 2010, Lindegren et al. 2012). Consequently, alternative and complementary approaches are needed to inform decisions about the risk of upcoming transitions in ecosystems and change in ecosystem functionality and value.

The only way to conclusively detect a threshold is to cross it (Carpenter et al. 2001). Such a shift may result from excessive environmental forcing, the functional extinction or invasion of species, but may also occur well below these limits due to changes in the architecture of interaction networks that connect the biological, chemical, and physical components in the ecosystem (Scheffer et al. 2001). The loss of positive feedbacks is particularly important in shifting the system into a fundamentally different state (Scheffer et al. 2012). Such shifts in the architecture of ecosystem interaction networks have been detected along environmental gradients, suggesting the potential for critical transitions (Thrush et al. 2012). Whole-lake experimental manipulations have provided empirical evidence of the importance of positive feedbacks and regime shifts (Carpenter 2003). However, questions remain as to whether we can experimentally manipulate an open and dynamic marine system to
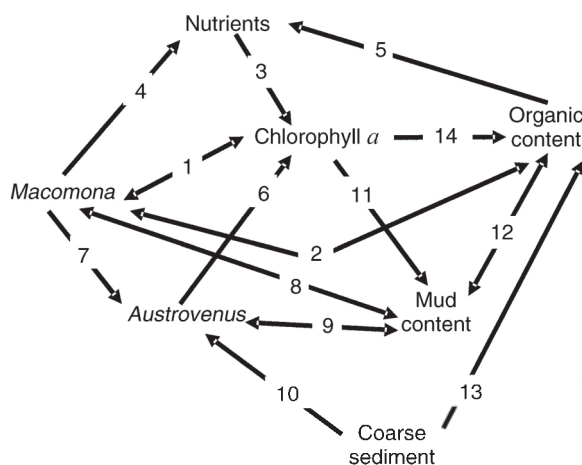
Fig. 1. Conceptual diagram of the potential interaction network linking infaunal bivalves (here marine species *Macomona liliana* and *Austrovenus stutchburyi* in New Zealand) to benthic chlorophyll *a* and sediment characteristics. (1) Grazing by deposit-feeding *Macomona* affects microphytobenthos (MPB, represented as chlorophyll *a*), and MPB has a positive relationship with *Macomona* density. (2) Sediment organic content increases food resources for *Macomona*. (3) MPB are highly productive and exploit nutrients remineralized in sediments. (4) *Macomona* affect pore water nutrient concentrations directly and (2, 5) indirectly. (6) *Austrovenus* has a positive effect on MPB. (7) Large *Macomona* and small *Austrovenus* interact negatively. (8, 9) Sediment mud content negatively affects density of both bivalve species; high densities of both species can increase fine-sediment erosion. (10) In coarse sediments, *Austrovenus* density increases. (11) MPB and mud content have a positive relationship, (8, 9) mediated by resident macrofauna. (12) Mud and sediment organic content are tightly correlated and (13) coarse sediments influence sediment organic content by increasing permeability and decay. (14) Degrading MPB also contributes to sediment organic matter, which (5) is positively correlated with nutrient concentration in pore water through microbial degradation. See *Methods* for further details and references.

demonstrate changes in interaction networks and the loss of positive feedbacks. We provide a path to address critical transitions that facilitate a formal linkage between empirical and theoretical study of ecosystem dynamics. As predicted by theoretical studies, our experiment demonstrates that stress-induced changes in ecosystem interaction networks can occur in real-world ecosystems, and this allows us to determine whether or not a specific ecosystem is predisposed to undergo transitions. Such empirical demonstration helps to ground theory and provide real-world advice to support managers, policy makers, and society about the limits to resilience of ecosystems under change.

There is a long history of ecological experimentation in marine systems, with early recognition of the role of interactions among species and disturbance influencing community dynamics (Dayton 1971, Woodin 1978). New analytical techniques allow us to assess the strength of both direct and indirect effects, define the architecture of interaction networks, and assess its validity relative to empirical data (Grace et al. 2012). Structured equation

models (SEMs) allow us to integrate causal and exploratory techniques, beginning with the development of a conceptual model supported by empirical evidence.

Our conceptual model (Fig. 1) is focused on interactions among primary producers, two sediment-dwelling bivalves (the deposit feeder *Macomona liliana* and the suspension feeder *Austrovenus stutchburyi*), sediment type, and pore water nutrient and organic matter pools, justified by empirical research and knowledge of ecosystem functioning. The potential for interaction between these variables and analogous species is typical of shallow, non-eutrophic, coastal and estuarine sandflat systems. This interaction network has some of the same elements as those previously used to look for thresholds across environmental gradients (Thrush et al. 2012). The conceptual model represents an ecosystem interaction network that supports coastal ecosystem services associated with habitat stability, nutrient recycling, and productivity (Barbier et al. 2011). In this paper we test for changes in the architecture of the ecosystem interaction networks (Fig. 1) associated with decreased light levels, an important consequence of increased turbidity in coastal ecosystems. We developed SEMs based on experimental data derived from either shaded or unshaded experimental plots. Changes in land use often elevate terrestrial sediment and nutrient loading in many estuarine and coastal ecosystems. Elevated turbidity is generally recognized because of its negative effects on seagrass (Duarte 2002), whereas effects on microphytobenthos are often overlooked despite their central role in primary productivity, nutrient interception, and basal food resource provisioning for many benthic invertebrates.

Methods

SEM starts with the definition of the potential interaction network (numbered effects discussed here refer to numbers in the Fig. 1 network). Specifically, (1) there is a direct negative effect of the large deposit-feeding *Macomona* on microphytobenthos (MPB; represented as chlorophyll *a*) due to grazing (Lelieveld et al. 2003). MPB are an important food source for *Macomona*, but there is also a positive relationship between chlorophyll *a* biomass and *Macomona* density (Thrush et al. 2006). Similarly, (2) sediment organic content increases the food resources for *Macomona* (by analogy to the functionally similar species *Macoma balthica* [Peterson and Skilleter 1994]). (3) MPB are highly productive (Cahoon 1999) and rely on nutrients remineralizing in sediments to sustain that production (Lohrer et al. 2004). *Macomona* affects pore water nutrient concentrations directly (4) and indirectly (2 and 5) through influencing organic matter pools via grazing and behaviorally induced pressure gradients in permeable sediments (Volkenborn et al. 2012, Woodin et al. 2012). (6) *Austrovenus* has a positive effect on chlorophyll *a* (Thrush et al. 2006), although this effect is density dependent (Sandwell et al. 2009, Lohrer et al. 2011). (7) Negative interactions between large *Macomo-*

na and small *Austrovenus* have specifically identified (Thrush et al. 1996). (8 and 9) Densities of both bivalve species are negatively impacted by mud (Thrush et al. 2003, 2004), but high densities of both species can increase the erosion of fine sediments by bioturbation (Thrush et al. 1996, Jones et al. 2011). (10) In coarse sediments, *Austrovenus* density increases (Thrush et al. 2008). (11) A positive relationship between benthic chlorophyll *a* and sediment muddiness exists (Van de Koppel et al. 2001), due to fine-sediment binding by MBP, a relationship (8 and 9) mediated by resident macrofauna (Van Colen et al. 2013). (12) Mud and sediment organic content are tightly correlated (Sloth et al. 1995) and (13) coarse sediments influence sediment organic content by increasing permeability and accelerating decay rates (Huettel and Rusch 2000). Degrading chlorophyll *a* (14) also contributes to the pool of organic matter in the sediment (Ehrenhauss et al. 2004), and (5) the concentration of pore water nutrients is positively correlated with the sediment organic content through microbial degradation processes (Sloth et al. 1995, Grabowski et al. 2011).

The experiment was conducted at Wiroa Island, Manukau Harbour, New Zealand (37°01.3′ S, 174°49.2′ E; see Plate 1). The intertidal sandflat is ~1.8 km wide and has a shallow gradient of 0.097° (Thrush et al. 1997). The macrofaunal community of the Wiroa Island sandflats is dominated both numerically and in terms of biomass by the tellinid *Macomona liliana* (~100/m^2 for individuals with shell length >20 mm), and the venerid *Austrovenus stutchburyi* (~32/m^2 for individuals with shell length > 10 mm). To investigate differences in the architecture of the ecosystem interaction network, we experimentally manipulated nutrient concentrations, *Macomona* densities, and light. The experiment was established on 25–29 October 2011 in seven blocks that encompassed about 800 × 350 m of sandflat. Experimental plots (2 × 2 m) were situated about 3 m apart in three rows to encompass an area of about 56 m alongshore and 14 m downshore. The experiment consisted of three density treatments of *Macomona* (200, 50, and 0 individuals/m^2 for individuals with shell length > 20 mm) crossed with three light treatments (shade, shade control, and open) crossed with three nutrient addition treatments (high, medium, none) and one ambient sediment treatment. This resulted in 28 experimental treatments, replicated once per block.

The central 1 m^2 in each 4-m^2 plot, excluding one treatment of ambient sediment, was excavated to 18 cm depth and the sediment sieved on 10-mm mesh to extract shell hash and large macrofauna. Sediments were then returned to the excavated plots and *Macomona* (>20 mm shell length) were spread evenly across the 1 m^2 achieve treatment densities.

Shade cloth designed to cut ~70–80% of the incident light was supported on a 4-m^2 metal grid (mesh size 150 × 150 mm) suspended 15–20 cm above the sediment surface. Shade controls were the metal grid only

covering the plots. Shading of plots was used to mimic changes in light levels due to elevated suspended sediment concentrations, SSC (Billerbeck et al. 2007). Direct field-based manipulation of SSC is very difficult in the medium to long term. Although SSC has multiple effects on the benthos (Thrush et al. 2004), we focused on effects mediated through the MPB. Benthic chlorophyll *a* is a measure of MPB standing stock, not productivity. This is important in the interpretation of our experiment due to the potential for bedload transport of MPB under shaded plots, potentially weakening treatment effects.

Nutrient addition consisted of adding four (high), one (medium), or zero 10 cm long sections of dialysis tubing filled with 15 g (±0.1 g) of a granular slow-release fertilizer (nutrient ratios: 18.9 N, 2.1 P, 0.0 K, 4.1 S, 3.0 Mg, 7.2 Ca). Our nutrient addition treatments were expected to have a direct stimulatory effect on MPB, because New Zealand sandflat studies show that MPB respond to nutrient released from the sediment as a result of bioturbation (Rodil et al. 2011).

Before destructive sampling at the end of the experiment (about +100 days, 7–10 February 2012), pore water nutrients samples were collected from each plot using reservoirs sampling the permeable sediments 5 cm below the sediment–water interface. Pore water was pressure-filtered through a 2.5-cm Whatman GF/C glass fiber filter in a Swinnex filter holder (ED Millipore, Billerica, Massachusetts, USA) and stored on crushed ice in the dark for transport to the laboratory, where they were frozen to –20°C pending analysis. Analysis for dissolved inorganic nutrients followed standard methods for seawater using an Astoria-Pacific 300 series segmented-flow autoanalyzer (Astoria-Pacific, Clackamas, Oregon, USA) with detection limits of <0.1 μmol/L for N and P. Three cores (2.3 cm diameter, 2 cm deep) were collected from each plot and were pooled for chlorophyll *a*, sediment particle size, and organic content analyses. The remaining sediment within the central 1 m^2 was excavated to a depth of about 15 cm and sieved on 10-mm mesh to extract large macrofauna, which were then identified and sized.

Sediment for chlorophyll analysis was freeze-dried and homogenized. A small quantity of sediment (~0.1 g) was soaked in 10 mL of MgCO$_3$-buffered acetone (90%) for ~20 h. Samples were shaken after 12 h and again prior to centrifugation. Samples were centrifuged for 10 min at 3300 rpm before fluorometric analysis (Turner 10-AU, Turner Designs, Sunnyvale, California, USA). An acidification step (0.15 mL 0.1N HCL) was used to separate phaeophytin from photosynthetic pigments (Arar and Collins 1997). Total organic matter content (as a percentage) was determined through loss on ignition from homogenized dried sediments (105°C for 24 h or until stable mass), after combustion for 5.5 h at 550°C (Dean 1974). Sediments for particle size analysis were digested in 10% hydrogen peroxide to remove organic matter, until bubbling ceased before using the

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PLATE 1.   Outplanting *Macomona* in one of the experimental plots on the sandflat (Wiroa Island, New Zealand). Photo credit: Rachel J. Harris.

standard operating procedure for marine sediments on a Malvern mastersizer-S (300 FR lens; Malvern Instruments, Malvern, UK) to determine grain size fractions in the range of 0.05–2000 μm.

SEMs were developed using M-Plus software (Muthén and Muthén 2007), based on Fig. 1, to contrast the networks apparent in the shaded and unshaded experimental treatments. We developed best-fit models for shaded and unshaded treatments and compared these with the results from applying the best shaded network to the unshaded data and vice versa, in order to ensure that there were real differences in the networks. Data transformations ($\log_e$) to improve the linearity of responses, or normality of errors, were utilized for bivalve abundances, coarse sand, and mud. The initial SEM (Fig. 1) was examined for respecification by removal of direct pathways based on parameter tests of significance, while maintaining nonsignificance tests for goodness of fit (χ^2) and the root mean square error of approximation, increasing values of the comparative fit index (above 0.95) (Vile et al. 2006) and decreasing Akaike's information criterion (see Appendix). The sensitivity of the model to new direct pathways was also investigated, with the decision on whether or not to include new links being based on parameter significance tests and no decreases in goodness of fit (Grace et al. 2012).

RESULTS

Consistent with using SEM as a tool to integrate causal and exploratory techniques (Grace et al. 2012), we have not focused on the more traditional analyses of the experimental data. Preliminary analysis did not indicate any experimental artefacts associated with shading (see Appendix). Treatment differences in *Macomona* density were maintained in the experiment, although slightly higher densities in shaded plots were apparent, while *Austrovenus* decreased. Lower pore water NO_x concentrations were found in higher *Macomona* density and zero nutrient addition treatments. Pore water dissolved reactive phosphorus concentrations were significantly and negatively related to *Macomona* density, but not nutrient addition. No significant differences in benthic chlorophyll *a* concentration or pore water ammonia concentrations were detected. Although mean benthic chlorophyll *a* concentrations in the shaded plots were low, high variability limited the detection of significant differences (see Appendix).

Shading drastically changed the nature of the interaction network (Fig. 2). In the unshaded treatments, there were a total of 13 interactions; although three were weak ($P > 0.15$ for estimates), they were required for model stability. A positive feedback loop was identified between *Austrovenus*, benthic chlorophyll
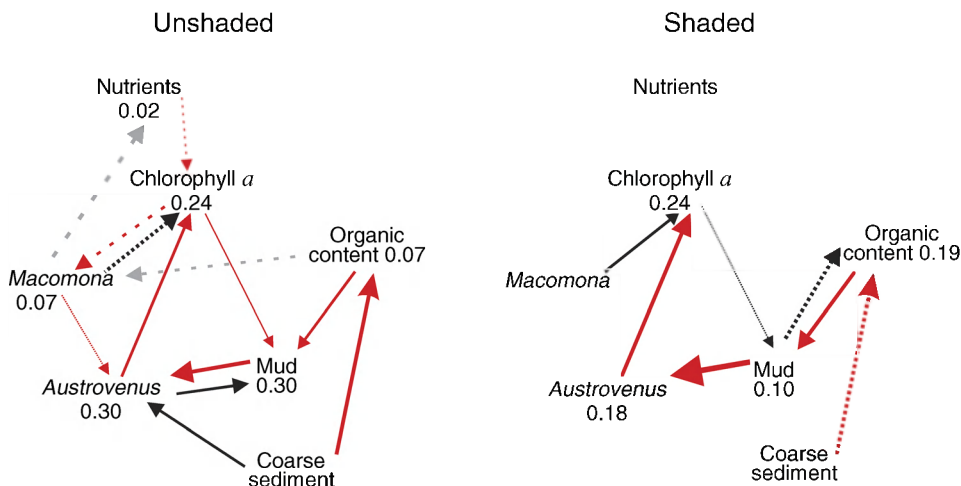
FIG. 2. Changes in ecosystem interaction networks associated with experimental shading, showing R^2 values for each factor. Red arrows indicate positive effects, black lines indicate negative. Solid lines denote parameter estimates with $P < 0.05$; dotted lines with P values 0.05–0.15; dashed lines with $P > 0.15$, but the relationship needs to be retained in the model for stability. Line thickness increases with the size of the parameter estimate, standardized by the relevant range standardization procedure (Grace et al. 2012); actual values are presented in the Appendix.

a, and mud. A positive coarse sediment–organic matter link fed into this positive feedback loop. Another weak positive feedback loop involving *Macomona* releasing nutrients to support chlorophyll standing stock fed into the stronger feedback loop.

In contrast, in the shaded plots, only seven connections were made and there were no positive feedbacks. The positive feedback between *Austrovenus*, benthic chlorophyll a, and mud was broken at the link between benthic chlorophyll a and mud, which was now negative, and the positive effect of *Macomona* on *Austrovenus* was also lost. Additionally, the negative effect of *Macomona* on benthic chlorophyll a was now significant and the positive effect of chlorophyll a on *Macomona* had been lost. Although both bivalves play a central role in the interaction network under ambient light, when the sediment is shaded, their role, and in particular the positive feedbacks, are not apparent. Under shaded conditions, we see mostly simple unidirectional relationships between biological and physical variables, with no role for nutrient additions.

DISCUSSION

Our empirical evidence of a break point is consistent with theoretical predictions of a system predisposed to a threshold shift, which would occur in response to changes in sediment loading and eutrophication. These stressor-induced changes imply important shifts in ecosystem interactions that determine organic matter degradation, nutrient recycling, and productivity that drive the functional capacity of coastal soft sediments.

The reconfiguration of the interaction network, as a result of shading, occurred in about 100 days and resulted in the loss of positive feedbacks both directly by linking large *Macomona* with MPB and indirectly

mediated through large *Austrovenus* (Fig. 2). In addition, the nutrient additions mediated the interaction between *Macomona* and MPB only in the unshaded sediments. Although mean MPB was lower in shaded treatments, high variability precluded detecting a significant difference. An important factor on this sandflat is the bedload transport of surficial sediments and associated MPB (Turner et al. 1997). This process provides a mechanism to resupply MPB to shaded sediments and add variability to our data. Nevertheless, our experiment was able to detect significant changes in the ecosystem interaction network. At the scale of our experiment, the mechanisms of change induced by large *Macomona* are behaviors (bioturbation, feeding, gill cleaning, gut voiding) that affect pore water oxygen concentrations and nutrient cycling (Volkenborn et al. 2012). Mediation of the effects of nutrient additions by large bivalves only in unshaded plots highlights the potential for cumulative effects associated with increased turbidity and eutrophication.

SEMs revealed that shading the sediment decoupled the ecosystem role of *Macomona* in sediment biogeochemistry. The range of data encompassed in model building is important in generalizing the SEM. Although the differences in environmental conditions encompassed in this experiment were subtle, the interaction network models developed from this experiment were similar to those previously developed from broadscale surveys of large bioturbating fauna, sediment grain size, organic characteristics, and benthic chlorophyll a (Thrush et al. 2012). The previous analysis revealed shifts in network architecture across a benthic chlorophyll a threshold of 11.6 µg/g chlorophyll a. Despite the smaller range of data in our more recent experiment, a similar threshold was detected, implying that the

networks are reasonably stable and consistent. Fundamental shifts associated with a loss of positive feedbacks and restrictions in the importance of indirect effects were apparent in both this experimental study and the previous broadscale analysis. Providing empirical information to define how a set of ecosystem components are connected in an interaction network helps to elucidate ecosystem function. Moreover, if specific types of connections are present, but can be changed by particular stressors, this provides a useful means for predicting the risk of critical transition related to a specific type and magnitudes of stress. It also allows insight into ecosystem function after the transition. Although there is often a gap between theory and practice, we have been able to experimentally shift the architecture of an interaction network, providing more impetus for scientists and managers to use these indicators of critical transitions. Our results show that well-designed and scaled manipulative field experiments can contribute to identifying warnings of increased risk for upcoming ecosystem transitions by testing for changes in interaction networks. For example, specific experiments manipulating the level of shading could be designed and implemented in different locations to define key break points for resource management. Shifts in functional performance associated with shading may not be gradual if interaction networks fundamentally shift. In our experiment, we see changes associated with interactions that affect key attributes of the system ranging from primary productivity and the stabilization of fine sediments to the ability of the system to recycle key nutrients. This indicates that the maintenance of community function plays critical roles in the resilience of sandflats to elevated suspended-sediment concentrations and eutrophication.

Change associated with non-point-source land use, sediments, and nutrients are notoriously difficult to manage. However policies that generate inertia and are blind to other surprises are dangerous and ultimately may be very costly in terms of the loss of ecosystem services and associated societal values (Horan et al. 2011). This is why the risks of threshold shifts are important. If not properly accounted for, our futures may be marked by sudden, unexpected reductions in ecosystem functionality and value. If there is a credible risk that a particular system can change in a nonlinear way associated with subtle but cumulative stress, then management down to a predetermined limit will be highly risky. Our approach of investigating the architecture of ecosystem interaction networks, and how they are changed by stressors, provides real-world empirical evidence to support many of the theoretical developments in regime shifts and resilience. This will allow us to more tangibly understand the implications of thresholds in ecosystems that affect our daily lives. Although we cannot yet predict when break points in dynamics will occur, our approach does identify mechanistic links and the key connections between ecosystem elements that will facilitate interventions. Such interventions are important in averting regime shifts, especially where the drivers of change are difficult to adjust or generate huge legacy effects (Biggs et al. 2009).

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SUPPLEMENTAL MATERIAL

Appendix

Description of experimental effects and potential artifacts and base statistical tables structured equation modeling (*Ecological Archives* E095-127-A1).