UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

Ocean and Earth Sciences

Species compensatory responses and biodiversity-ecosystem function relations

by

Matthias Schmidt Thomsen

Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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Anthropogenic activities affect ecosystems and alter community dynamics and species interactions, which can have with significant consequences for biodiversity-function relations. Current knowledge on the role of biodiversity in mediating ecosystem processes and functions is largely derived from controlled, biodiversity manipulation experiments. However, these studies rarely account for species compensatory responses that potentially represent an important ecological response to perturbations in natural systems. Incorporating species compensation into empirical studies or predictive models has the potential to fundamentally change perceptions of the ecosystem consequences associated with changing biodiversity, but has received little attention.

Here, I explicitly incorporate aspects of biodiversity change that have not previously been included within the biodiversity-ecosystem function framework. By adopting a range of approaches, including trait-based models, laboratory-based mesocosm experiments and field observations, I explore the role of compensation in marine benthic communities. Results show that scenarios of species loss that include community compensatory responses are fundamentally different to those where response mechanisms are excluded. However, the ecosystem consequences of compensation depend on the type and expression of compensation. I demonstrate that the functional traits of the species driving the compensatory response, and their relative abundance within the community, is highly important in determining the functional outcome of altered biodiversity. Although, a consistent feature across communities, irrespective of the driver of perturbation, the functional consequences of compensatory responses are also dependent on environmental context.

The general paradigm that emerges is that compensatory responses exist in natural systems and are likely to alter the form of biodiversity-function relations, leading to changes in ecosystem properties that differ from current expectation. I conclude that, in order to project the ecosystem consequences of anticipated levels of biodiversity change, it will be necessary to acknowledge the role of compensation in natural systems to ensure the benefits that ecosystems provide society are sustained.

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Academic Thesis: Declaration of Authorship

I, Matthias Schmidt Thomsen declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

Incorporating compensation effects into predictive models of shelf sea biodiversity-ecosystem.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

Thomsen, M. S. et al. Consequences of biodiversity loss diverge from expectation due to post-extinction compensatory responses. Scientific Reports, 7, 43695; doi: 10.1038/srep43695 (2017).

Signed: ....

Date: ....

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Chapter 1: General Introduction

1.1 Introduction

Current trends in human activity, from development, land use and resource exploitation, place unprecedented pressures on ecological systems on a global scale (Butchart et al. 2010, Halpern et al. 2008). Such pressures alter and reconfigure the web of interacting species (Barnosky et al. 2011, Brook et al. 2008, McCauley et al. 2015, Elahi et al. 2015) that are essential for the supply of goods and services to human society (Cardinale et al. 2012, Isbell et al. 2017). Play a crucial role in the mediation of ecosystem processes (e.g. decomposition) and functions (e.g. resource capture, primary and secondary production; Balvanera et al. 2006, Roher et al. 2016), which in turn regulates the flux of materials and energy (nutrients and biomass) as well as the provisioning of ecosystem services (e.g. production of floral and faunal biomass, water purification, soil formation retention and fertility, and regulation of pathogens and climate; Chapin et al. 2000, Diaz et al. 2006, White et al. 2010). The exacerbating impact on biodiversity at local and global scales has prompted concern regarding the imperilment of ecosystem function and associated services to society, upon which human standard of living depends (Millenium Ecosystem Assessment 2005, Hooper et al. 2005, Cardinale et al. 2012, Mulder et al. 2015).

Such changes in ecosystems are not limited to various aspects of biodiversity alone, but simultaneously affect many levels of ecological organization (Fussmann et al. 2014). While the effects of change are mediated through the response of individuals (e.g. physiological changes), depending on life history, changes in consumer-resource (Woodward et al. 2010, Fussmann et al. 2014) or predator-prey interactions are key mechanisms through which change affects populations and entire ecosystems (Sydeman et al. 2015). Reconfigurations of foraging constraints by for example, climate change or species invasions, can modify abiotic conditions (e.g. lightscape or habitat structure; Thomsen et al. 2011, Langbehn and Varpe 2017), leading to a weakening, complete relief, strengthening and/or the development of novel foraging constraints, influencing predator behaviour. Modifications of trophic interactions in response to change can alter bottom-up control through primary productivity and top-down control (e.g.; via vision-based foraging; Langbehn and Varpe 2017), which can have consequences for the structure, stability and functioning of food webs (Yvon-Durocher et al. 2011, Petchey et al. 1999, Binzer et al. 2016, O’connor et al. 2009, Schwarz et al. 2017, Ripple and Beschta 2012, Schmitz et al. 2004). However, individual-level responses and associated niche shifts to biodiversity change can adversely affect species’ production efficiency (Mueller et al. 2013, Fründ et al. 2013). Hence, both processes that occur between and within trophic levels can have significant implications on ecosystem properties (Duffy et al. 2007, Allhoff and Drossel 2016).

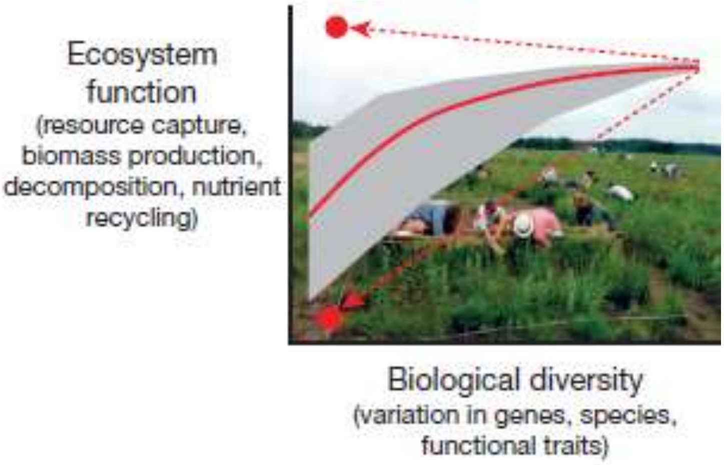

Figure 1.1. Biodiversity-ecosystem function relations based on summaries of several hundred experiments. The red line indicates the average change across all aspects of biodiversity (genes, species, traits). The grey polygon represents the 95% confidence interval, while the red points show the maximum and minimum values of the most or least productive species in monoculture (after Cardinale et al. 2012).

A plethora of empirical studies have established that the alteration of biodiversity leads to reduced functioning of ecosystems (Stachowicz et al. 2007, Cardinale et al. 2006, Worm et al. 2006, Cardinale et al. 2012, Hooper et al. 2012), taking the shape of saturation curve (Figure 1.1; Cardinale et al. 2011, 2012, Mora et al. 2014). However, the shape and form of this relationship is subject to variation and has been tested using a multiplicity of approaches (e.g. Tilman et al. 2001, Jaillard et al. 2014). A global survey of reef fish assemblages, for example, showed that standing biomass scales in a non-saturating manner with biodiversity (species and functional richness; Mora et al. 2011). A range of theoretical and empirical studies subsequently found that the history of community colonisation Fukami and Morin 2003, Fukami 2004 Fukami et al. 2010) as well as the relative influence of disturbance and dispersal across spatial scales (Cardinale et al. 2004) affected the shape and magnitude of this relationship. More recently, species evenness and dominance have shown to affect biodiversity-function relations (Wohlgemuth et al. 2016). In this context, trait variability between different species populations have been highlighted as a source of diverging ecosystem consequences to biodiversity loss (Wohlgemuth et al. 2017).

As current conservation and management strategies continue to move towards ecosystem-based approaches (Millenium Ecosystem Assessment 2005), accuracy and confidence that the shape of the biodiversity-ecosystem function relationship is representative of altered biodiversity in natural systems become increasingly important, as the shape of the relationship forms the basis upon which predictions about the ecosystem consequences of biodiversity change are modelled (Naeem 2009). However, the relationship between biodiversity and ecosystem functioning has been demonstrated to conform to alternative curve-fits besides that of the Michaelis-Menten function. Biodiversity-function relations are influenced by seabed morphology and heterogeneity (Zeppilli et al. 2016) and have shown exponential decline in functioning with benthic biodiversity loss in the deep sea (Danovaro et al. 2008). Because of its application in ecosystem assessments which are used to inform decision-makers in formulating and implementing long-term policies which would ensure sustainable ecosystem futures, the shape of the biodiversity-ecosystem function curve has vital implications for ecosystem management. Thus, if the current understanding of biodiversity-function relations is based on data that is misrepresenting biodiversity loss in natural communities, this could have far reaching implications and ultimately compromise human wellbeing. Hence, it is crucial for research to accurately determine the relationship between biodiversity and ecosystem functioning.

Evidence in support of the saturating relationship between biodiversity and ecosystem functioning (Cardinale et al. 2012) is mostly based on experiments manipulating biodiversity (predominantly species richness) on individual ecosystem functions (Cardinale et al. 2012, Naeem et al. 2012). Such experimental systems are often homogeneous and lack the environmental and biological complexity of the natural communities (Bracken et al. 2008) and do, for example, not allow for the development of community responses and dynamics in response to change. This suggests, that these experimental studies, due to their randomly assembled species from a single trophic level, may provide insufficient insight into biodiversity-ecosystem function relations of natural ecosystems, where communities are multi-trophic (Duffy et al. 2007).

However, ecosystems are far from random species assemblages, rather natural systems are structured by ecological networks interlinked (Montoya et al. 2006, Williams et al. 2002) by species, which respond in different ways to global change (Gonzalez and Loreau 2009). Natural ecosystems are highly dynamic and heterogeneous environments that are subject to various interconnected processes

(Lefcheck et al. 2015) exposed to a multitude of environmental and anthropogenic forces (e.g. pollutants, habitat transformation and climate warming), which cause local extinctions or fundamental shifts in the distribution and abundance of species with considerable effects on structure and functioning of ecosystems (Suttle et al. 2007, Gonzalez and Loreau 2009). Species diverge in their response to disturbance, depending on stressor-sensitivity, traits (Williams et al. 2008, Jump and Peñuelas 2005) and life history (Paine et al. 1998). Disturbance may, therefore, impair species that are more susceptible or stress-sensitive, whilst providing opportunities (i.e. resource) for others (Ghedini et al. 2015, Sih 2013, Sih et al. 2011, Tuomainen and Candolin 2011, Candolin and Wong 2012).

Apart from diverging directional response patterns, species can respond via various types of expressions. In response to perturbation, species can, for example, switch their behaviour (Carnicer et al. 2008, Underwood et al. 2017, Frainer et al. 2018), adjust their physiological regulation (Van Dievel et al. 2016) with direct implications for the rate at which they mediate ecological processes (Frainer et al. 2018, Pascal et al. 2016, Oulette et al. 2004), exhibit elevated somatic growth (Suding et al. 2006) or increase their reproductive investment and offspring output (Buechling et al. 2016). Consequences related to climate warming can increase organism metabolism (Brown et al. 2004) and intrinsic population growth (Savage et al. 2004) and modify feeding parameters associated with predatory-prey interactions (Rall et al. 2009, Englund et al. 2011, Rall et al. 2012). The role of specific trophic levels has also been demonstrated to be critical for ecosystem resilience, as such, herbivory regulates the capacity of intertidal rocky shore communities to resist warming, by maintaining trophic and competitive interactions (Korads et al. 2017). Yet, how exactly species respond to change may differ across timescales. Species might, for example, not necessarily be impacted by the effects of climate change in the short-term, but, such effects may manifest over longer timescales and induce gradual changes in the behaviour of species (Godbold et al. 2013).

Besides variation in temporal species responses, different responses operate at different spatial scales. Recruitment is a key mechanism that can affect ecosystems by influencing population and community via demographic buffering and compensatory recruitment (McDonald et al. 2016). In this context, species in perturbed communities (e.g. by disease) are capable of increasing rates of recruitment to compensate for reduced survival probability (Muths et al. 2011, Connell et al. 1984). However, dispersal between habitat patches can act as an important stabilising mechanism, through which communities can retain composition and structure across larger spatial scales. These natural patterns of dispersal are lost in laboratory-based experiments, which is of particular concern, as connectivity has been highlighted to be important in modifying the effect of species diversity on ecosystem properties at the metacommunity-level (Matthiessen et al. 2007, Thompson and Gonzalez 2016).

Nonetheless, not all consequences of species responses to change are as predictable as the direct effect of organisms. Indirect effects can induce cascading effects (e.g. via co-extinction; Brodie et al. 2014, Sanders et al. 2015) that propagate through intermediaries to affect other species, separated by several links (McClean et al. 2015, Montoya et al. 2006, Sanders et al. 2013, Säterberg et al. 2013) and can be considerably more difficult to predict (Wernberg et al. 2012). Hence, the extinction of a single species can have dramatic consequences for ecosystem structure and dynamics (Dunne and Williams 2009, Estes et al. 2016, Estes and Palmisano 1974, Estes et al. 2011, Koh et al. 2004, O'Connor and Donohue 2013, Paine 1966). The loss of species that trigger secondary extinctions are predicted by both theory (Borrvall and Ebenman 2006, Dunne and Williams 2009, Dunne et al. 2002, Ebenman et al. 2004, Eklöf and Ebenman 2006, Fowler 2010, 2013, Pimm 1980) and empiricism (Estes and Palmisano 1974, Paine 1966, Springer et al. 2003, Terborgh et al. 2001) to be a common consequence of biodiversity change, depending on the trophic position of the expired species (Donohue et al. 2017). Thus, such co-extinctions and mechanisms of coexistence are likely to modify the curve of biodiversity-ecosystem functioning. Hence, how species respond to environmental and anthropogenic change and their drivers need to be prioritized in the context of exploring the repercussions of biodiversity change upon ecosystems.

Ample evidence from the geological record show that communities undergo fundamental shifts in the relative abundance of taxa and the dominance of species in each successive assemblage that follows an extinction event (Wagner et al. 2006, Hull 2015, Pimiento et al. 2017). Among marine benthic assemblages there is evidence that surviving lineages strongly dominated, the majority of which were rare prior to the extinction event, in both inshore and offshore environments due to changes in relative abundance (Aberhan and Kiessling 2006). Only few of the new dominant taxa in these assemblages were newly evolved, suggesting that biotic interactions and in particular incumbency effects suppressed post-extinction diversity compensation by radiating and invading species (Aberhan and Kiessling 2006). More recently, these regime shift have been found to be part of a global pattern, in which ecospace utilisation and the functional traits of benthic assemblages shifted to a system of different structure (Aberhan and Kiessling 2015). Such community turnover resembles that of recovering post-disturbance communities (Lotze et al. 2006, Hillebrand et al. 2008, Suding et al. 2005, Grman et al. 2010), where a variety of compensatory interactions amongst surviving species (Harries et al. 1996) develop and offset, wholly or in part, the functional contributions made by species that have been extirpated (Gonzalez and Loreau 2009).

Although an extensive body of empirical research has comprehensively studied the positive effect of biodiversity on various ecosystem functions, critical gaps continue to persist in the understanding of consequences associated with altered biodiversity (Figure 1.2, Bracken et al. 2017, Brose and Hillebrand 2016, Wright et al. 2016). One such knowledge gap is the scaling-up of biodiversity-function relations (Cardinale et al. 2012, Naeem et al. 2012, Snelgrove et al. 2014, Lohrer et al. 2015, Bracken et al. 2017). Because experiments lack the complexity of natural ecosystems and realistic scenarios of species loss, there is great uncertainty with regards to the generality of the relationship between biodiversity and ecosystem functioning derived from small-scale, short-term, homogenous experimental studies, which provide limited understanding of how this relationship changes in time and space (Cardinale et al. 2012, Naeem et al. 2012, Bracken et al. 2017, Hillebrand 2009, Duffy 2009, Yasuhara et al. 2016). Natural systems can be highly variable across even very fine spatial scales and experience substantial temporal fluctuations and environmental heterogeneity, enhancing niche exploitation by species (Cardinale et al. 2012). Thus, small-scale experiment are likely to under- (Duffy 2009) or over-estimate the impact of biodiversity loss on ecosystem functioning in natural systems (Cardinale et al. 2012). Although the results from these studies provide insufficient insight into realistic scenarios of biodiversity change and the consequences on ecosystem functioning (Bracken et al. 2008, Hillebrand et al. 2009), they have explored potential ecological consequences of a wide range and aspects of global change scenarios (Hillebrand et al. 2009). Hence, consequences associated with altered biodiversity are likely to be very different from current expectation of biodiversity-ecosystem function relations based on conclusions reached from biodiversity-ecosystem functions studies (Cardinale et al. 2012).

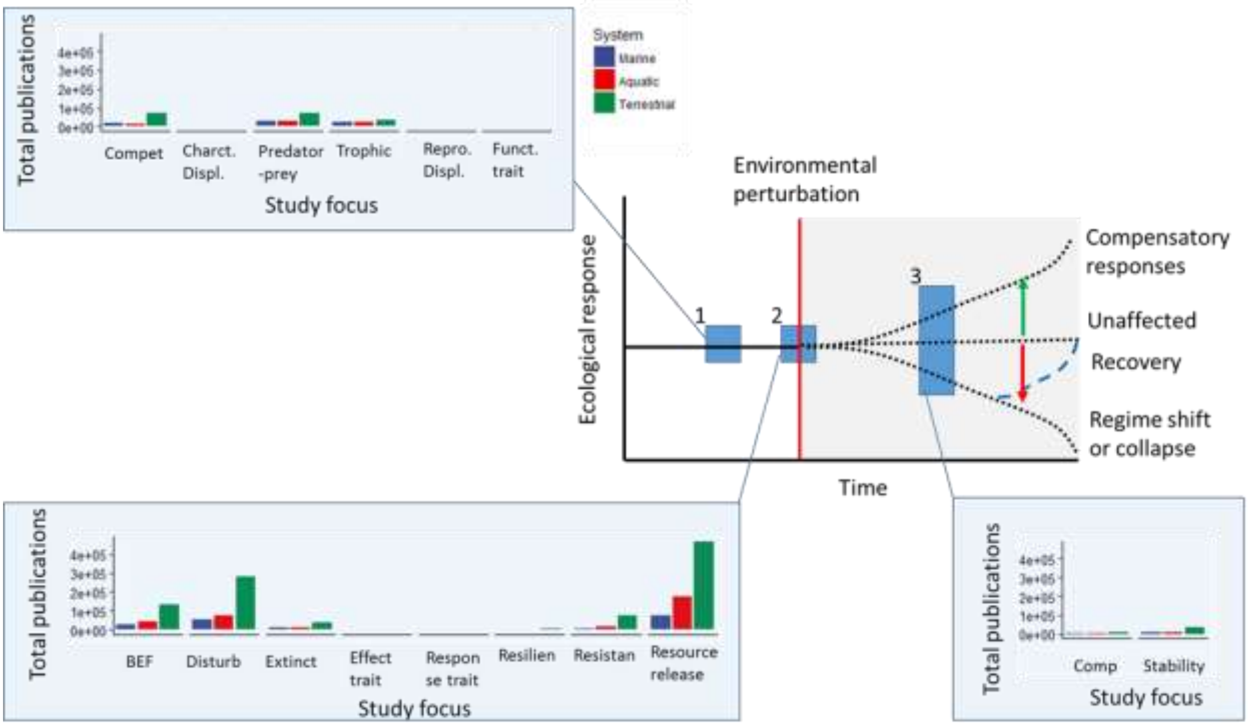

Figure 1.2. Total number of published articles along the time axis/spectrum of environmental change (1) before change; competition, character displacement, predator-prey, reproductive displacement and functional trait, (2) at the time of impact; biodiversity-ecosystem functioning, disturbance, extinction, functional effect trait, functional response trait, resilience, resistance and resource release, (3) post-impact; compensation and stability and their relative effort intensity for marine, aquatic (aquatic and freshwater), and terrestrial (plant, soil and terrestrial) systems. What is clear is that studies that have considered compensation are vastly underrepresented in terms of research effort, particularly in the marine environment. Secondly, post-impact aspects of environmental change are strongly underdeveloped. Data were compiled from a Web of Science (https://apps.webofknowledge.com; date of access: 28.02.2018) literature search, see Appendix A table A.1 for details on the search terms.

Another key knowledge gap that exist within current biodiversity ecosystem functioning research is the ignorance of compensatory response to change, which only few studies have accounted for. Compensatory responses are the response of stress tolerant species that – partially or completely – buffer the ecological role of declining or extinct species. Thus compensation is more likely to occur in communities where species responses differentiate to environmental and/or anthropogenic change (Gonzalez and Loreau2009, Loreau 2010, Cardinale et al. 2012) and can manifest at different hierarchical scales. Compensatory responses are diverse and include various types of responses. The majority of studies that have accounted for compensation have focused on numeric or density compensation, through asynchronous dynamics between community populations (e.g. MacArthur et al. 1972, Ernest and Brown 2001, Klug et al. 2000, Hector et al. 2010, Houlahan et al. 2007, Valone and Barber, 2008) in response to perturbation (Gonzalez and Loreau 2009, Ghedini et al. 2015). However, species are also known to compensate through; somatic growth (biomass), increased reproductive output (abundance), rate regulation (per capita physiology; Ruesink and Srivastrava 2001) as well as behavioural switching, in which species can change their function or behaviour (Maire et al. 2010). Recently, organismal homeostasis has also been suggested to provide a basis for compensatory dynamics and the buffering against environmental change (Ghedini and Connell 2016). While species responses and the variation in species abundances may be a direct measure of compensation, the actual effect of compensatory responses on ecosystem functioning are more difficult to quantify and thus remain largely unknown. Underlying mechanisms of compensation are believed to be associated with competitive interactions between species (Gonzalez and Loreau2009, Loreau 2010, Cardinale et al. 2012), and are seldom incorporated in models predicting the ecosystem consequences of biodiversity change. Despite having known about these processes for a long time (McNaughton 1977, MacArthur et al. 1972), compensatory mechanisms are poorly understood and markedly underdeveloped both in general ecology and in particular within the marine realm (Figure 1.2).

1.2 Thesis aims and objectives

This thesis aims to explicitly address the disconnect that exists between the representation of biodiversity-ecosystem function relations in experimental systems and those observed in natural systems facing multiple sources of change. Using marine sediment invertebrate communities, I examine the role of compensatory responses to change using trait-based modelling to inform alternative scenarios of local extinction complimented by experimentation and observations of representative shelf sea habitats. Key foci of the thesis include:

1) Compensatory responses may change the ecosystem consequences of altered biodiversity, but the response of communities to different types of compensation have not previously been explored. Using empirically derived relationships of how species moderate ecosystem function, I will test the **Hypothesis (H1)**: *The type of compensation expressed (biomass and numeric) is not an important determinant of ecosystem process and function* **(Chapter 2)**;

2) Whilst paleo-ecological evidence and theoretical reasoning may indicate that compensatory responses can change biodiversity-function relations, compensatory responses have not been extensively evaluated in extant communities. I will quantify the functional consequences of biomass compensation in representative benthic communities and test the **Hypothesis (H2)**: *The compensatory response of communities cannot be demonstrated in model communities that differ in community structure* **(Chapter 3)**;

3) Natural communities are undergoing rapid change associated with unsustainable levels of human activity, increasing impetus to establish the ecosystem consequences of continued resource exploitation. Here, I will examine whether changes in ecosystem functioning following bottom fishing in a representative

shelf sea are completely or partially mitigated by the compensatory responses of surviving species. By identifying community responses to bottom-fishing, I will parameterise models that explore the potential for community-level compensation across a range of fishing pressure intensity scenarios to test the **Hypothesis (H3):** *Compensatory dynamics are invariant to perturbation intensity at a regional scale* **(Chapter 4)**;

4) The frequency and extent of compensatory processes in natural systems experiencing change is often assumed, but has not generally been evaluated in relation to specific perturbation events. In this chapter, I will use a time-series of macrofaunal assemblage structure to identify occurrences of compensatory responses in a natural system to test the **Hypothesis (H4)**: *Compensatory responses to perturbation cannot be detected above natural variation in compensatory dynamics* **(Chapter 5)**;

Collectively, addressing these hypotheses will improve understanding of the response of communities to perturbation and increase capability in predicting the ecosystem consequences of natural and anthropogenic forcing.

Chapter 2: Consequences of biodiversity loss diverge from expectation due to post-extinction compensatory responses

The contents of this chapter have been published as:

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2.1 Abstract

Consensus has been reached that global biodiversity loss impairs ecosystem functioning and the sustainability of services beneficial to humanity. However, the ecosystem consequences of extinction in natural communities are moderated by compensatory species dynamics, yet these processes are rarely accounted for in impact assessments and seldom considered in conservation programmes. Here, I use marine invertebrate communities to parameterise numerical models of sediment bioturbation – a key mediator of biogeochemical cycling – to determine whether post-extinction compensatory mechanisms alter biodiversity-ecosystem function relations following non-random extinctions. I find that compensatory dynamics lead to trajectories of sediment mixing that diverge from those without compensation, and that the form, magnitude and variance of each probabilistic distribution is highly influenced by the type of compensation and the functional composition of surviving species. These findings indicate that the generalized biodiversity-function relation curve, as derived from multiple empirical investigations of random species loss, is unlikely to yield representative predictions for ecosystem properties in natural systems because the influence of post-extinction community dynamics are under-represented. Recognition of this problem is fundamental to management and conservation efforts, and will be necessary to ensure future plans and adaptation strategies minimize the adverse impacts of the biodiversity crisis.

2.2 Introduction

Species extinction and the associated degradation of ecosystems are proceeding at an accelerating pace (Pereira et al. 2010, Pimm et al. 2014, Urban 2015), but the consequences of the current decline in biodiversity for socio-ecological systems represent a critical knowledge gap for policy-makers(Halpern et al. 2015). Consensus reached from experiments that have manipulated biodiversity and measured various ecosystem functions, including primary productivity, nutrient cycling and decomposition, predict an accelerating decline in ecosystem properties with increasing biodiversity loss (Cardinale et al. 2012), yet it is not clear how appropriate it is to apply this general relationship at the landscape scale (O'Connor et al. 2016). A major difficulty is that the complexities of natural communities (Brown et al. 2001, Strong et al. 2015), including the role of rare species (Hull et al. 2015) and the occurrence of co-extinctions (Koh et al. 2004), have been poorly articulated in controlled experiments, and very few studies have focussed on realistic trajectories of species loss that factor in a predisposition to community dynamics (Bracken et al. 2008). Indeed, the role of population dynamics in moderating the consequences of extinction have received little attention (Ives and Cardinale 2004, Gross and Cardinale 2005, Gonzalez and Loreau 2009), despite direct evidence that communities undergo fundamental shifts in the relative abundance of taxa and the dominance of species in each successive assemblage that follows an extinction event (Wagner et al. 2006, Hull 2015, Lotze et al. 2006). Such community turnover resembles that of recovering post-disturbance communities (Lotze et al. 2006), where a variety of compensatory interactions amongst surviving species (Harries et al. 1996) develop and offset, wholly or in part, the functional contributions made by species that have been extirpated (Gonzalez and Loreau 2009). Compensatory responses tend to be asynchronous within a perturbed community and can lead to partial (Smith and Knapp 2003, Davies et al. 2012), complete (Bai et al. 2004, Vross and Harte 2007, Peters et al. 2009), or over (Yvon-Durocher et al. 2015) compensation in ecosystem functioning. Species can also switch behaviour (Carnicer et al. 2008), make physiological regulation adjustments (Van Dievel et al. 2016), exhibit elevated growth (biomass compensation; Suding et al. 2006) or increase reproductive investment (numeric compensation; Ensign et al.1997) in response to perturbation, especially following release from competition/predation (Holbrook and Schmitt 1995) or during niche expansion (Lister 1976). These responses may not be immediate, in some instances taking months (Godbold and Solan, 2013) to years (Touchton and Smith 2011) to develop, but once expressed they can be critical in influencing further species interactions(Werner 1992) and can dramatically affect ecosystem properties (Ruesink and Srivastava 2001, Gardmark et al. 2006, Lorenzen 2008, Ghedini et al. 2015). Furthermore, where extinction events are localized and communities are interconnected (Bernhardt and Leslie 2013), immigration and re-colonization from the surrounding area (Godbold et al. 2011), as well as recruitment from the wider species pool (Sanz-Aguilar et al.2016), can play a pivotal role in stabilizing local population decline and ecological processes (Thompson and Shurin 2012). Ultimately, however, the degree of functional compensation will depend on the amount of functional redundancy in the surviving community, which, in turn, will reflect the spatial extent and consistency of the perturbation compromising biodiversity and the level of covariation between the extinction driver and the traits that mediate functioning (Solan et al. 2004).

Despite the range of compensatory mechanisms and variety of ways in which species interactions can affect the functional properties of natural communities

(Brown et al. 2001, Harries et al. 1996), few studies have explored how surviving species moderate the consequences of extinction (Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007, Allgeier et al. 2015) and the relative role of different compensation mechanisms remain largely unexplored. Here, I use probabilistic numerical simulations to test how the loss of sediment dwelling marine invertebrates may affect the sediment mixing depth, an important mediator of biogeochemical cycling (Botto et al. 2005, Solan et al. 2008). These simulations assume that the sequence of species loss is either random or ordered by body size or rarity to reflect likely sources of extinction risk. The probabilistic distributions are compared to further simulations in which populations of surviving species maintain total abundance (numeric compensation) or total biomass (biomass compensation) sourced from different components (common or rare species, within or between bioturbation functional groupings, same or different/lower or higher level of activity) of the surviving community. In doing so, the objective is to establish the extent to which alternative compensatory dynamics alter biodiversity-function relationships.

2.3 Methods

2.3.1 Sampling and study site

Field data were collected at station Margaretta (22 m water depth, 53 ° 13.50′ N, 09 ° 6.50′ W) in Inner Galway Bay on the central west coast of Ireland. Samples of macro-invertebrates (retained on a 500μm sieve; n = 5, 0.1 m^2 van Veen grab) were collected approximately on a monthly basis over a one-year period (December 1996–November 1997, n = 11), returning a total of 139 invertebrate species (Solan et al. 2004). Measurements of the sediment mixing depth were obtained using sediment profile imaging (SPI; n = 10) camera system (Solan et al. 2004).

2.3.2 Extinction simulations

Using a comprehensive study of the macrofaunal assemblages of Galway Bay, west coast of Ireland (Solan et al. 2004), it is predicted how species extinction is likely to affect the mixing depth, an indicator of invertebrate bioturbation. The relationship was established between an index of bioturbation potential that uses per capita bioturbation potential (BP_i, Appendix B, Equation A1) to estimate population-level (BP_p, Appendix B, Equation A2) and community-level bioturbation potential (BP_c, Appendix B, Equation A3), which accounts for each species body size, abundance, activity level (4 levels, scored on a categorical scale reflecting increasing activity, 1 = in a fixed tube, 2 = limited movement, 3 = slow movement through sediment profile, 4 = free movement via burrow system; Solan et al. 2004), and mode of sediment mixing (5 levels, scored on a categorical scale reflecting increasing impact on sediment turnover, 1 = epifauna, 2 = surfical modifiers, 3 = upward or downward conveyorbelt feeders, 4 = biodiffusers, 5 = regenerators; Solan et al. 2004), and measurements of mixing depth obtained from sediment profile images. This relationship (Appendix B, Equation A4) was used to parameterise probabilistic, numerical simulations that test how alternative extinction scenarios might affect sediment mixing depths. As environmental forcing in natural systems can target different components of the community (Payne et al. 2016), simulations are considered in which species go extinct at random ($\frac{1}{n}$, where n = the number of species) versus extirpations ordered by body size (largest expire first) or rarity (least abundant expire first). As the functional consequences of extinction also depend on the response of surviving species, models were developed in which species either do not exhibit compensatory responses or in which the abundance (numeric compensation) or biomass (biomass compensation) of the surviving community are held constant following extinction. In doing so, it was recognized that compensating species are not randomly assigned, rather they represent different components of the species pool:

2.3.3 Compensation by common species

Compensatory responses by common species is arguably one of the most likely pathways of compensation in a community, both probabilistically in terms of their relative proportion of abundance, and ecologically as numeric success reflects their disproportionate share of resources and competitive advantage over less numerous species (Smith and knapp 2003). In addition, this type of compensation has been observed in natural communities (Pan et al. 2006).

2.3.4 Compensation by rare species

The majority of community species are rare, but some species are equipped with unique functional traits (Lyons and Schwartz 2001) and may become important if they increase in abundance (MacDougall et al. 2013, Jian et al. 2014).

2.3.5 Compensation by species from within/outwith or lower/higher functional grouping or which exhibit similar/distinct or lower/higher levels of activity

It was assumed that species within the same functional group (e.g. sediment reworking mode; Solan et al. 2004) will have similar functional traits and thus employ a similar ecological role, and that functional buffering can also be carried out by species from a different but adjacent functional group (e.g. grass versus forbs (Smith and knapp 2003), local versus non-local distribution of sediment particles by bioturbators; Solan et al. 2004, Clapham 2016), or species selected from any lower or higher functional group. Compensating species can also exhibit similar or contrasting levels of activity (mobility categorisation; Solan et al. 2004) relative to the species that has been extirpated, such that functional buffering can also be carried out by species from a different but adjacent mobility group, or species selected from any lower or higher mobility group. In the absence of an adjacent functional group, compensation stems from the next available functional group of greater/lesser or equal standing. Each of these model scenarios (i.e. 3 extinction orders, 2 compensation mechanisms and 11 compensation types, n = MacDougall et al. 2013) was run for 1000 simulations (from 139–1 species). The R code for executing each of these simulations are provided in (Appendix B, Code A1).

2.4 Results

In the absence of compensatory dynamics, the form of the biodiversity function curve approximates expectations (accelerating loss of function with declining species richness, moderated by how extinctions are ordered), and the simulations include a previously documented (Solan et al. 2004) prominent bifurcation of the mixing depth that reflects whether a burrowing brittlestar, *Amphiura filiformis*, is present (deeper mixing depth) or absent (shallower mixing depth) in the surviving community (panels a,l,w in Figure 2.1and Figure 2.2). The disproportionate contribution of this species is evident throughout all of the simulations (Appendix B, Figures A1-2), although it is clear that the loss of other species can also result in stepped changes (abrupt shifts in mixing depth, most prominently featured in Figure 2.1)that show a tendency to only partially compensate for the loss of the extirpated species (Figure 2.1). When compensatory mechanisms of the surviving community are based on numerical responses, the mixing depth is largely maintained as species richness declines (Figure 2.1), when extinctions are random (panels b–k) or ordered by rarity (panels x–ag). However, when extinctions are ordered by body size (panels m–v), compensatory responses, independent of how they are expressed, are unable to fully mitigate the functional consequences associated with species loss, yet notable differences exist depending on which species drive the compensatory response. However, when compensatory mechanisms of the surviving community are based on biomass, with a few exceptions, there is a tendency for overcompensation to take place along the main species-function trajectory (colour intensity in Figure 2.2). Despite implementing these fundamentally different compensatory mechanisms, these simulations reveal that most probabilistic trajectories overlap one another to form a narrow band of likely ecosystem functioning (colour intensity in Figure 2.1 and Figure 2.2). The variation of the outcome under numeric versus biomass compensation increases at low and high levels of species richness; this is particularly evident for compensatory responses driven by lower and higher functional groupings and activity level, but at intermediate levels of species richness there is some evidence to suggest similar levels of mixing depth, irrespective of the type of compensation mechanism (Figure 2.3). The same general patterns persist in the absence of *A. filiformis*, although variation is considerably reduced for numeric compensation (Appendix B, Figure A3). When compensation is realized via the most common species in the surviving community, these models indicate that numeric compensatory mechanisms (Figure 2.1, panels b,m,x) can reduce, maintain, or increase the mixing depth relative to when there is no compensation, whilst biomass compensatory mechanisms (Figure 2.2, panels b,m,x) show a tendency to increase the mixing depth. In contrast, when compensation is realized by the rarest species in the surviving community (panels c,n,y in Figure 2.1 and Figure 2.2), the mixing depth tends to increase relative to the no compensation scenarios under both numeric and biomass compensation, albeit with high variability at low levels of species richness (panels c,n,y in Figure 2.3). When compensating species stem from the same or different functional group, or exhibit identical or contrasting levels of activity relative to the species that have been extirpated (compare panels d-e, o-p, z-aa and h-i, s-t, ad-ae between Figure 2.1 and Figure 2.2), there is little influence of compensation because compensation is sourced from all possible functional groups. Hence, over multiple species losses, compensation does not occur disproportionately in any one functional group.

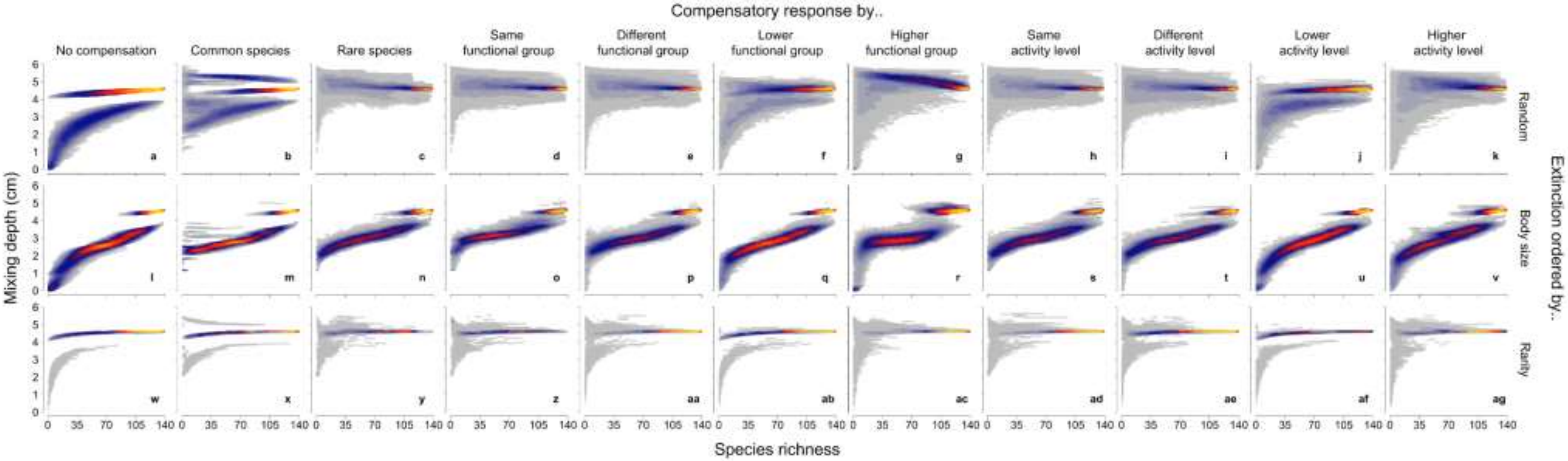

Figure 2.1. Predicted changes in sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction numeric compensation. Simulations (n = 1000 per panel) represent species losses that occur at random (panels a-k) or which reflect trait-based vulnerabilities to extinction governed by body size (panels l-v) or rarity (panels w-ag). It was assumed that the surviving community shows either no compensatory response (a, l, w) or full numeric compensation by common (b, m, x) or rare (c, n, r) species, species from within (d, o, z), between (e, p, aa), lower (f,q,ab) or higher (g,r,ac) functional groups, or species with the same (h, s, ad), different (i,t,ae), lower (j,u,af) or higher (k,v,ag) level of activity to the species that have gone extinct. Colour intensity (cold to warm colouration; grey - blue – red - yellow) reflects an increasing density (low to high) of data points.

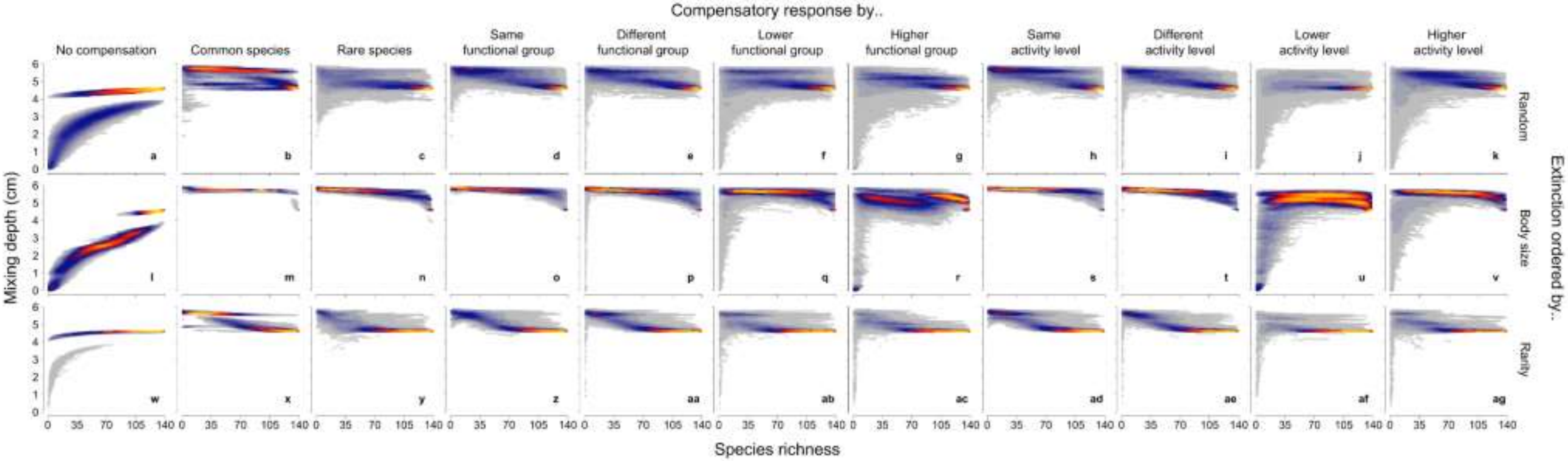

Figure 2.2. Predicted changes in sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction biomass compensation. Simulations (n = 1000 per panel) represent species losses that occur at random (panels a-k) or which reflect trait-based vulnerabilities to extinction governed by body size (panels l-v) or rarity (panels w-ag). It was assumed that the surviving community shows either no compensatory response (a, l, w) or full biomass compensation by common (b, m, x) or rare (c, n, r) species, species from within (d, o, z), between (e, p, aa), lower (f,q,ab) or higher (g,r,ac) functional groups, or species with the same (h, s, ad), different (i,t,ae), lower (j,u,af) or higher (k,v,ag) level of activity to the species that have gone extinct. Colour intensity (cold to warm colouration; grey - blue - red - yellow) reflects an increasing density (low to high) of data points.

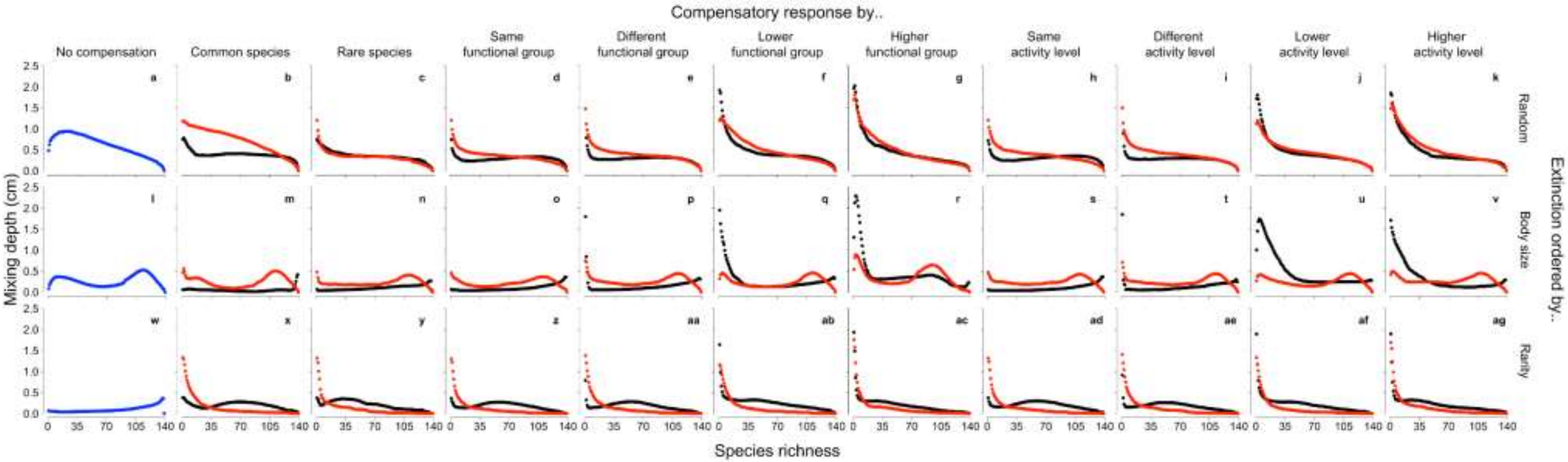

Figure 2.3. Variability of sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction compensation. Standard deviations are shown for the probabilistic distributions (n = 1000) at each level of species richness for the extinction scenarios depicted in Figures 1 and 2, assuming no compensatory response (blue), full numeric compensation (red) or full biomass compensation (black).

When compensation is directed towards lower functional groups (Figure 2.1f,q,ab and Figure 2.2 f,q,ab) and/or activity levels (Figure 2.1j,u,af and Figure 2.2 j,u,af), the loss of functioning accelerates relative to the other functional group and/or activity level scenarios because bioturbation capacity is reduced. Alternatively, when compensation is directed towards higher functional groups (Figure 2.1g,r,ac and Figure 2.2 g,r,ac) or activity levels (Figure 2.1k,v,ag and Figure 2.2 k,v,ag), the mixing depth tends to be maintained at similar or higher levels than those observed when compensation stems from species with the same or different functional group/activity level because bioturbation capacity continues to be maintained or is increased. These observations suggest that certain traits may well be linked to the mediation of ecosystem functioning, but their role in determining observed levels of functioning will depend on how influential such traits are for underlying ecosystem processes (Wooding et al. 2016).

2.5 Discussion

Using numerical models parameterised with data from a marine benthic community, it has been demonstrated that incorporation of compensatory dynamics, irrespective of the mechanism of compensation (numeric or biomass) or how a species extinction risk is determined (random, ordered by rarity or body size), have the potential to lead to clear differences in aggregate community responses to species loss that do not always conform to expectations based on the generalised biodiversity-function relation curve (Cardinale et al. 2012). The models showed that the probabilistic distributions for sediment mixing depth were deeper when compensatory mechanisms were present relative to when they were absent, and when compensatory dynamics reflected post-extinction increases in biomass rather than abundance. Moreover, simulations indicate that the way in which numeric or biomass compensation is expressed within the surviving species pool is most influential. These observations highlight the importance of post-extinction compensatory mechanisms in determining how traits are expressed and mediate function, and suggest that the ecological status of soft-sediment benthic habitats is unlikely to conform to expectation as current visions of future scenarios of extinction lack the necessary sophistication. Numerous studies investigating the consequences of environmental forcing for ecosystem functioning have focused on the decline of the number of species and their functional traits or attributes. Whilst the effect of various attributes of biodiversity on ecosystem functioning, including evenness (Schmitz et al. 2013), dominance (Wohlgemuth et al. 2016), and functional traits (Mason et al. 2005) have been studied, the relative importance of compensatory mechanisms in natural ecosystems and the concept of compensation as a whole has largely been ignored despite evidence for the occurrence of compensation in natural systems (Pan et al. 2016). Importantly, these simulations reveal that the mixing depth of sediment-dwelling invertebrate communities will depend on how compensatory behaviour is expressed, and the extent to which the functional attributes of compensating species affect bioturbation. A difficulty with determining the latter is that recent work has shown that differences in how species interact with sediment biogeochemistry and other aspects of the environment can converge in terms of absolute effects of ecosystem properties (Woodin et al. 2016, Mason et al. 2005). This may explain previous inconsistencies in linking particular species traits to ecosystem functioning (Solan et al. 2008) and why community compensation does not appear to be dominated by a limited number of species that host specific sets of traits; a conclusion consistent with recent studies that demonstrate the importance of common species in maintaining ecosystem functioning (Gaston et al. 2007, Winfree et al. 2015, Inger et al. 2016). Whilst the differences between alternative compensatory scenarios may be subtle, they can form crucial differences. Consequently, the repercussions of species loss are more effectively offset by a subset of species that share the same functional group or level of activity, especially at low levels of species richness. Whether these mechanisms can be identified and operate in natural communities, however, remains an open empirical question (Bracken et al. 2008). It is important to acknowledge that the current study is an abstraction of community dynamics and to recognize that the model assumptions that were adopted represent an oversimplification of community interactions under environmental forcing. The focus was not to predict the depth of sediment mixing for specific biodiversity futures, but rather to explore the relative importance of compensatory mechanisms in determining ecosystem properties. Whilst the study was unable to incorporate the occurrence of co-extinctions (Koh et al. 2004), non-indigenous invasive species (Gallardo et al. 2016) or other cascading effects that can have further consequences for community structure and ecosystem functioning, it was possible to establish divergent patterns in response for alternative extinction scenarios that hold promise for exploring new strategies of ecosystem management and governance. An important next step in predicting future biodiversity change, however, is to quantify the prevalence of local extinction drivers in the ecological landscape (Elahi et al. 2015) and understand how these interact in natural systems (Brook et al.

2008, Darling and Côté 2008) to influence the risk of extinction, altering community dynamics and ecosystem properties, both locally and across regional scales. Extensive uncertainties exist in the responses of species and communities to environmental forcing, hence the use of empirically-based scenarios of the future to explore the potential consequences of species loss will continue to be a necessity for ecological advancements. This study has shown, that the incorporation of important aspects of post-extinction community dynamics can lead to sharp contrasting forecasts of future ecosystem properties. Such information will help advance the predictability of community responses to change, provided that regionalised vulnerability assessments that determine the response of functionally important species under realistic future environmental conditions become available (Pearson et al. 2014, Pinceel et al. 2016). However, it is unlikely that all of these details will be available and incorporated into next generation models in the short-term, nor is this likely to be necessary. Consistency in community responses in the presence of compensation reveal patterns that may be general. Based on the available evidence, it should expect that the loss of species will be compensated by less efficient species over the long term (Séguin et al. 2014), resulting in alterations to ecosystem properties. However, the discrepancy in ecosystem consequences between biomass and numeric compensatory responses emphasise the need to identify which, or whether both, compensatory processes prevail in natural assemblages.

Estimates of the functional consequences of biodiversity loss that incorporate the error associated with such variation are needed, and will allow more confidence in simulations of the future and provide improved levels of certainty on the consequences of future global change.

2.6 Acknowledgements

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Chapter 3: Compensatory responses can modify the form of the biodiversity-function relation curve contingent on post-extinction community composition

This chapter has been submitted to Proceedings of the Royal Society B.:

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3.1 Abstract

There is now strong evidence that ecosystem properties are influenced by alterations in biodiversity and the consensus that has emerged from over two decades of research is that the form of the biodiversity-functioning relationship follows a saturating curve. However, the foundation on which these conclusions are drawn mostly stem from empirical investigations that have not accounted for post-extinction changes in community composition and structure, or how surviving species respond to new circumstances and modify their contribution to functioning. Here, I use marine sediment-dwelling invertebrate communities to experimentally assess whether post-extinction compensatory mechanisms could alter biodiversity-ecosystem function relations. Consistent with recent numerical simulations, I find that the form of the biodiversity-function curve is highly dependent on whether or not compensatory responses are present, the cause and extent of extinction, and how the density of individual species are distributed within the community. When species losses are combined with the post-extinction compensatory responses of surviving species, both community composition and the pool and relative expression of functionally important traits are altered, whilst changes in dominance structure affect species interactions and behaviour. These observations emphasise the importance of post-extinction community composition in determining the resilience of ecosystem functioning following extinction and caution against use of the generalized biodiversity-function curve when generating probabilistic estimates of post-extinction ecosystem properties for practical application.

3.2 Introduction

Species populations can respond to the loss of, or reduction in, the number of individuals or species in a community through various compensatory mechanisms, including numeric (Ernest and Brown 2001, Klug et al. 2000, Hector et al. 2010), biomass (Bai et al. 2004, Pan et al. 2016) and/or *per capita* processing rate responses (Ruesink and Srivastrava, 2001), or via mechanisms that effectively absorb disturbances through changes in trophic interactions (Ghedini et al. 2015). Such expressions are often associated with adjustments in the competitive balance between species (Pickett and White 1985, Paine et al. 1998, Connell et al 2013), contributing to resource-release and new opportunity in the face of environmental disturbance (Ghedini et al. 2015, Sih 2013, Sih et al. 2011, Tuomainen and Candolin 2011, Candolin and Wong 2012). Intuitively, such fundamental changes in community structure are likely to modify community contributions to functioning and, ultimately, the long-term legacy of perturbation. Yet, the effects of compensatory responses on ecosystem functioning are not well understood, despite recognition that there are multiple instances of species compensation in the geological record following major perturbation events (Aberhan and Kiessling 2006, Tu et al. 2016, Lotze et al. 2006, Pimiento et al. 2017), some of which appear to be a part of a global pattern (Aberhan and Kiessling 2015). Many of these events are associated with regime shifts, in which substantive shifts in functional trait composition and the utilisation of ecospace take place that have concomitant effects on ecosystem properties (Aberhan and Kiessling 2015). It follows, therefore, that the general form of biodiversity-ecosystem functioning curve that emerges from two decades of experimentation (Cardinale et al. 2012) is unlikely to represent the most likely post-disturbance outcome for ecosystem functioning, as the many community processes and dynamics that are known to have compensatory attributes (Gonzalez and Loreau 2009, Thomsen et al. 2017) have not been fully considered within the biodiversity-function experimental framework.

Recent studies have shown that the cause and order of species loss are important determinants of extinction risk (Solan et al. 2004, McIntyre et al. 2007, Thomsen et al. 2017), and that the potential of the surviving community to compensate for the loss or reduction of functionally important species will be dependent on the level of functional redundancy (Walker, 1992, Lawton and Brown, 1993, Chapin et al. 2000, Bihn et al. 2010) and on realized levels of species richness (Naeem and Li, 1997, Yachi and Loreau, 1999, Blüthgen et al. 2016, Houadria et al. 2016). Evidence suggests that the effects of compensation can increase (over-compensate, Pan et al. 2016, Hoover et al. 2014, Hallet et al. 2014), maintain (complete compensation, Ernest and Brown, 2001) or reduce (partial to no compensation, Davies et al. 2012) ecosystem functioning, and that the ecosystem consequences of biodiversity loss could be buffered by the presence of a low number of functionally important species (Reich et al. 2012, Pan et al. 2016). Whilst this may be appealing from a management or conservation perspective, such a synthesis ignores other important aspects of post-perturbation community dynamics. In particular, recent numeric simulations suggest that ecosystem responses to perturbation may be dependent on the type of compensation that develops in the surviving community (Thomsen et al. 2017), but these conclusions have not been empirically tested and are yet to be incorporated into ecosystem models.

Here, I experimentally explore how the effects of biomass compensation following the loss of sediment dwelling marine invertebrates may affect sediment mixing and associated levels of nutrient generation in model benthic communities. Specifically, invertebrate communities were assembled to reflect a sequence of species loss that was random or ordered by body size or rarity to represent likely generic sources of extinction risk (Larsen et al. 2005, Seguin et al. 2014, Hull et al. 2015, Payne et al. 2016) and I simulated post-extinction compensation by increasing the biomass of the 'surviving' species. It was anticipated that functional compensation would be less prominent in communities in which extinction order is related to body size, as body size is often correlated with benthic ecosystem functioning (Solan et al. 2004) and is considered a key species trait at the population level (Brose et al. 2016). Similarly, given that species that occur at low abundances generally contribute little to the ecosystem function inventory, compensation in response to the loss of rare species was expected to lead to elevated levels of functioning (*sensu*, the insurance hypothesis, Ives et al. 2000, Loreau et al. 2003). Irrespective of extinction scenario, I anticipated that compensatory effects would be greater accentuated in communities of high evenness, as traits are more evenly distributed, relative to those assembled to reflect natural evenness levels where functional dominance is a consistent feature of community structure.

3.3 Methods

3.3.1 Faunal and sediment collection

Sediment and the gastropod *Peringia ulvae* were collected from the Hamble Estuary, United Kingdom (50˚52'22.8"N 1˚18'48.9"W), whilst the amphipod *Corophium volutator* was collected from Hayling Island, United Kingdom (50˚49'56.9"N 0˚58'36.8"W) in April 2015. Both *P. ulvae* and *C. volutator* were collected by sieving surface sediment (1 mm and 500 μm mesh respectively). The polychaete *Hediste diversicolor* was collected by hand from Langstone Harbour, Portsmouth (50˚50'46.5"N 1˚00'05.3"W). All species co-occur at all sites, but sampling location reflected logistical convenience. The sediment was sieved (500 μm mesh) in a seawater bath to remove macrofauna, allowed to settle (48 hours to retain the fine fraction, <63 μm), and homogenized by stirring prior to distribution between experimental aquaria.

3.3.2 Experimental design

I assembled replicate (n = 4) transparent acrylic aquaria (12 × 12 cm, 35 cm high; 10 cm sediment overlain by 20 cm seawater, salinity ~ 33) containing all possible permutations of species composition (no macrofauna, species in monoculture and in unique combinations of 2 or 3 spp.) for three scenarios of species loss (Figure 3.1), where the probability of extinction was either random (8 assemblages) or in proportion to body size (4 assemblages) or relative abundance (rarity; 4 assemblages). To test the effects of post-extinction biomass compensation, this set of aquaria were duplicated in order to include a set of non-interactive communities that experienced no biomass compensation, i.e. species biomass declined with loss of species; versus a set of interactive communities in which complete biomass compensation was simulated by maintaining the total biomass of each community across the remaining species (Appendix D, Table A1 and A2).

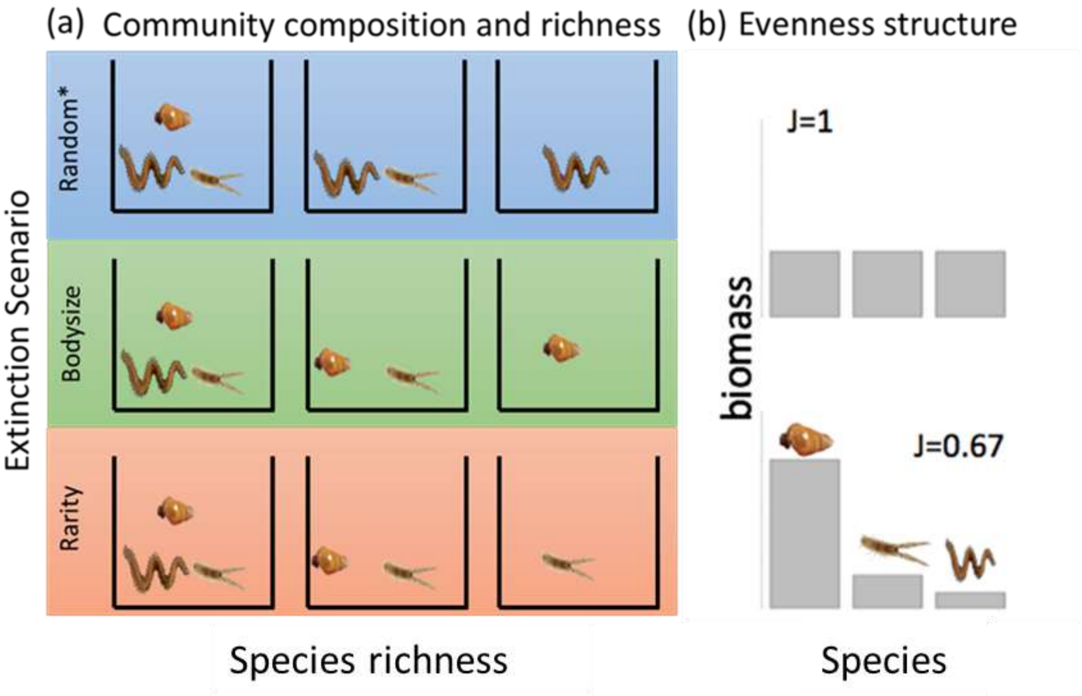

Figure 3.1. Summary of the experimental design. Communities were assembled to reflect extinction scenarios that assumed (a) random extinction, representing the full spectrum of possible species combinations, versus trait-based extinctions ordered by body size (i.e. body mass) or by species relative abundance (rarity), and (b) each extinction scenario was repeated to include a set of non-interactive communities that experienced no biomass compensation (J^{1}) versus a set of interactive communities that experienced complete biomass compensation ($J^{0.67}$). Abbreviations: A, *Peringia ulvae*; B, *Hediste diversicolor*; C, *Corophium volutator*.

This design was repeated across two levels of evenness that represent organism density distributions that are either evenly distributed and typical of most biodiversity-ecosystem function experiments (J^1), or that contain a dominance hierarchy more typical of a natural system ($J^{0.67}$, based on field observations; Biles et al. 2003, Yamanaka et al. 2010, Wohlgemuth et al. 2016). Hence, the experimental design required a total of 256 aquaria (Figure 1), all of which were maintained in a water bath at 12 ºC under a 12:12h light:dark regime and continually aerated for 12 days.

3.3.3 Measurements of ecosystem process and functioning

Fluorescent sediment profile imaging (f-SPI) was used to quantify the extent of infaunal particle reworking (Solan et al. 2004). This technique allows the redistribution of an optically distinct particulate tracer (60 g red coloured sand aquaria^{-1}, fluorescent under ultraviolet light; Brianclegg Ltd, UK) to be quantified from a composite image (Canon 400D, set to 10 s exposure, aperture f5.6 and ISO400; 1864 × 2185 pixel, effective resolution 62.5 μm pixel^{-1}) of the four sides of each aquarium using a custom made, semi-automated macro within ImageJ (1.47v). From these data, the mean (${}^{f\text{-}SPI}L_{mean}$), median (${}^{f\text{-}SPI}L_{med}$) and maximum (${}^{f\text{-}SPI}L_{max}$) depths of particle redistribution were calculated as an indicator of faunal reworking (Hale et al. 2014). In addition, surface boundary roughness (SBR, the maximal vertical deviation of the sediment-water interface), was determined as an indication of surficial activity.

Burrow ventilation was estimated from changes in the concentration of the inert tracer sodium bromide ($\Delta[Br^-]$, mg L^{-1}; Forster et al. 1999) over a 4-hour period (aeration disabled) following the addition of sodium bromide (2.74 g) to raise water column concentration to 9.25 mmol L^{-1} on day 12, determined using a Tecator flow injection auto-analyser (FIA Star 5010 series).

Water column nutrient concentrations ($[NH_4\text{-}N]$, $[NO_x\text{-}N]$ and $[PO_4\text{-}P]$) were determined (Tecator flow injection auto-analyser, FIA Star 5010 series) from samples (10ml, 0.45 μm pre-filtered, day 12) taken from the centre of each aquarium approximately 5 cm above the sediment-water interface.

3.3.4 Statistical analyses

A total of seven statistical models were developed, one for each of the dependent variables (SBR, ${}^{f\text{-}SPI}L_{mean}$, ${}^{f\text{-}SPI}L_{med}$, ${}^{f\text{-}SPI}L_{max}$, $\Delta[Br^-]$, $[NH_4\text{-}N]$, $[NO_x\text{-}N]$, $[PO_4\text{-}P]$). The control treatments were excluded from the statistical analyses, as the focus is to assess the effects of different extinction scenarios and not the presence/absence of macrofauna on ecosystem properties. The initial linear models were assessed visually for normality (Q-Q-plot), homogeneity of variance (plotted residual vs. fitted values), as well as for influential data points (cook's distance) (Zuur et al. 2007). In cases where data exploration indicated heterogeneity of variances, relationships were defined using restricted maximum likelihood (REML) and generalized least squares (GLS) estimation (Pinheiro and Bates, 2000). The use of GLS allows the variance structure to be modelled using appropriate variance functions (here "varIdent" for nominal explanatory variables) rather than transforming the data (Pinheiro and Bates, 2000; Zuur et al. 2007). To identify the optimal random effects structure for each response variable, the model including a variance-covariate term was compared to a model without the variance covariate term using AIC (Akaike Information Criterion) and visually by plotting residuals versus fitted values (Zuur et al. 2007, Zuur et al. 2009). The optimal fixed effects model was estimated using maximum likelihood estimation (ML) determined using a backward selection procedure informed by AIC. (Zuur et al. 2009). All statistical analysis were performed using the 'R' statistical and programming environment (R Development Core Team 2016) and the "nlme" R package (version 3.1-128, 2016; Pinheiro et al. 2017).

3.4 Results

The analyses confirm that both the sequence in which species are extirpated, the level of species richness and the degree of species evenness are important for both ecosystem process (SBR, $^{f\text{-}SPI}L_{mean}$, $^{f\text{-}SPI}L_{med}$, $^{f\text{-}SPI}L_{max}$, $\Delta[Br^-]$) and functioning ($[NH_4\text{-}N]$, $[NO_x\text{-}N]$, $[PO_4\text{-}P]$), and that post-extinction community dynamics are particularly influential in determining ecosystem properties. Indeed, the addition of biomass in the experiments dramatically altered the type and extent of particle reworking and led to changes in nutrient generation. These effects were stronger in even communities (J^1, Figure 3.1 and 3.3) relative to those observed for uneven communities ($J^{0.67}$, Figure 3.2 and 3.4).

3.4.1 Effects on particle reworking and burrow ventilation

In even communities (J^1) surface boundary roughness (SBR) was dependent on a three-way interaction between compensatory response × order of extinction × species richness (L-ratio = 12.4925, d.f. = 4, p = 0.014; Appendix C, model A1,

Figure A2a). Specifically, SBR decreased in non-compensatory communities with decreasing species richness when extinction was ordered by body size or by rarity. In communities with compensatory responses, SBR also decreased with declining species richness when extinction was ordered by body size, but not when extinction was ordered by rarity (Figure 3.2a). However, when extinction was random there was little change in SBR with species richness in both compensatory and non-compensatory communities (Figure 3.2a). Median maximum depth of particle reworking (${}^{f\text{-}SPI}L_{med}$) and the maximum mixed depth of particle reworking (${}^{f\text{-}SPI}L_{max}$) were dependent on the interactive effects of compensatory response × order of extinction × species richness (${}^{f\text{-}SPI}L_{med}$: L-ratio = 32.2030, d.f. = 4, $p < 0.0001$; Appendix C, model A2, Figure A2b; ${}^{f\text{-}SPI}L_{max}$: L-ratio = 18.9542, d.f. = 4, p = 0.0008; Appendix C, model A3, Figure A2c). In communities with compensation, ${}^{f\text{-}SPI}L_{med}$ decreased when extinction occurred randomly and when ordered by body size, but in communities without compensation, ${}^{f\text{-}SPI}L_{med}$ decreased when extinction was ordered by body size or by rarity. Overall, the maximum mixing depth (${}^{f\text{-}SPI}L_{max}$) decreased strongly with declining species richness irrespective of extinction scenario, with little difference between communities with and without compensation (Figure 3.2c). Burrow ventilation ($\Delta[Br^-]$) significantly reduced with species richness irrespective of extinction or compensation scenario (L-ratio = 6.4222, d.f. = 2, p = 0.0403; Appendix C, model A4, figure A1).

For uneven communities representative of natural systems ($J^{0.67}$), the results revealed that surface boundary roughness and the median mixed depth of particles reworking was dependent on the interaction compensatory response × order of extinction × species richness (SBR: L-ratio = 12.5304, d.f. = 4, p = 0.0138; Appendix C, model A8, figure A3a; ${}^{f\text{-}SPI}L_{med}$: L-ratio = 23.8706, d.f. = 4, p = 0.0001; Appendix C, model A9, figure A3b). Patterns for SBR under random extinction showed a small net decline with decreasing species richness, with a slightly greater decrease in the presence of compensation (Figure 3.3a). When extinction was ordered by body size, SBR in both compensatory and non-compensatory communities was highest at intermediate levels of species richness and decreased with species loss (Figure 3.3a). In contrast, when extinction was driven by species rarity (Figure 3.3a), SBR increased with decreasing species richness for both compensatory and non-compensatory communities.

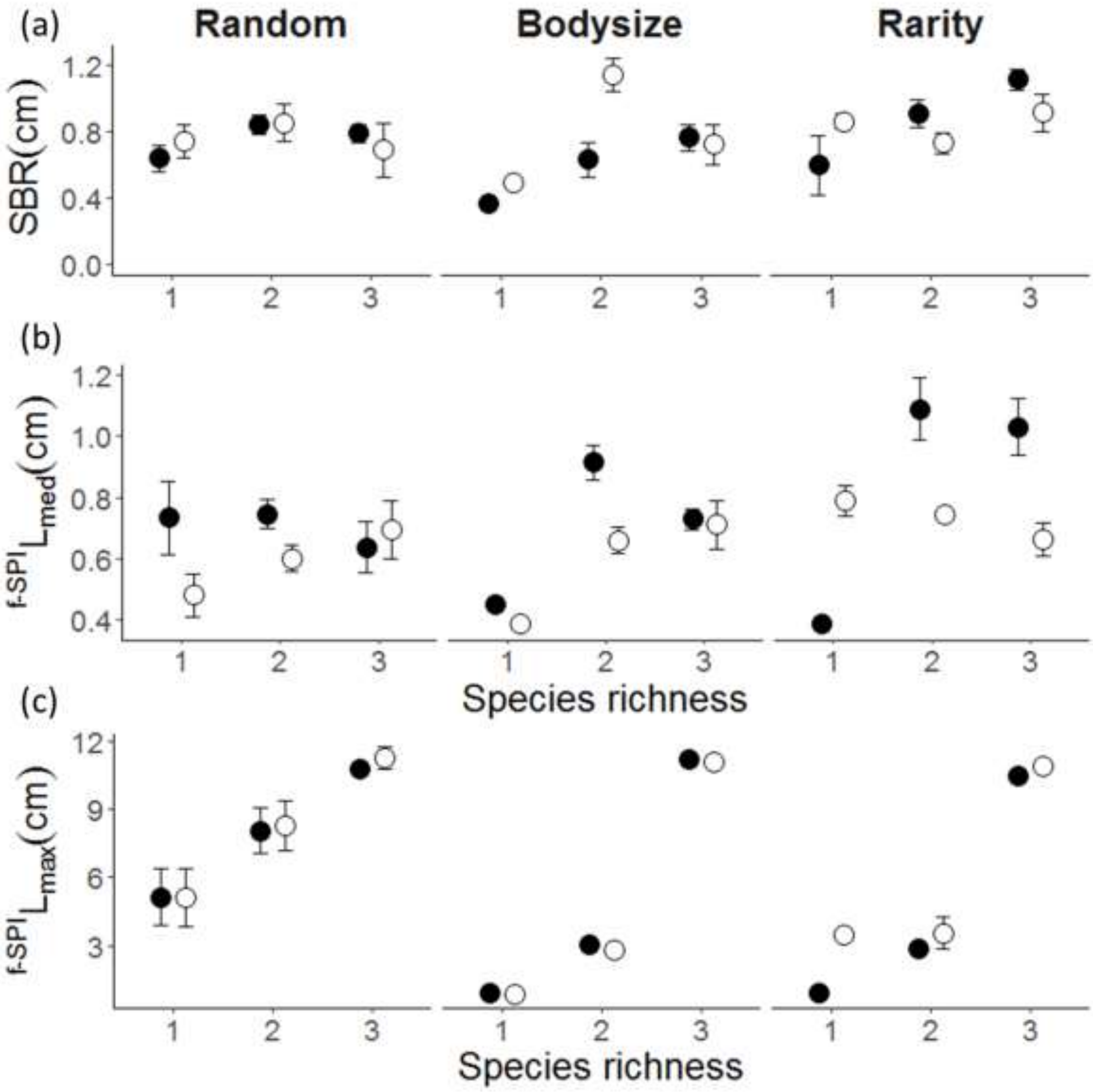

Figure 3.2. Interactive effects of extinction scenario (random or ordered by body size or rarity), species richness and biomass compensation (present, closed circle; absent, open circle) on mean (± s.e., n = 4) (a) surface boundary roughness (SBR), (b) median depth of particle reworking ($^{f\text{-}SPI}L_{med}$) and (c) maximum depth of particle reworking ($^{f\text{-}SPI}L_{max}$) for communities with even species distribution (J^1). For visual clarity, compensation levels are horizontally offset.

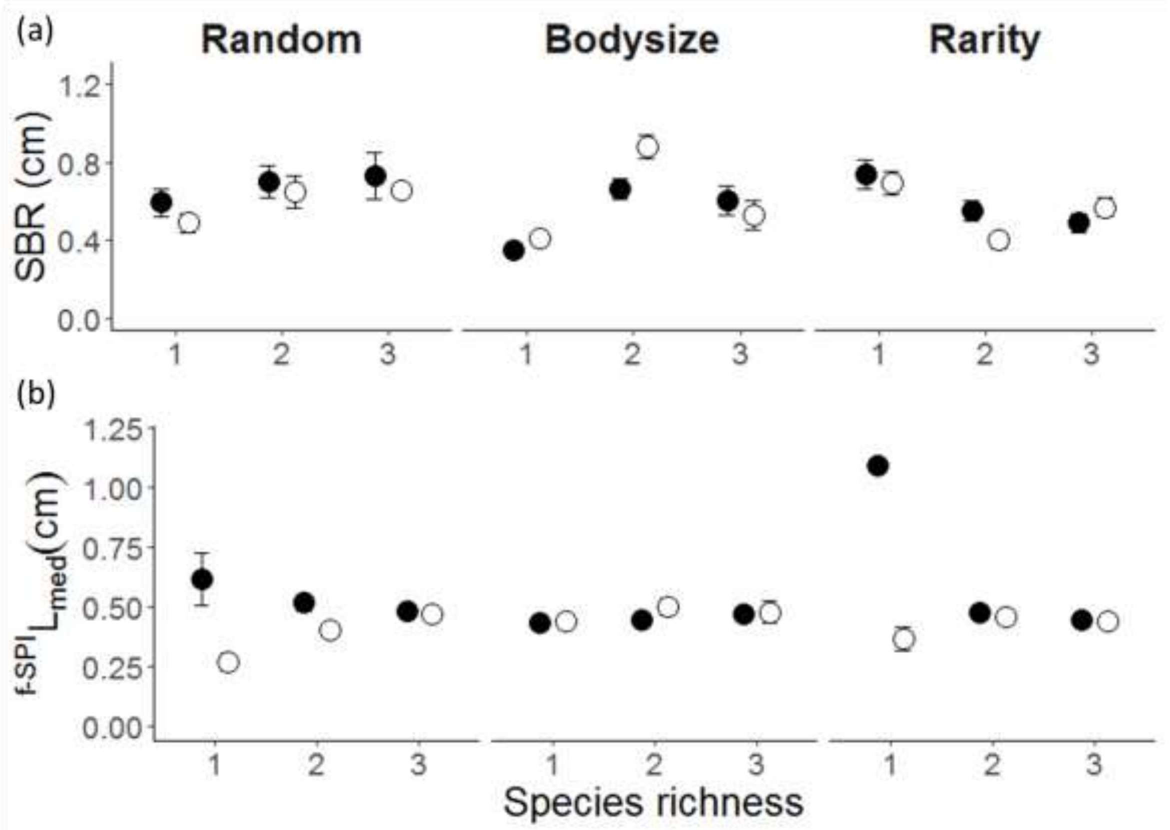

Figure 3.3. Interactive effects of extinction scenario (random or ordered by body size or rarity), species richness and biomass compensation (absent, open circle; present, closed circle) on mean (± s.e., n = 4) (a) surface boundary roughness (SBR) and (b) maximum depth of particle reworking (f-SPILmax) in uneven communities (J0.67). For clarity, compensation levels are offset horizontally.

When extinction was random or ordered by rarity, median mixing depth decreased with species richness in communities without compensation, but increased in communities with compensation (Figure 3.3b). When extinction was ordered by body size, irrespective of compensatory dynamics, ${}^{f\text{-}SPI}L_{med}$ was maintained as species richness declined (Figure 3.3b). There was no effect of compensation on the maximum mixed depth of particle reworking or on burrow ventilation, both of which were dependent on an interactive effect of species richness × order of extinction (${}^{f\text{-}SPI}L_{max}$: L-ratio = 52.8775, d.f. = 4, $p < 0.0001$; Appendix C, model A10; $\Delta[Br^-]$: L-ratio = 16.2130, d.f. = 4, $p = 0.0027$; Appendix C, model A11, figure A2a and b).

3.4.2 Effects on nutrient generation

In community assemblages with even species distribution, water column nutrient concentrations were affected by the interactive effects of compensatory response × order of extinction ([NH_4-N]: L-ratio = 23.3478, d.f. = 2, $p < 0.001$; Appendix C, Model A5, figure A4a); [NO_x-N]: L-ratio = 7.4958, d.f. = 2, $p = 0.0236$; Appendix C, Model A6, figure A4c; [PO_4-P]: L-ratio = 8.3114, d.f. = 2, $p = 0.0157$; Appendix C, Model A7, figure A4e), as well as compensatory response × species richness ([NH_4-N]: L-ratio = 25.4207, d.f. = 2, $p < 0.001$; Appendix C, Model A5, figure A4b; [NO_x-N]: L-ratio = 26.2201, d.f. = 2, $p < 0.001$; Appendix C, Model A6, figure A4d). In the presence of compensatory dynamics [NH_4-N] and [NO_x-N] showed similar patterns to one another, irrespective of extinction scenario (figure 3.4a and 3.4c respectively), however in the absence of compensatory dynamics [NH_4-N] and [NO_x-N] substantively decreased when extinctions were ordered by rarity. For compensatory response × species richness, [NH_4-N] decreased with species loss when compensation was present (figure 3.4b), whilst [NO_x-N] increased with decreasing species richness, irrespective of compensation scenario (Figure 3.4d).

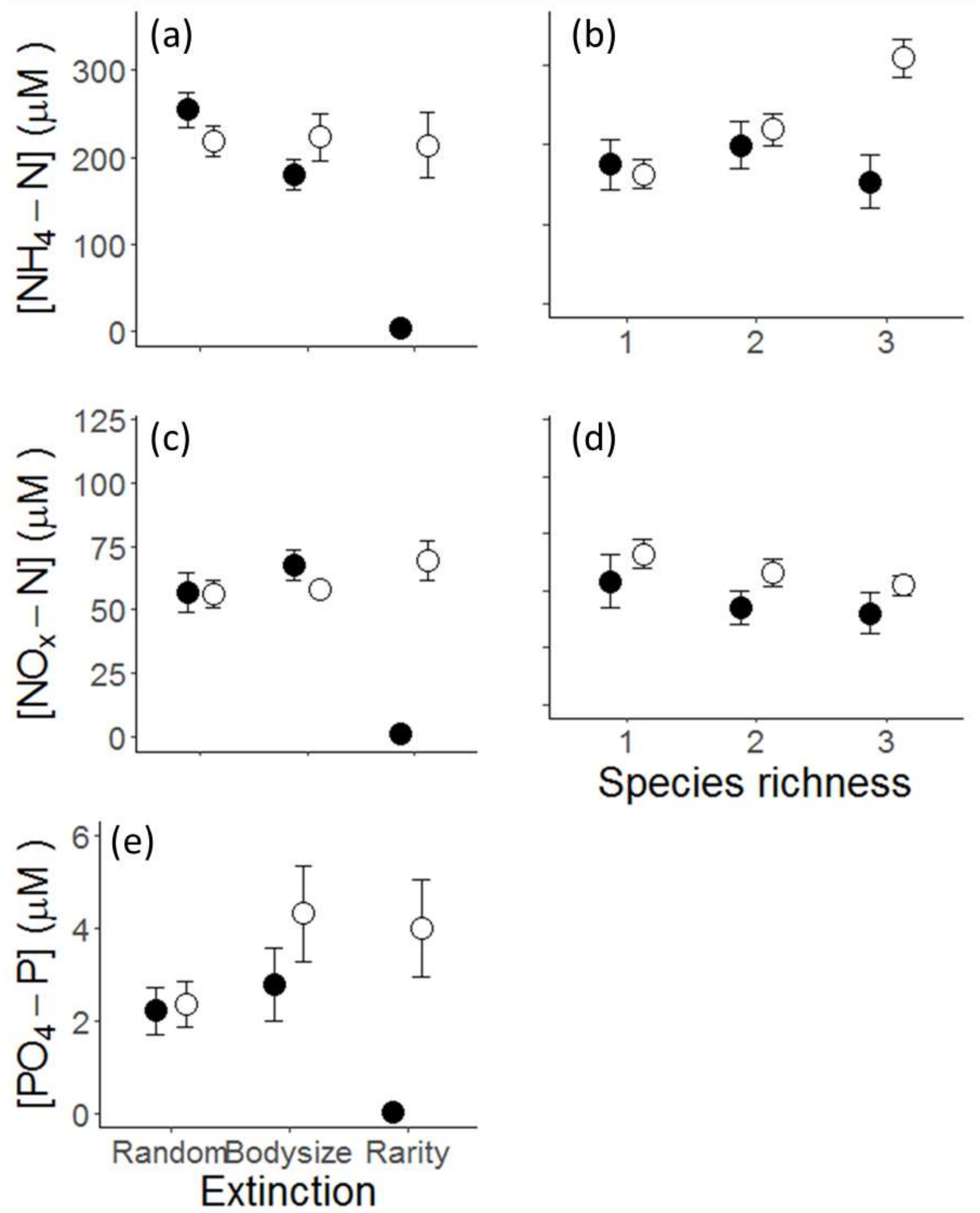

Figure 3.4. Effects of extinction scenario (random, body size, rarity) in the absence (open circle) versus (filled circle) presence of compensation in even ($J^{1.00}$) communities on mean (± s.e., n = 4) [NH_4-N], [NO_x-N], and [PO_4-P].

[PO_4-P] was highest in communities with compensation when extinction was ordered by body size or rarity, but lowest in the absence of compensatory dynamics when extinction was driven by rarity.

In uneven communities, irrespective of compensation scenario, [NH_4-N] and [NO_x-N] were dependent on the interactive effects of species richness × order of extinction ([NH_4-N]: L-ratio = 24.6755, d.f. = 4, p = 0.0001; Appendix C, Model A12, figure A3a; [NO_x-N]: L-ratio = 9.78363, d.f. = 2, p = 0.0442; Appendix C, Model A13, figure A3a). In contrast, [PO_4-P] was dependent on an interaction between compensatory response × species richness ([L-ratio = 6.51340, d.f. = 2, p = 0.0385; Appendix C, Model A14, figure A5). Overall [PO_4-P] increased with decreasing species richness and was higher in the presence of compensatory dynamics (Figure 3.5).

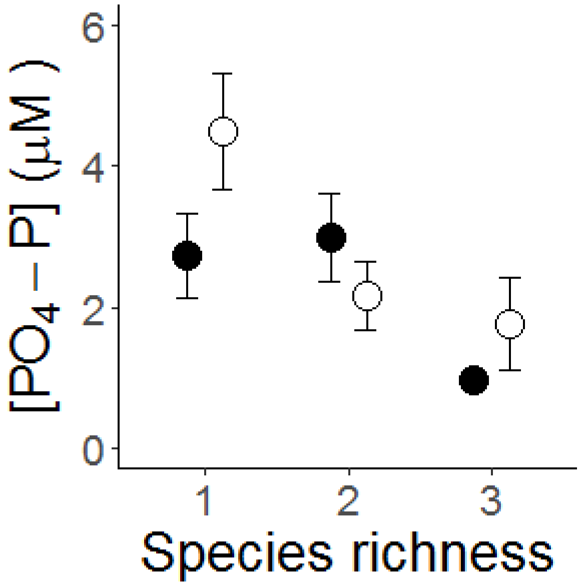

Figure 3.5. The interactive effects of species richness and compensatory dynamics (present, filled circle; absent, open circle) for uneven ($J^{0.67}$) communities on mean (± s.e., n = 4) [PO_4-P].

3.5 Discussion

Our study provides empirical evidence that the ecosystem consequences of extinction can be fundamentally altered, beyond the effects attributable to the loss of biodiversity, by post-extinction compensatory responses within the surviving community (Thomsen et al. 2017). However, I find that the strength of such a response is contingent on compositional differences that arise from the order of species loss and the level of post-extinction species richness (Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007). Further, I find that the effects of biomass compensation, although not as strong as anticipated, are less prominent in uneven communities that typify natural community structure than they are in communities with an even species distribution, as per the archetypal design of biodiversity-ecosystem function experiments (Cardinale et al. 2012). This distinction is important because the majority of experimental manipulations of biodiversity fall short of allowing community dynamics and compensatory responses to fully develop (Langenheder et al. 2010, Langenheder et al. 2012), reducing the likelihood of conveying the most likely community response to extinction for a natural setting (Velland et al. 2013, Velland et al. 2017). Recent work has shown that adjustments to community structure in the absence of species loss can have consequential effects on ecosystem functioning that relate to the rank order of species dominance (Wohlgemuth et al. 2016), rather than dominant species identity (Orwin et al. 2014, Wilsey & Potvin 2000), and changes in species density and biomass (Ieno et al. 2006, Schmitz et al. 2013, McKie et al. 2008, Reiss et al. 2011, Winfree et al. 2015). Such transient changes in how dominance and identity are represented as communities respond to forcing over time (Hillebrand et al. 2018) have important ramifications for the design and analysis of contemporary biodiversity experiments (Bracken et al. 2008, Naeem 2008), as well as the relevance of their findings for practical application (Srivastava and Velland, 2005), and reinforce the role of species traits and trait variability (Albert et al. 2010) as a primary determinant of ecosystem functioning (Cardinale et al. 2012).

At a broader ecological level, our findings indicate that the ecological consequences of extinction are unlikely to be foreseeable when projections are based on extant community properties and dynamics (Dunhill et al. 2018) because the type, timing and severity of extinction generates a legacy that influences the capacity of, and way in which, the surviving community will respond and affect ecosystem properties. The complexities of how species respond to novel circumstances are difficult to anticipate and are yet to be fully explored, even in relation to near term aspects of climate change (Nicholls et al. 2018), but understanding variability in species responses to abiotic and biotic change (Godbold and Solan 2009), as well as the context-dependent contributions they make to ecosystem functioning over time (Langenheder et al. 2010, Somero 2010, Godbold and Solan 2013) will help to refine the likelihood of various ecological outcomes against specific scenarios. Here, biomass compensation had a positive effect on sediment reworking in even communities, especially at intermediate levels of species richness, whilst incidences of overyielding were particularly pronounced at high levels of species richness (Lembrechts et al. 2018). For uneven communities, functioning was only maintained when extinctions were random or ordered by rarity. However, when extinction was driven by body size in both even and uneven communities, pre-extinction levels of sediment mixing could not be maintained in the surviving community, regardless of the identity and ordering of the compensating species because smaller species contribute little to bioturbation (Solan et al. 2004, Seguin et al. 2014). In contrast, where species shared physiological and/or behavioural traits across the species pool, as was the case for surface boundary roughness, functioning was generally maintained across the species richness gradient.

Our findings are in broad agreement with previous hypotheses that state that the potential or probability for compensatory dynamics countering the consequences of biodiversity loss will depend on the level of functional redundancy within a system (Naeem and Wright, 2003, Loreau and Mazancourt, 2013). I find that the effect of extinction order is driven by species-specific differences within community, especially the disproportionate effect of *Hediste diversicolor* on the depth of particle mixing and the inability of the mud snail *Hydrobia ulvae* to replace the loss of bioturbation activity previously performed by other species (Davies et al. 2012, Hale et al. 2014, Huijbers et al. 2015). Whilst this demonstrates that compensatory effects are not always able to buffer the deterioration of ecosystem processes and functions associated with species loss (Hale et al. 2017), our data suggests that, on average, compensatory mechanisms are sufficient to provide some relief, in whole or in part, to the negative ecological consequences of species loss. Indeed, nutrient release was either maintained or increased in the presence of compensation, even when extinction was driven by body size, and there is some evidence to suggest that other mechanisms may lead to overyielding prior to the development of community dynamics. Although the present study was unable to account for processes that act over longer time scales, such as adaptation (Torres Dowdal et al. 2012, Wong and Candolin 2015) and evolutionary change (Pfennig et al. 2010, West-Eberhard 2005), our study suggests that the immediate challenge is to determine the circumstances under which species exhibit compensatory responses and whether or not the presence of compensatory processes refine understanding of biodiversity-function relations. In the meantime, I advocate that a focus for management efforts should be the need to prioritise the conservation of species with functional traits, whilst recognizing the importance compensatory capacity as ecosystems change with the biological and environmental context (Fetzer et al. 2015), that are important for maintaining key ecosystem functions and the delivery of services.

3.6 Acknowledgements

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Chapter 4: Capacity of benthic communities in sustaining ecosystem functioning depends on the intensity of anthropogenic forcing

This chapter is in preparation for submission to the Journal of Applied Ecology: **Thomsen M S**, Garcia C, Bolam S G, Parker R, Godbold J A, Solan M, *Capacity of benthic communities to support shelf sea ecosystem functioning through compensatory responses depends on the intensity of anthropogenic forcing*. Journal of Applied Ecology.

4.1 Abstract

Anthropogenic activities that lead to a loss of biodiversity can vary in intensity, yet it is not clear whether the compensatory responses of surviving species are sufficient to offset any associated loss of ecosystem function across the full extent of a perturbation gradient. Here, I identify changes in marine benthic invertebrate community abundance and biomass associated with bottom trawling to parameterise models that explore the potential for community-level compensation to maintain ecosystem functioning across four scenarios of trawling intensity. Our models show that several indicators of ecosystem functioning (oxygen penetration depth, total organic carbon, total organic nitrogen, chlorophyll and phaeopigment) are largely maintained across different scenarios of fishing intensity, despite considerable changes in community structure and composition, but the ability to compensate is less pronounced at low and high levels of perturbation. The ability of communities to functionally compensate reflects increases in faunal activity and abundance that translate into a small proportional change in the traits most important for ecosystem functioning. The ability of compensatory responses to offset declines in ecosystem functioning at regional scales will depend on local variations in assemblage structure, the spatio-temporal distribution of perturbation intensity and historical precedent. Understanding when compensatory mechanisms that support multifunctional ecosystems are activated, their relative contribution to ecosystem functioning, and the long term viability of any response will be important to the development of long-term management strategies that ensure the future sustainability of ecosystems.

4.2 Introduction

Understanding the effects of alterations to biological systems on ecosystems processes and functions remains one of the greatest challenges facing conservationists and environmental managers (Pereira et al. 2012, Butchart et al.

2012). Current understanding is based on a plethora of experimental studies that have manipulated different aspects of biodiversity and measured various ecosystem functions, including primary productivity, nutrient cycling and decomposition, and confirm declining trends of ecosystem properties with reduced biodiversity (Cardinale at al. 2012). The complexities of how natural communities respond to the influence of environmental forcing represent a major obstacle in determining the most likely ecosystem outcome (Velland et al. 2013, Velland et al. 2017) due to post-disturbance community turnover and restructuring, including functionally important shifts in relative abundance and dominance of species (Stachowicz et al. 2007). Moreover, the ecosystem consequences of altered biodiversity in natural communities are moderated by compensatory species dynamics (Thomsen et al. 2017), leading to partial (Davies et al. 2012), complete (Peters et al. 2009), or over (Pan et al. 2016) compensation in ecosystem functioning. Such changes can lead to new opportunities (e.g. *via* competitive release, Bolnick et al. 2010, Holbrook and Schmitt 1995) and have disproportionate effects of functioning (Wohlgemuth et al. 2016) that are difficult to anticipate, yet the form, prevalence and relative importance of compensatory responses in extant communities have received limited attention and are largely unknown (Houlahan at al. 2007, Bai at al. 2004), despite a strong theoretical support base (Gonzalez and Loreau 2009, Loreau 2010, Loreau 2001).

While it is important to acknowledge the difficulty in detecting and quantifying the effect of compensatory dynamics in natural systems (Houlahan at al. 2007), numeric simulations generate an expectation that compensatory responses will be an important determinant of post-disturbance levels of ecosystem functioning (Solan at al. 2004, McIntyre et al. 2007, Chapter 1). Moreover, global extinctions are preceded by extirpations at both local and regional scales, and local loss of species has been demonstrated to lead to direct impacts on local ecosystem services (Riggio et al. 2013). Empirical evidence demonstrates the importance of compensation by dominant species in maintaining ecosystem functions (Bai et al. 2004). When dominant species are lost from a system ecosystem functions decline dramatically, however when present, dominant species mitigate the functional consequence associated with the loss of other species (Pan et al. 2016, Smith and Knapp 2003). Further, the magnitude of functional effects depends on which functional traits are removed from the species community, highlighting that the effects of compensation are identity-dependent (Pan et al. 2016). As compensation matters for ecosystem function, there is an urgent need to examine the effect of compensatory responses along gradients of disturbance.

Bottom trawling is the most widespread source of anthropogenic physical disturbance to seabed habitats (Halpern et al. 2008, Hiddink et al. 2017, Foden et al. 2011). Although several fisheries have demonstrated complete recovery following reductions in fishing pressure (Costello at al. 2016) recovery rates tend to vary and can be difficult to predict (Hutchings 2000, Neubauer at al. 2013). Here, I use marine sediment-dwelling invertebrate communities to parameterize numerical models of bioturbation – a key mediator of sediment community functioning – to establish the extent to which compensatory dynamics are able to moderate ecosystem functioning across a gradient of fishing intensity. Our expectation was that the compensatory response of the community would peak at intermediate levels of disturbance, and that ecosystem functioning would be maintained for low to medium levels of fishing intensity, but not for the highest levels of fishing intensity. In doing so, our objective was to understand whether there are habitat specific thresholds that delimit the natural capacity of the system to absorb perturbation, and to determine whether abrupt changes in ecosystem functioning occur should such thresholds be crossed.

4.3 Methods

4.3.1 Area of study

Data for the present study were collected in the Celtic Sea, southwest coast of the UK, during the Shelf Seas Biogeochemistry program (RRS Discovery, cruise DY021, March 2015). A region within the southern Celtic Sea was selected and found to be representative of the Celtic Sea and the UK shelf as a whole with respect to the range and diversity of its sedimentary habitats and macrofaunal assemblages and sediment biogeochemical processes (Thompson et al. 2017). Using observed data from this constrained region of the Celtic Sea reduces the effect of a number of confounding variables (depth, temperature, hydrography) which are otherwise known to have large-scale influences on seabed benthic-pelagic coupling and processes which affect carbon and nutrient storage within sediments (Thompson et al. 2017).

4.3.2 Sample collection

Sediment cores were collected from 55 stations (Appendix E, Figure A1) using a 0.08 m^2 NIOZ (Netherlands Institute for Sea Research, Texel) corer. The sediment composition of the cores varied in type, from mud, sandy-mud, muddy-sand, sandy mud, mixed to coarse sediments (for detailed site characterization see Thompson et al. 2017). Benthic macrofauna together with a suite biogeochemical metrics, including total organic carbon (TOC) and nitrogen (TON), chlorophyll *a* (chl-*a*) and phaeopigment were collected from the sediment cores at each station. These observations provide a baseline of the spatial environmental conditions of 2015 (Figure 4.1).

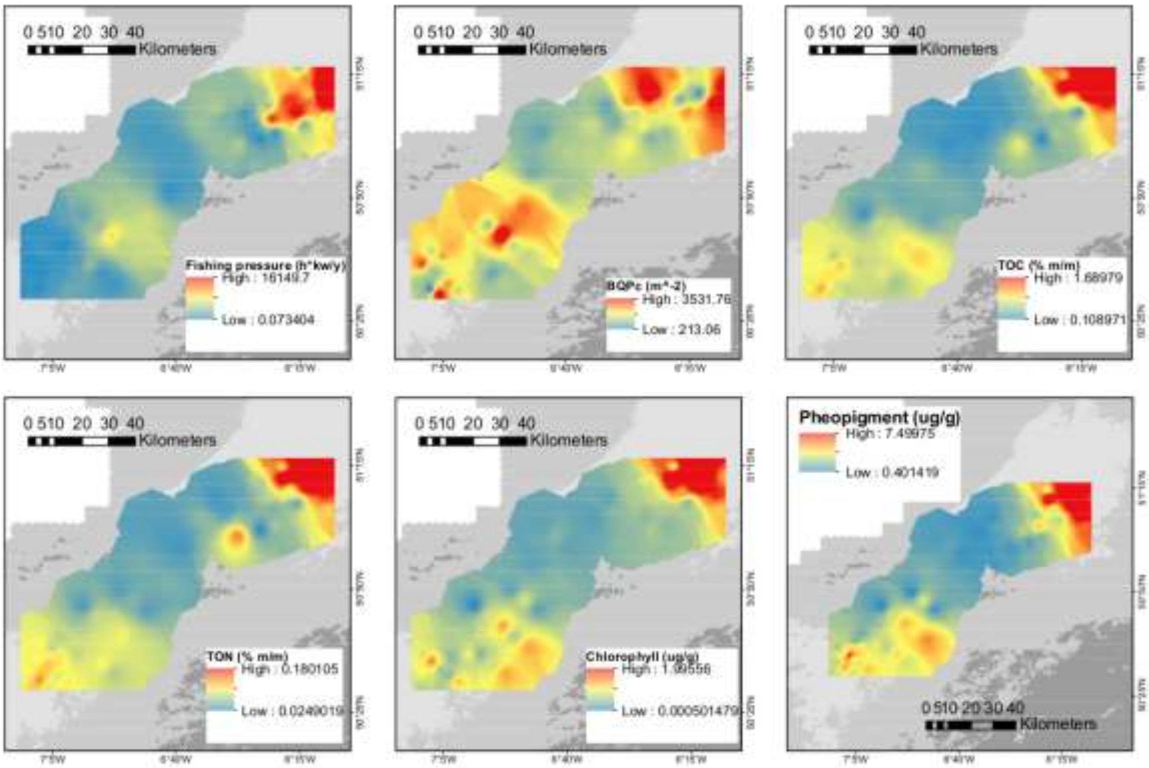

Figure 4.1. Spatial interpolation of fishing pressure and ecosystem properties; (a) trawling intensity ($h \times kw\ yr^{-1}$), (b) BQP_c (m^{-2}), (c) TOC (%), (d) TON (%), (e) Chl-*a* (μg g^{-1}), (f) phaeopigment (μg g^{-1}) across muddy (n=35) sandy (n=16), mixed (n=2), coarse (n=1) sediments.

The composition of macrofaunal seabed community was determined by sieving (1 mm), after which all taxa were preserved according to standard procedure (using formalin solution) and identified to the lowest possible taxon and enumerated (abundance) and wet biomassed (further details can be found in Godbold et al. 2017 or Hale et al. 2017). Sediment organic carbon and nitrogen content was estimated using an elemental analyser (Hedges and Stern 1984, Kirsten 1979), while sediment chl-*a* and phaeopigment concentrations were analysed using 90% acetone pigment extracts (before and after acidification) of known weights of freeze dried sediments (method modified from Tett et al. 1987). For further details see supplementary material in Thompson et al. (2017).

4.3.3 Approach, analysis and data

I modelled community species abundance and biomass using simple models parameterised by species responses to increasing demersal trawling pressure. The trawling gradient, ranging from 0 to 5411.3 k×hr yr^{-1} was established exclusively within muddy sediment habitats (n=35) on the basis of bottom trawling information (normalised by year) from vessel monitoring systems (VMS) data from 2009 to 2014 with cell size 0.05 decimal degrees (Lee et al. 2010). Gear type was derived from vessel speeds, which varied from 1-6 knots.

The trawling gradient was divided by quartiles, each quartile forming a scenario of increasing trawling intensity (Q1;0-172.0 k×hr yr^{-1}, Q2;172.0 691.0 k×hr yr^{-1}, Q3; 691.0-1789.0 k×hr yr^{-1}, Q4; 1789.0-5411.0 k×hr yr^{-1}). The change in median species abundance between each of the quartiles along the trawling gradient represents the median species response to changing intensity of trawling that parameterises the models and determines the four model communities, one for each of the trawling scenarios. This median difference was used as a species-specific multiplier for all possible combinations of directional change in trawling intensity relative to the reference level (i.e. the trawling intensity of 2015), enabling the calculation of species abundance and biomass for each of the novel communities in each trawling intensity (Figure 4.2). Only species biomass and abundance in stations that already lie within the desired level of trawling remain the observed macrofauna samples. The number of observed (i.e. non-modelled) macrofaunal data varies depending on the scenario of trawling intensity ($n_{Q1} = 10$, $n_{Q2} = 8$, $n_{Q3} = 8$, $n_{Q4} = 9$).

Changes in species biomass between trawling intensity quartiles were also modelled in congruence with the species-specific median abundance change. Where species went from absent to present, the median species biomass of all stations within the destination quartile became the novel biomass. Similarly, where species were previously not present with respect to abundance, the median abundance of all sites within the quartile of interest became the species abundance in the novel community.

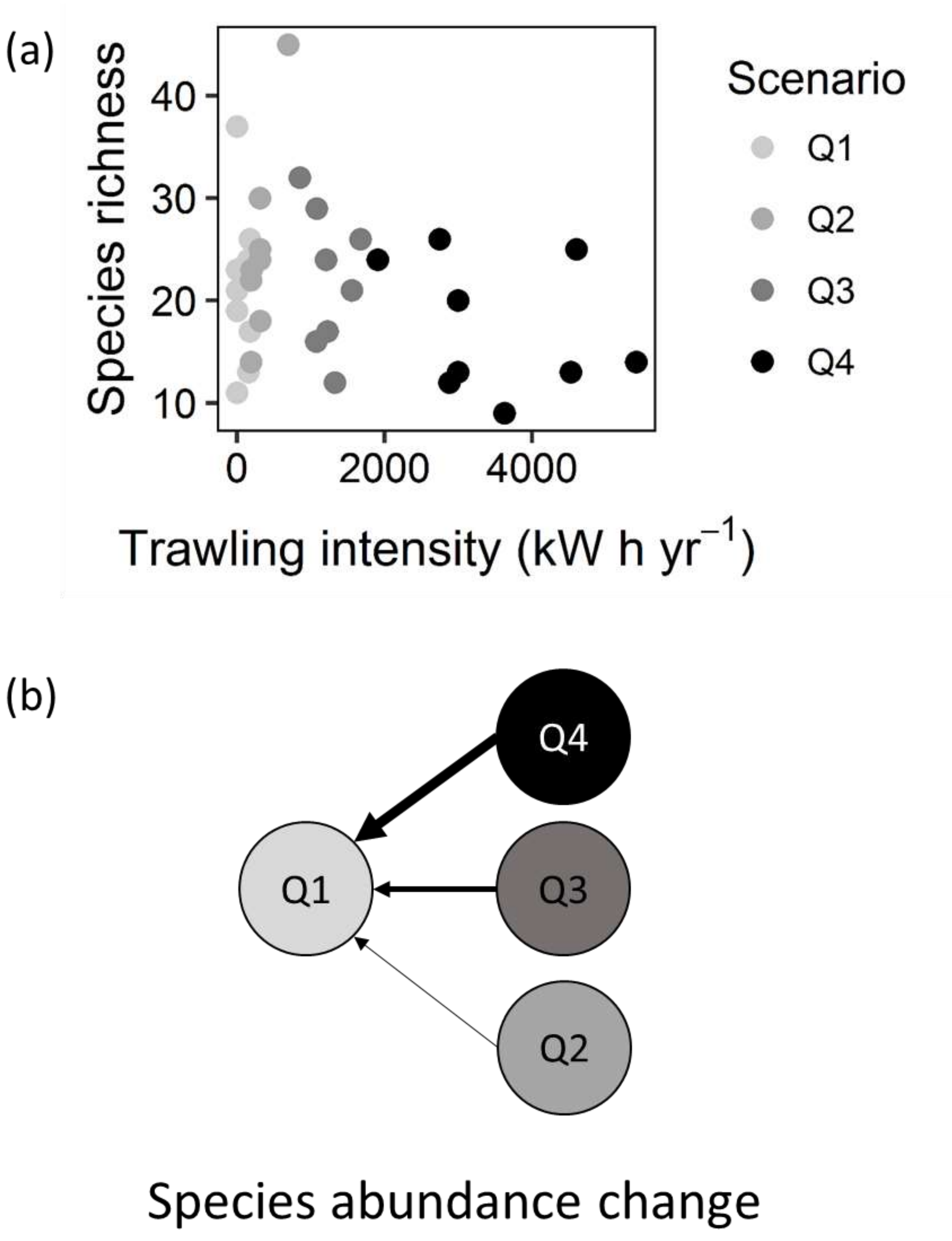

Figure 4.2. Schematic illustrating the methodology applied to create scenarios alternative trawling intensity. Trawling (vessel monitoring satellite 2009-2014) data for each station within area of study (a) form the basis of trawling gradient, spanning four individual scenarios of trawling intensity, each scenario (Q1, light grey; Q2, grey; Q3, dark grey; Q4, black) make up 25% of the observed data (b). Species-specific responses to trawling intensity were calculated based on the Δ median species abundance between each trawling scenarios. For instance, in the case of trawling scenario Q1 (b), differences in species abundance between

scenario Q2, Q3 and Q4 to abundance of Q1 were computed for each individual species. These unique species responses were used to model the community data for trawling scenario Q1 (b). Hence, one quarter of the data in scenario Q1 consist of observational (non-modelled) data i.e. stations already experiencing the trawling intensity of scenario Q1, while the other three-quarters consist of modelled data evenly distributed between scenario Q2, Q3 and Q4. Species responses were computed for each of the remaining trawling scenarios (as per scenario Q1; b), which parameterise the trawling scenarios. Species-specific biomass responses were calculated using the same methodology.

I calculated BQP_c (see section 4.2.4) for the muddy sediment communities (n=35), within the environmental context of 2015. The relationship between BQP_c2015 and each of the biogeochemical metrics were determined by a linear model (Table S1). The relationship between BQP_c2015 and the biogeochemical metrics was established for stations of low to intermediate fishing pressure to control for the effect of fishing on the relationships. Each of the 5 relationships was used to predict the respective ecosystem properties for each of the novel communities under the modelled scenarios of trawling. Juveniles, and species with a total biomass <0.01g across all stations, were excluded from the analysis.

Data were then interpolated using inverted distance weighted (IDW) method (ArcGIS version 10.5). The substrate map representing predictions of EUNIS habitats was also created in ArcGIS, the GeoTIFF was downloaded from the PANGAEA website (https://doi.org/10.1594/PANGAEA.845468; Stephens and Diesing 2015).

4.3.4 BQP$_c$

I calculated BQP_c, a novel index integrating the bioturbation potential, BP_c (Solan et al. 2004) and bioirrigation proceses, via the fluid transport potential (QP_c; Hale et al. in prep):

$$BQP_c = \sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times M_i \times R_i \times A_i \times {}^{a}Q_i \ \times {}^{p}Q_i$$

Where B_i is species biomass, A_i is species population abundance, M_i is activity level of an individual species, R_i is the species reworking trait, ${}^{a}Q_i$ is the ventilation rate of an individual species and ${}^{p}Q_i$ represents the sediment volume passively influenced by an individual species' ventilation (Meysman et al. 2006).

4.3.5 Species evenness J'

Pielou's index for species evenness was calculated, *J'* (Pielou 1975), which is a product expressed by the Shannon information scaled by the maximum information, to measure species evenness for each community:

$$J' = \frac{H'}{\ln(S)'}$$

Where *H'* represents the observed value of Shannon's diversity index, and *S* is the community species richness. Pielou's index of species evenness is widely used as it captures changes in biodiversity related to dominance, and thus complimenting other measures of biodiversity (Hillebrand et al. 2017).

4.4 Results

Increases in bottom trawling influenced the way in which seabed communities are structured. Total community abundance increased from 25163.75 to 35452.96 m^2 from trawling scenario Q1 to Q2, before drastically declining, reaching a new community low of 12757.28 m^2 at scenario Q4 (Figure 4.3a). Total abundance levels predicted for trawling intensity of scenario Q4 are similar to that of 2015 (14890.64 m^2; Figure 4.3a). Patterns of total community biomass revealed a different response to scenarios of trawling intensities relative to total community abundance. Total biomass increased considerably from 240.30g under scenario Q1 to 358.27g m^{-2} at scenario Q2, followed by a minor increase to 362.81g m^{-2} at scenario Q3 before decreasing to 222.10g m^{-2} under scenario Q4 (Figure 4.3b). Total biomass observed in 2015 was 247.10g m^{-2}, which is comparable to biomass levels of scenario Q1 and Q4. Trawling had no community-wide effect on species richness, which remained constant at 102 species, irrespective of the trawling intensity (Q1-Q4), this was also the value observed in 2015 (Figure 4.3c). However, other aspects of biodiversity were modified. Pielou's evenness *J'* experienced an overall shift in the relative abundance of species towards a more evenly structured community (higher values of *J'*), hence less influenced by a few common species, as trawling intensified. Pielou's evenness is relatively low at scenarios Q1 and Q2 ($J^{0.64}$). Elevated trawling intensities lead to an increase to $J^{0.71}$ at scenario Q3, peaking at scenario Q4 ($J^{0.77}$), which is just below observed levels ($J^{0.81}$; Figure 4.3d).

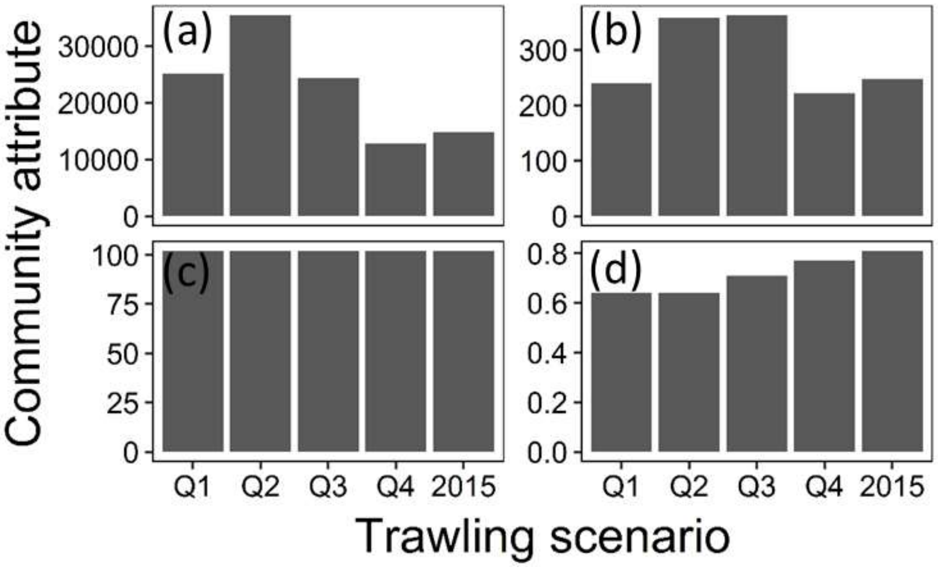

Figure 4.3. Community attributes; (a) total abundance, (b) total biomass, (c) species richness (d) evenness J' for each scenario of trawling (Q1-Q4, n = 35) and observations (2015).

Scenarios of trawling intensity revealed community restructuring in the relative distribution of functional traits associated with sediment reworking and burrow irrigation (Figure 4.4). The community response patterns followed the trend of total abundance, increasing from scenario Q1 to Q2, followed by a rapid decrease at a gradual rate from scenario Q2 to Q4. Generally, there was a strong congruence between the relative abundance and composition of functional traits in trawling scenario Q4 and the 2015 functional trait distribution (Figure 4.4a-d). Biodiffusers remained relatively stable irrespective of the scenario of trawling, whereas up/down-ward conveyors and surficial modifiers showed considerable fluctuation in relative abundance (Figure 4.4a). The abundance of sessile organisms showed strong trawling intensity dependency, increasing from Q1 to Q2 before rapid declining as the intensity of trawling increased. However, slow-moving species and tube-dwellers, in particular, displayed limited change across scenarios (Figure 4.4b). Species of intermediate ventilation potential (10-1000 ml hr^{-1} $individual^{-1}$) increased substantially in abundance from Q1 to Q2. However, beyond Q2, intermediate ventilators decreased, reaching similar levels of abundance to low-intensity trawling conditions at Q4. Low ventilating organisms (0-10 ml hr^{-1} $individual^{-1}$) decreased dramatically from trawling conditions of scenario Q2 to Q4 (Figure 4.4c). Increasing trawling intensity also altered the relative proportion of species that passively influence the sediment volume (Figure 4.4d). Abundance of organisms that provide a diffusive flow remained relatively unchanged, whereas species providing a constrained flow through or over body (e.g. bivalves) showed considerable variation in abundance depending on scenario of trawling intensity, increasing from Q1 to Q2, before drastically declining from scenario Q2 to Q4 (Figure 4.4d).

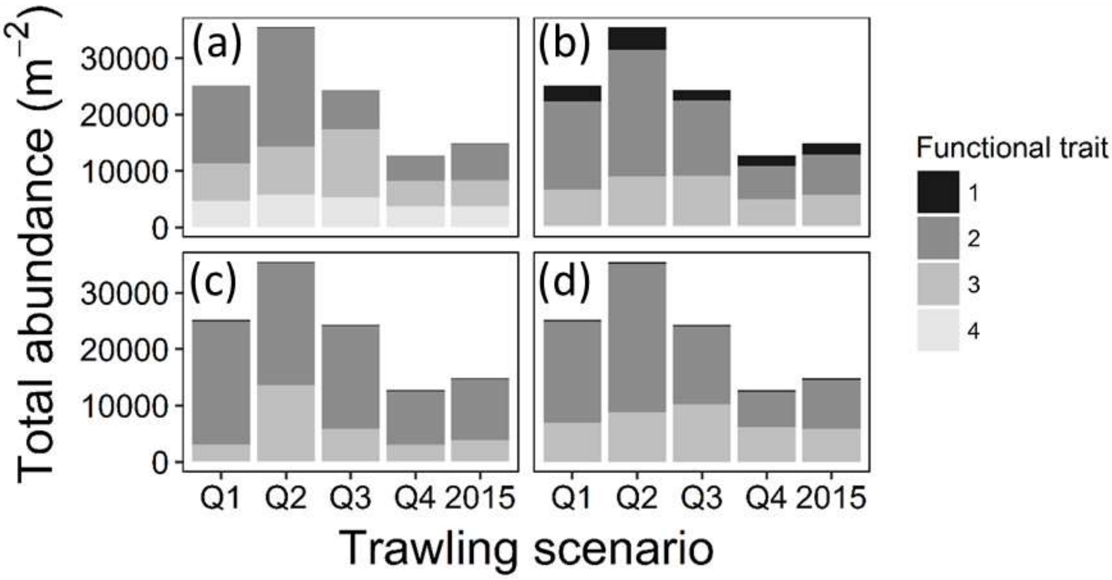

Figure 4.4. Total abundance of functional community trait; (a) reworking trait (R_i: 1; epifauna, 2; surficial modifiers, 3; head-down/head-up feeders, 4; biodiffusers), (b) activity level (M_i: 1; fixed tube, 2; limited movement or sessile, 3; slow movement through sediment, 4; free movement via burrow system), (c) ventilation rate (${}^{a}Q_i$: 1; no ventilation, 2; low ventilation rate [>0–<10 ml hr^{-1} $individual^{-1}$], 3; medium ventilation rate [10–1000 ml hr^{-1} $individual^{-1}$], high ventilation rate [>1000 ml hr^{-1} $individual^{-1}$]) and (d) sediment volume passively influenced (${}^{p}Q_i$: no flow directed towards or through the sediment, 2; flow is constrained through or over individuals body or within a tube that has an inlet or outlet connected to the sediment water interface, 4; Species generating advective flow through the sediment over a volume larger than that adjacent to the body) with increasing trawling intensity (scenario Q1-Q4, n = 35) and observations (2015; n = 35).

Scenarios of intensified trawling pressure ultimately predicted changes of ecosystem properties, including processes fundamental in the recycling of macronutrients, biogeochemical sediment concentrations as well as stock and decay of chlorophyll *a* (Figure 4.5a-f). Bioturbation and irrigation processes quantified by the BQP_c index and oxygen penetration depth (OPD) both show concave downward response patterns to increasing intensities of trawling (Figure 4.5a-b). It is notable, that the standard deviation of BQP_c and OPD is markedly larger in scenario Q2 and Q3, relative to scenario Q1 and Q4. In contrast, TOC and TON both exhibit patterns which conform to a concave upward curve with increasing scenarios of trawling intensity (Figure 4.5c-d). Indicators of labile carbon (chlorophyll *a* and phaeopigment) exhibit a concave upward response similar to that of biogeochemical patterns (Figure 4.5e-f). Spatially, the consequences of intensifying trawling on ecosystem properties proved disproportionate between stations across regional scales (Appendix E, Figure A1).

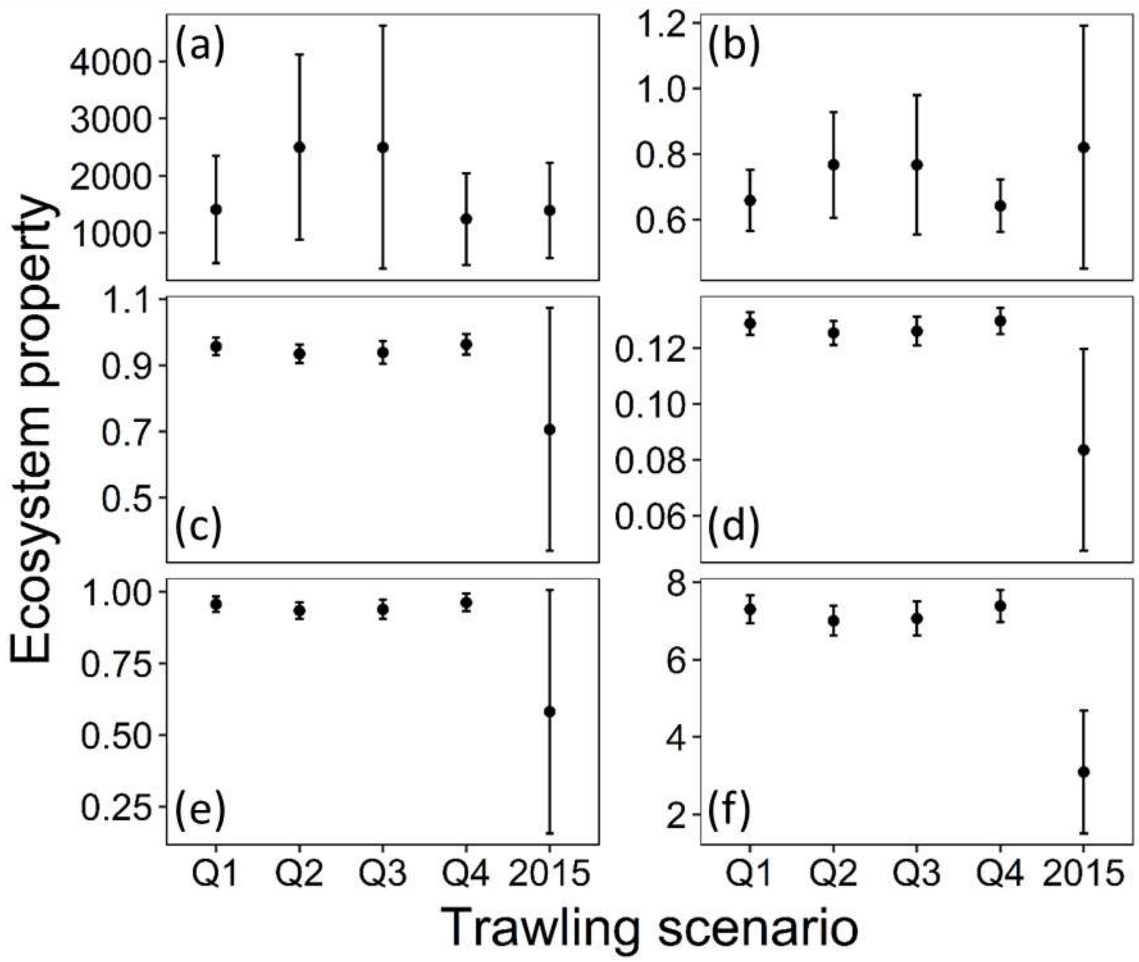

Figure 4.5. Ecosystem property; (a) BQP_c, (b) oxygen penetration depth, OPD (cm), (c) total organic carbon, TOC (%), (d) total organic nitrogen, TON (%) (e) chl *a* (μg g^{-1}), (f) phaeopigment (μg g^{-1}; mean ± standard deviation, n = 35) for each scenario of trawling intensity (Q1-Q4) and observations (2015).

Changes in community abundance reflect individual species responses to the transition in trawling intensity; some species decline while others increase under the novel circumstances and increase in population size (Figure 4.6). At regional scales, the transition from scenario Q1 to Q2, community abundance gain is markedly higher (54.26%) than the proportional loss (13.47%), hence a net increase in community abundance of 40.89% (Figure 4.6a). During the transition from scenario Q2 to Q3, however, the ratio between species abundance gain and loss decreases dramatically, shifting from a net gain (4.06 gain:loss) to a net loss (0.47

gain:loss). This community switch is mainly contributed to exacerbated loss in abundance concomitant with a substantial decline in abundance gain (Figure 4.6a). The community abundance continues to decline, contracting by 47.63% during the transition from scenario Q3 to Q4, as species abundance gained decreases to 10.88%, while the loss stabilises at 58.51% (gain:loss-ratio of 0.19; Figure 4.6a). The site-specific community change show limited loss of abundance in the transition from Q1 to Q2, where the majority of local communities display net growth (Figure 4.6b.Q1-Q2). However, the transition in trawling from Q2 to Q3 demonstrates a mixture of negative and positive community responses (Figure 4.6b.Q2-Q3), whist, transitioning from scenario Q3 to Q4, local community responses are overwhelmingly negative, despite a few communities still responding with abundance growth (Figure 4.6b.Q3-Q4). It is noteworthy that, irrespective of the intensity of transition, communities not only display contrasting directional responses, they also experience substantial variation in the magnitude of abundance across local scales (Figure 4.6b).

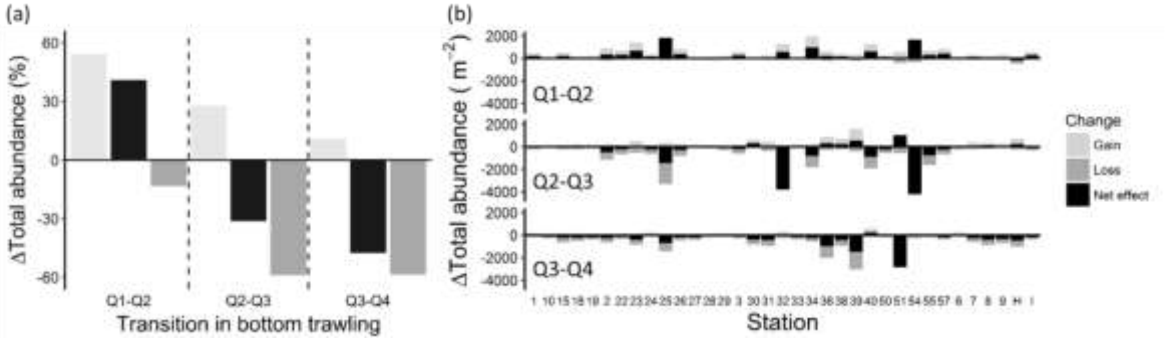

Figure 4.6. Total abundance change (a) on aggregate percentage and (b) absolute abundance change at the station-level for transition in bottom trawling intensity; Q1-Q2, Q2-Q3 and Q3-Q4.

Incremental transitions in perturbation intensity altered the functional trait composition within the pool of compensating species (Figure 4.7a) for traits important to burrowing and ventilation. Moreover our results demonstrate that taxa groups differ in their relative contribution of compensatory responses, highlighting various compensating polychaetes (Figure 4.7b), irrespective of trawling intensity. However, there was a mismatch between numerical and functional compensators species (Figure 4.7c). In other words, the species that were most important to functional compensation did not correspond to the the species exhibiting the highest numeric compensatory response.

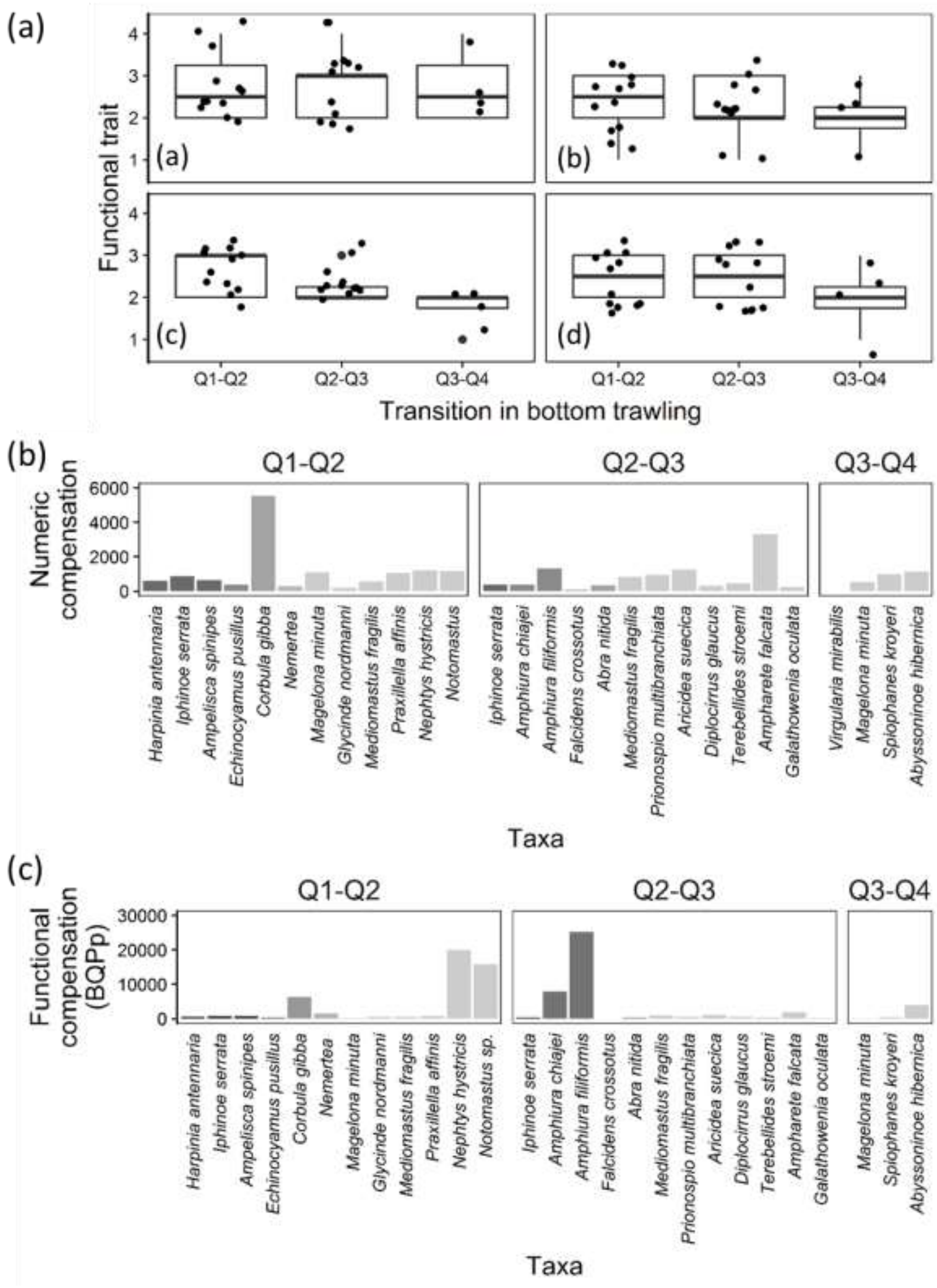

Figure 4.7. Compensatory responses by (a) trait composition (a) reworking trait, (b) activity level, (c) ventilation rate (aQi) (d) sediment volume passively influenced (pQi) (lower whisker represents smallest observation greater than or equal to lower hinge -1.5 × inter-quartile range (IQR), while upper whisker represents largest observation less than or equal to upper hinge +1.5 × IQR), (b) numeric compensation (abundance m^{-2}; bar fill represents taxa groups: Anthozoa, Crustacea, Echinodermata, Mollusca, Nemertea, Polychaeta; from dark to light grey), and (c) functional compensation (BQP$_p$ m^{-2}; bar fill represents taxa groups:

Crustacea, Echinodermata, Mollusca, Nemertea, Polychaeta; from dark to light grey) by compensating species for each transition in trawling intensity.

4.5 Discussion

Understanding how each individual species that make up a community respond to changing perturbation intensity is key if we want to predict the consequences on ecosystem properties as anthropogenic change proceeds to increase. Using empirical species responses across a gradient of trawling intensities to model the consequences of perturbation for ecosystem properties, the present study demonstrates that compensatory species responses moderate the consequences for sediment biogeochemical properties, but that the strength of the compensatory expression depends on the trawling intensity. While numeric species compensation decreases with increasing perturbation intensity (from low to high), the response to increasing trawling intensity is non-uniform within each transition scenario and subject to variation at the station level. Increasing trawling intensity reduces the frequency and magnitude of numeric (abundance) compensatory responses and thus the ability of compensatory responses to mitigate the ecosystem consequences of perturbation on sediment biogeochemical properties. Furthermore, the functional trait composition of the compensating species changes with transitions in perturbation intensity (from low to high), altering the compensatory effect and compromises the community capacity to mitigate consequences for ecosystem properties. Hence the compensatory capacity of the community is substantially stronger at low perturbation intensity, allowing communities to maintain or even increase ecosystem properties. However, as the intensity of perturbation continues to increase, this compensatory capacity is eroded, rendering communities unable to mitigate the ecosystem consequences associated with perturbations. In addition, transitions in perturbation intensity were characterised by high species turnover among the species that provide the compensatory response with only few reoccurring species, suggesting that compensation is provided by a number of species, the identity of which changes with increasing perturbation intensity. Therefore, species that may not seem important for ecosystem functioning because they do not compensate at low perturbation intensity may suddenly become important in high-intensity perturbation environments.

While different types of compensatory responses (e.g. numeric and biomass) can differ in their contribution towards functioning (Chapter 2), the relative of importance of these two responses in natural ecosystems remain poorly understood (Chapter 2). Our findings show that both biomass and numeric compensation are important in muddy species communities, although compensatory responses (biomass and numeric) continue to persist along the bottom-trawling gradient, the compensation magnitude and the pool of compensating species declined with increasing perturbation intensity. This may suggest that disturbance intensity overrides the effect of community attributes to compensate or recover from loss (Avila et al. 2018). The majority of studies in the compensation literature focusses on compensatory dynamics (Gonzalez and Loreau 2009) – i.e. changes in species or community abundance or biomass – our findings indicate that numeric species compensation is not proportional to the species contribution on ecosystem functioning. Furthermore, compensatory responses were generally driven by a few species, however, major groupings of taxa differed in their relative compensatory response both numerically as well as functionally. This is in line with findings from biomass recovery of trees in tropical forests (Avila et al. 2018).

Our findings show that compensatory species responses moderate the consequences for sediment biogeochemical properties. However, the extent to which such responses can be sustained depends on the level of trawling intensity. High-intensity perturbation repercussions on ecosystem properties reduced the magnitude of compensatory responses together with changing functional community composition. Alterations to the function composition of communities can affect the cycling of nutrients and carbon (Carreño-Rocabado et al. 2012). However, recent research demonstrates that low to moderate intensities of management intervention can maintain and even enhance the sequestration of carbon (Avila et al. 2018). Therefore, identifying the level of intensity to which ecosystems are able to absorb the effects of disturbances and subsequently recover various ecosystem properties and functions represent information that is critical to management (Chazdon and Arroyo 2013, Avila et al. 2018).

While some ecosystem services are beginning to be accounted for in management programs (Oliver et al. 2015), empirical measurement, monitoring, and direct management of ecosystem functions, resilience to anthropogenic perturbation from local to regional scale it still lacking (Spears et al. 2015; https://doi.org/10.1111/1365-2664.12497). I believe that the insight into community functioning presented here using our species-response models fill this gap by identifying community mechanisms and attributes at the species level driving ecosystem functioning at both local and regional scales that are relevant to resilience-based management of socio-ecological systems. Furthermore, our study demonstrates how species community responses to different intensities of perturbation can be used to make predictions about how potential future scenarios of perturbation may impact ecosystem properties and that present systems provide better information about future consequences than previously thought (Pearson et al. 2014). However, further research is needed to understand the way in which perturbation intensity affects compensatory responses in scale and time, especially climate-related perturbations, which continue to increase in frequency and magnitude.

I have shown that compensatory responses by surviving species to perturbation can offset and even increase ecosystem properties, but that the magnitude and frequency of such responses depend on the perturbation intensity. Our findings indicate that ecosystems can absorb the consequences of perturbation to a certain extent. However, as perturbation continues to intensify, compensatory responses weaken and eventually become insufficient at maintaining ecosystem properties. In this context, changes in the functional trait composition of species driving the response may affect the compensatory capacity (of the community) further. While community species exhibit a clear (directional) response pattern at the regional level, local community species may respond very differently to the effects of perturbation intensity at the station level. Due to modifications of the functional contribution and decreasing magnitude of numeric compensatory responses, our findings suggest that consequences of perturbation on ecosystem properties and the delivery of associated services may be subject to more variability at the landscape scale than previously thought. In addition, these findings revealed dynamic compensatory responses with high species turnover along the perturbation gradient, indicating that different species compensate at different levels of perturbation intensity. This means that diversity potentially play an important role in sustaining compensatory responses and that species which are not important for compensation at low-intensity perturbation could indeed become relevant at elevated intensities of perturbation. This study demonstrates the importance to recognise that different intensities of perturbation can lead to community responses that are fundamentally different, ultimately resulting in contrasting ecosystem outcomes depending on the local conditions. As scenario-based research matures, there is a growing need for future research to incorporate local variability into models that predict ecosystem consequences of changing biodiversity across spatial scales. Doing so will improve the relevance of model predictions (Snelgrove et al. 2017) and uncertainty of ecosystem responses to specific global change stressors, making predictions more applicable to management strategies.

4.6 Acknowledgements

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Chapter 5: Environmental perturbation destabilises benthic community structure and dynamics

5.1 Abstract

Compensatory dynamics are important mechanisms contributing to the stability of communities and the functioning of ecosystems in the context of environmental change. However, as few studies have investigated the effects of compensatory dynamics in complex multitrophic systems, existing evidence overwhelmingly stem from experiments using simple systems. Here, I explicitly test if sediment-dwelling communities compensate following the cumulative effects of heatwave disturbance and how this affect key aspects of biodiversity, community composition of functional traits to infer subsequent effects on functioning, using benthic community time series data. Community responses to perturbation was quantified through changes in species dynamics and biomass before, during and after impact of perturbation. I find that although species fluctuated independently or covaried positively with each other, increases in biomass by species within certain functional groups, indicated the occurrence of compensatory responses. This would explain why community stability was maintained, despite alterations in biodiversity, which reconfigured the composition of functional traits with respect to sediment reworking and activity level. These findings suggest that shallow benthic communities may be resilient to the effects of certain short sharp shocks. However, whether community stability can be maintained under additional or prolonged shock events is uncertain, especially as the disturbance had modifying effects on community composition.

5.2 Introduction

Communities respond in various ways to the effects of perturbation (Gonzalez and Loreau 2009, Ruesink and Srivastava 2001) and, irrespective of the direction of response, can fundamentally alter the functioning of ecosystems (Pan et al. 2016). Species are known to respond to the novel circumstances that follow perturbation through a variety of mechanisms, including behavioural switching (Maire et al. 2010), physiological regulation adjustments (Van Dievel et al. 2016), elevated growth (biomass compensation; Pan et al. 2016), or increasing reproductive investment (numeric compensation; Ensign and Leftwich 1997). Evidence from the paleoecological record shows that compensatory responses have played an important role in shaping the composition of communities following extinction events (Aberhan and Kiessling 2015, Wagner et al. 2006, Hull 2015). This is particularly clear in benthic assemblages, in which previously rare species exploited novel circumstances and became more dominant post-perturbation, altering functional trait composition and shifting the way in which species utilised ecospace (Aberhan and Kiessling 2015). Such community restructuring resembles that of recovering extant post-disturbance communities (Lotze et al. 2006, Hillebrand et al. 2008, Suding et al. 2005, Grman et al. 2010), in which the interplay between various compensatory responses amongst surviving species (Harries et al. 1996) develop and offset, wholly or in part, the functional contributions of extirpated species (Gonzalez and Loreau 2009). Whilst the long-term record demonstrates that the compensation capacity of communities has been sufficient to maintain ecosystem functioning, despite community reorganization, the relevance of such extended dynamics to contemporary forcing regimes is not clear.

It is clear that the effects of global change are changing the character of environmental forcing, by increasing the frequency and intensity of climatic events, whilst shortening the duration. Heatwaves, cyclones and other intense storms (Meehl and Tebaldi 2004, Rahmstorf and Coumou 2011) may cause localized high temperatures and pulses of rainfall and terrestrial run-off (Dosio et al. 2018) that can negatively affect ecological communities (Smale et al. 2017). Indeed, extreme events can cause high species mortality (Marba and Duarte 2010), manifest by deleterious impacts on populations (Van De Pol et al. 2010, Smale and Warnberg 2013) and reconfigure communities (Thibault and Brown 2008, Warnberg et al, 2013, 2016). Whilst it is known that communities are able to compensate to gradual changes in perturbation intensity (Chapter 4), it is not clear whether compensation occurs in response to a short life span sudden change. Hence, there is an urgent need to explore whether species are able to; absorb the short term effects of extreme events, compensate for the loss of others, or alternatively if they are lost from the system and change community structure or the functional contribution of the community through reorganisation. Here, I use a time series of sediment-dwelling invertebrate communities from shallow marine embayments along the Estonian coast to explicitly test whether communities compensate following a heatwave disturbance. It was anticipated that the compensatory response of the community would initially include opportunistic and functionally inferior species that, collectively, would be unable to fully compensate for any losses. Hence, our *a priori* expectation is that communities will require an extended time period to recover from the perturbation event.

5.3 Methods

Sampling. Field data were collected across 15 stations (see Appendix F, Table A.1 for location coordinates) from Soft-bottom communities using Van Veen grab samples (0.1 m^2) Kõiguste lath, Estonia, in the Eastern Baltic Sea. This area is located within the Kahtla-Kübassaare marine protected area.

The analysis was restricted to data collected on a subannual basis (2003-2017) at these stations to increase the temporal resolution sufficient to allow detection of fine scale intra-annual variations. The analysis focus on the immediate community response to the heatwave event of July 2006 (Figure 5.1). The analysis was consequently limited to the time period from 2005 (the year prior to perturbation impact) to 2008 (two years following perturbation impact). Because heatwaves have a disproportionate impact on shallow benthic communities the analysis is therefore limited to stations in shallow waters (< 5m), where the intensity of disturbance is at its maximum. The rationale for the 4-year timescale of this analysis was chosen on the basis that effects of heatwaves often are associated with relatively short snaps of alteration to the environmental conditions.

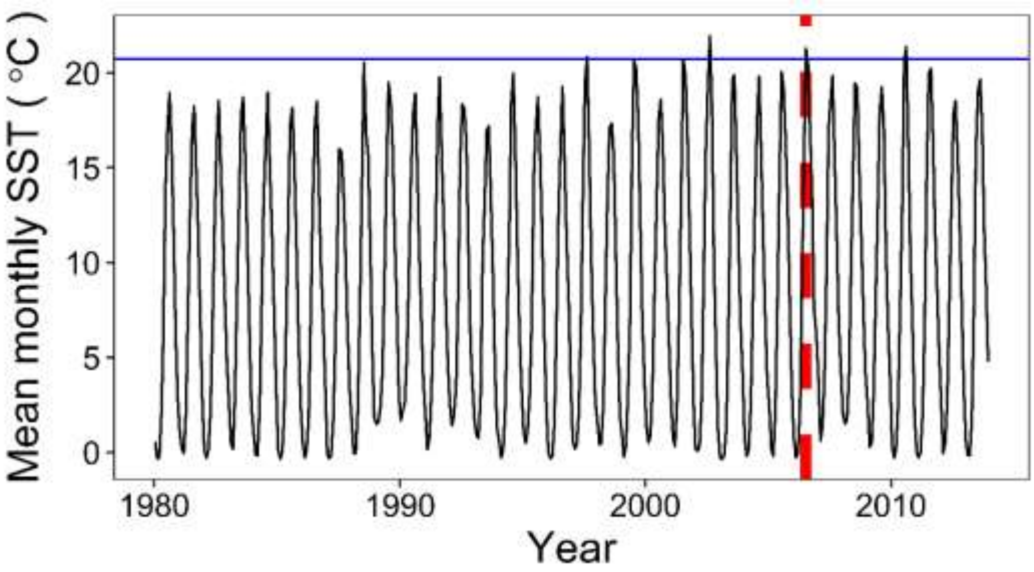


Figure 5.1. Mean monthly SST (sea surface temperature) time series (1980-2013) from the Gulf of Riga, Eastern Baltic Sea. The horizontal blue line represent the 99th percentile (20.72816 ˚C), while the vertical dotted red line represent the heatwave of July 2006.

Functional Traits. Species functional traits for sediment reworking trait (R_i) and activity level (M_i) as per the Bioturbation Potential (*BP*; Solan et al. 2004, Chapter 2) framework. Functional trait values were assigned using a combination of the current literature (Gogina et al. 2017 and Queirós et al. 2013) and on the basis of expert opinion, where such information was not available. (see Appendix F, Table A.1 for list of species and traits).

Statistics. T-test and effect size, Cohen's *d* was used to test differences between pre, during and post disturbance communities to test the mean difference between two groups. An effect size of $d = 0.2$ is considered a 'small' effect size, this means that the two groups' means don not differ by 0.2 standard deviations or more. All statistical analysis were performed using the 'R' statistical and programming environment (R Development Core Team 2014) and the "compute.es" package (version 0.2.4; Del Re 2013).

Mean-variance scaling. Mean-variance scaling relationship is a measure of community stability (Grman et al. 2010) and is based on Taylor's power law (Taylor 1961). Taylor's power law predicts that the (temporal or spatial) variance of a species' biomass σ2 increases with mean biomass μ according to the power law ($\sigma^2 = \alpha\mu^\beta$; Taylor 1961), and used to observe the temporal mean variance relationship of total community biomass. Empirical observations confirm a slope between 1 and 2 of the linear log-log relationship for most species (Mellin et al. 2010).

z-test. The z-test was used to test the difference between two regression slopes and was computed as the difference between two slopes divided by the standard error of the difference between the slopes (Cohen et al. 2013):

$$z = \frac{b_1 - b_2}{\sqrt{S_{b1}^2 + S_{b2}^2}}$$

Variance ratio. The variance ratio was used to determine the occurrence and significance of compensatory dynamics (Schluter 1984, Grman et al. 2010). The variance ratio calculates the variance of the community (*C*) as a whole relative to the sum of variances of the individual species population (x_i):

$$VR = \frac{Var(C)}{\sum_i^N Var(x_i)}$$

Where:

$$Var(C) = \sum_{i=1}^{N} Var(x_i) + 2\left(\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} Covar(x_i, x_j)\right)$$

A variance ratio = 1 indicates that species vary independently to each other (i.e. no covariance), while a variance ratio > 1 indicates predominantly positive covariance among species and a variance ratio < 1 indicates negative covariance between species (Schluter 1984). Here, the variance ratio was computed for species biomass in shallow (<5m depth) benthic communities (bootnumber; n = 100, see Hallet et al. 2014 for further detail), in the 'R' statistical and programming environment (R Development Core Team 2014) using the "codyn" package (version 1.1.0; Hallett et al. 2016).

Community stability. Community stability was calculated for total community biomass, as the temporal mean divided by the temporal standard deviation (Tilman 1999). This reveals whether or not diversity has an impact on stability (z = 2, no impact; z < 2, stability decreases as community stability increases; z > 2, stability increases as diversity increases). Stability was computed in the 'R' statistical and programming environment (R Development Core Team 2014) using the "codyn" package (version 1.1.0; Hallett et al. 2016).

Species turnover and rate of change. Metrics of species turnover (total, appearance and disappearance), rate of directional change in community composition described by Euclidean distances (Collins et al. 2000) were calculated in the 'R' statistical and programming environment (R Development Core Team 2014) using the "codyn" package (version 1.1.0; Hallett et al. 2016).

5.4 Results

Although, the majority of benthic community dynamics were driven by species fluctuating independently or exhibiting positive covariance among species, increases in biomass within certain functional groups, indicated the presence of compensatory responses in the first year following perturbation impact. The effects of perturbation also caused initial reduction in species richness and community evenness at the time of impact, before increasing the following year, exceeding pre perturbation conditions, leading to a reconfiguration of the composition of functional traits within communities.

Irrespective of year relative to perturbation, community biomass was not affected by the effects of heatwave. However, there was a trend of decreasing biomass from pre perturbation conditions to the first year following perturbation impact, before increasing in biomass (Figure 5.2a). Species richness was not affected by perturbation initially, but in fact increased the first year following perturbation impact before a minor decrease (Figure 5.2b). Comparison of community evenness from year of impact to first year following perturbation impact revealed a difference between communities ($t(14) = -2.2319$, $p = 0.03$, $d = -0.44$), in which species evenness increased from $J^{0.49}$ to $J^{0.52}$. Although, there was no difference from comparisons from pre perturbation conditions to time of impact, there was a clear evenness trend (Figure 5.2c).

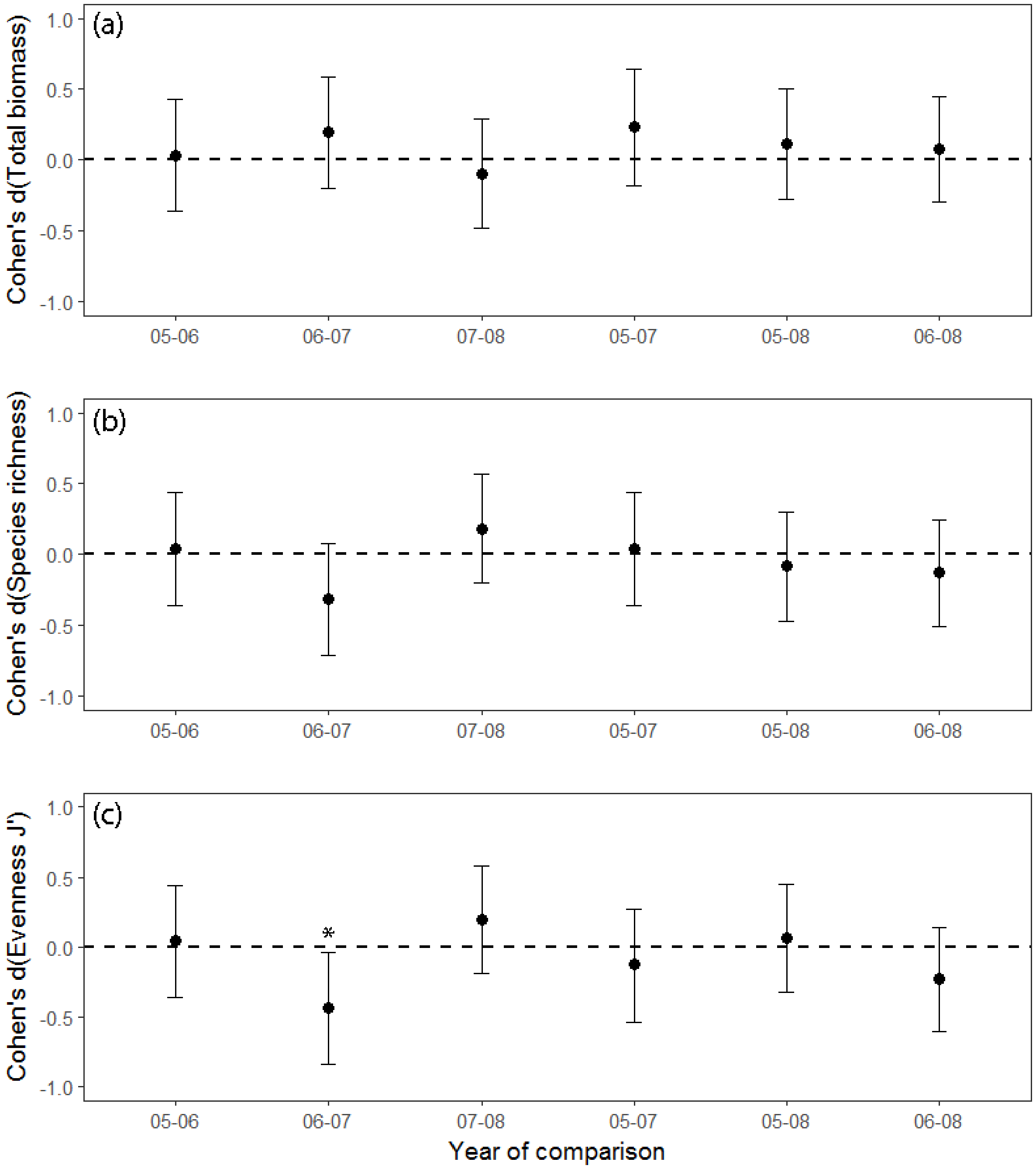


Figure 5.2. Effect of environmental disturbance on (a) total biomass, (b) species richness and (c) evenness J' in shallow soft-bottom communities. The mean and 95% confidence interval are shown for separate analyses for the respective community attributes between; pre and during disturbance (2005-06), pre and 1 year post disturbance (2005-07), during impact and 1 year post disturbance impact (2006-07), . The zero line indicates no effect, and significance of mean effects is determined when the 95% confidence interval does not overlap zero. Evenness *J'* pre and year of disturbance (2006-07) responses are significantly negative (*), while the others show no effect but clear trends.

Benthic macrofauna decreased in biomass by 35.55% from pre perturbation conditions to the year of perturbation impact, before increasing by 27.18% biomass the first and second year post perturbation impact, these changes in biomass affected the relative distribution of functional traits with regards to reworking trait and activity level (Figure 5.3). Functional groups of reworking and mobility displayed predominantly two contrasting responses to the effects of perturbation (1) an initial decline at the impact of perturbation followed by (2) an increase in biomass.

Tube-dwelling organisms (M_i = 1), organisms limited in movement or sessile (M_i = 2) and Slow moving species (M_i = 3) all decreased in biomass initially from pre perturbation to the year of impact. While both tube-dwellers and organisms limited in movement or sessile increased in biomass post perturbation impact, slow moving species continued to decrease. In contrast, free-moving species via burrow systems (M_i = 4) benefitted from the effects of perturbation and remained unaffected initially at time of impact, before increasing in biomass post perturbation impact (Figure 5.b; Appendix F, Table A4).

Epifaunal organisms (R_i = 1), surficial modifiers (R_i = 2) and regenerators (R_i = 5) decreased in biomass initially from pre perturbation to the year of impact. However, both epifaunal organisms and surficial modifiers increased, while regenerators continued to decrease in biomass from year of perturbation impact to post perturbation. While up- and down-ward conveyors (R_i = 3) increased slightly in biomass initially in response to the effects of perturbation, only followed by a decrease post perturbation, biodifusers (R_i = 4) exhibited the exact opposite response by a slight initial decrease at the time of impact, followed by an increase in biomass post perturbation (Figure 5.3b, Appendix F, Table A5).

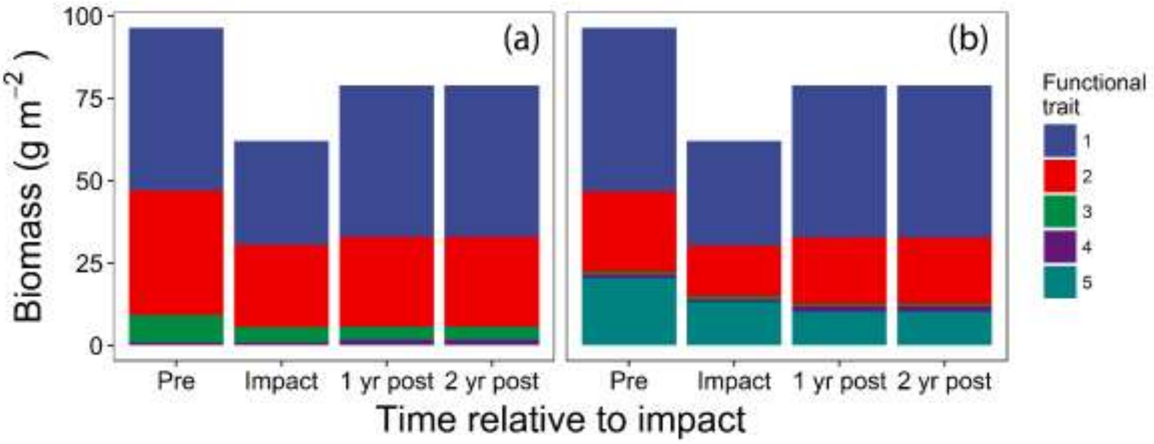


Figure 5.3. Effects of heatwave disturbance on (a) activity level (1; fixed tube, 2; limited movement or sessile, 3; slow movement through sediment, 4; free movement via burrow system) and (b) reworking trait (1; epifauna, 2; surficial modifiers, 3; head-down/head-up feeders, 4; biodiffusers, 5; regenerators) in shallow soft bottom communities pre, during, 1 year post, 2 year post impact; n = 47, 53, 48, 60, respectively.

In most communities, species varied independently of each other (variance ratio ~ 1, within the 95% confidence interval of the null model), such species dynamics were remained relatively unaffected by the effects of perturbation (Figure 5.4; Appendix F, Table A.5). The year prior to perturbation only 6.7% soft bottom communities exhibited positive covariance between species, whereas during the year of impact and the first year following perturbation impact 13.3% of communities exhibited positive covariance between species. However, by the second year following perturbation 20% soft bottom communities exhibited positive covariance between species. In contrast, no communities exhibited negative covariance among species (beyond the 95% confidence interval of the null model).

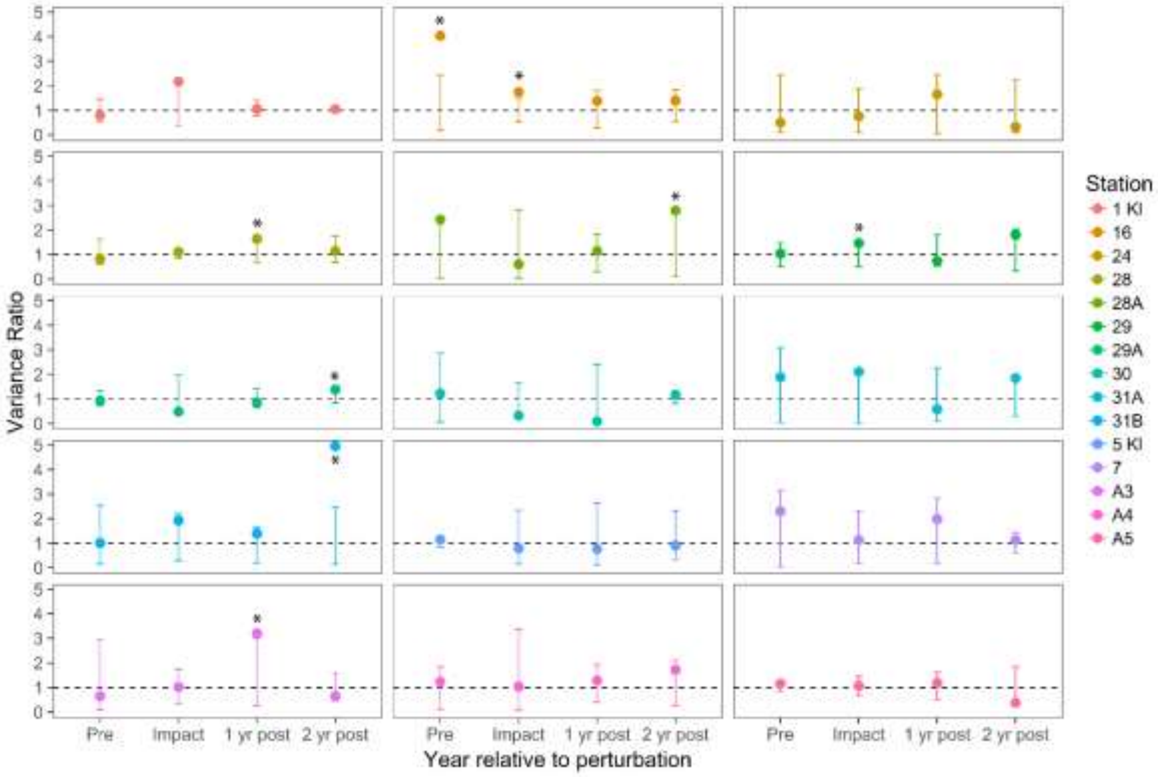


Figure 5.4. Effects of environmental disturbance on the variance ratio ± critical interval of null model (bootnumber; n = 100) in shallow soft-sediment communities for each station (indicated by colour) pre, during, 1 and 2 year post perturbation impact. The dashed line (VR = 1) indicates the threshold, between negative covariance (VR<1) and positive covariance (VR>1) among species, at which species in a community are said to fluctuate independently to each other. Significance of mean effects (*) is determined when VR exceeds the 95% confidence interval of the null model.

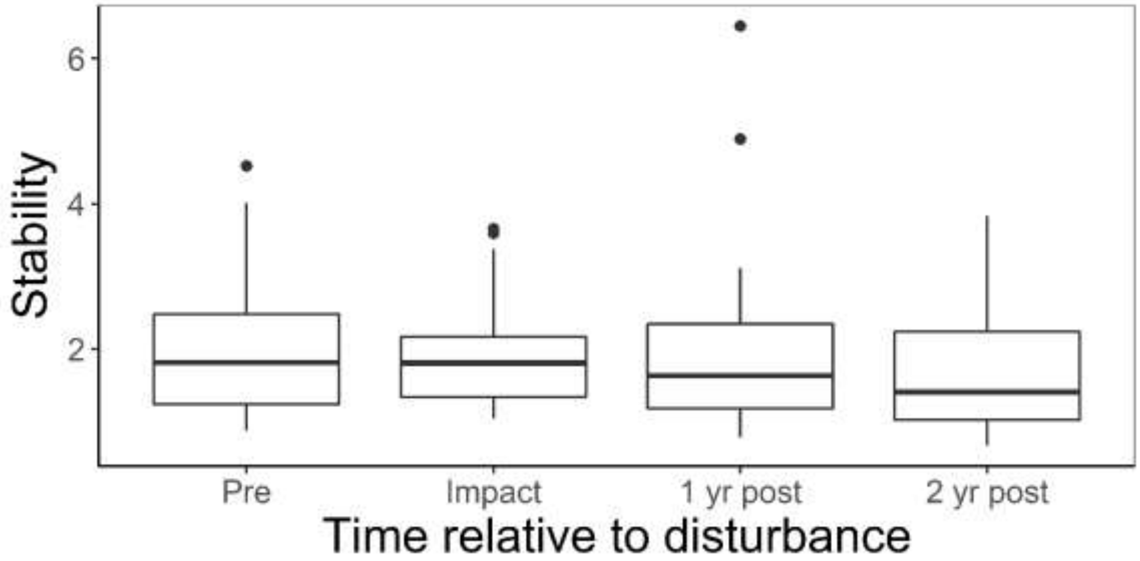


Figure 5.5. Effects of environmental disturbance on stability of total community biomass in shallow soft bottom communities; pre, during, 1 and 2 year post perturbation impact.

Trends in community stability (Figure 5.5) were confirmed by reduced scaling coefficient (larger slope) in communities initially following the impact of perturbation in the mean-variance scaling relationship for total biomass (Figure 5.6), however two year post perturbation impact the scaling relationship increased near pre perturbation conditions, although, regression slopes were not affected by perturbation ($z = 3.05$, $z = 1.14$, $z = 0.56$, $z = -0.13$, z = -1.62 and $z = -0.77$ for pre-impact versus impact, pre-impact versus 1 year post impact, pre-impact versus 2 year impact, impact versus 1 year post impact, impact versus 2 year post impact and 1 year versus 2 year post impact, respectively).

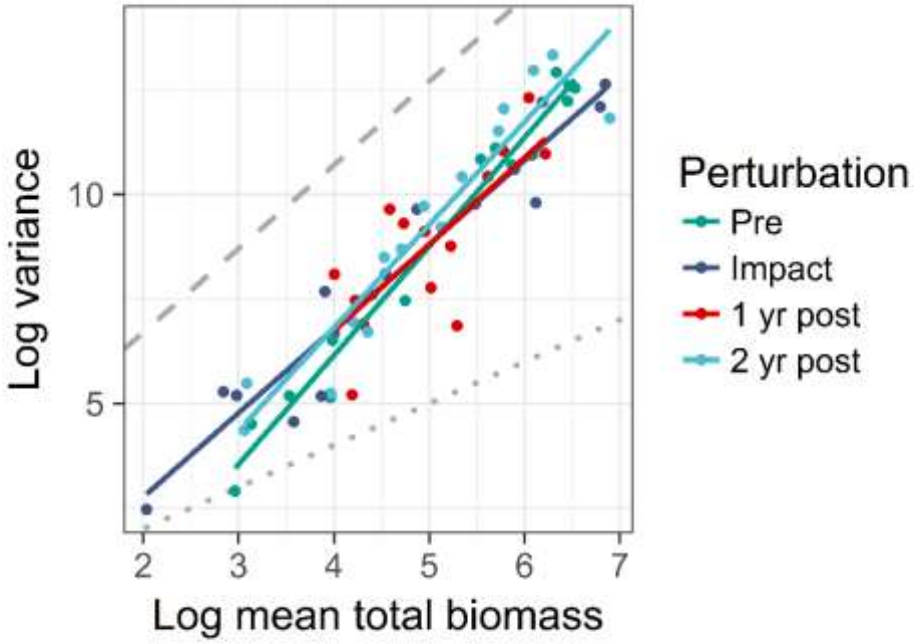


Figure 5.6. Mean-variance scaling relationship for total biomass in shallow water communities (<5m). The solid lines are the actual scaling relationship for the year pre (green; 2005), the year of impact (dark blue; 2006), 1 (red; 2007) and 2 (light blue; 2008) year post perturbation impact. The power laws with slope = 1 (dotted line) and slope = 2 (dashed line) are plotted for comparison.

Irrespective of year relative to perturbation, total turnover, appearance nor disappearance of species was not affected by the effects of the heatwave (Appendix F, Table S1-S3). Trends in total species turnover were driven by species disappearance, while species appearance remained relatively stable from pre to post perturbation (Figure 5.7).

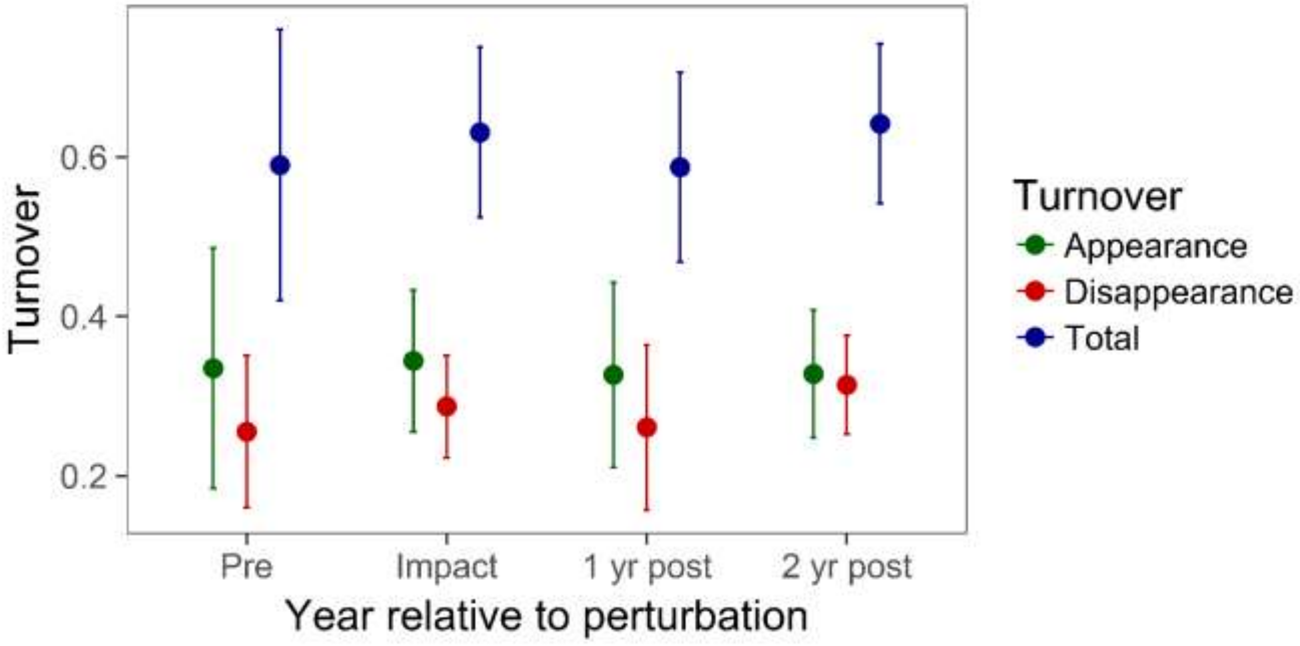


Figure 5.7. Species turnover (total = blue, disappearance = red, appearance = green; mean ± standard deviation; n = 15) for each; pre, upon, 1 and 2 year post perturbation impact.

5.5 Discussion

Better understanding into the short-term ecological response of communities to high frequency extreme events is needed to improve future projections of ecological consequences and long-term processes (Smale et al. 2017). The motivation here, was to examine whether compensatory responses develop in response to the effects of a heatwave perturbation event, and to provide insight of how it manifest within the community. My focus is not to investigate the direct functional consequences of a perturbation event, but to determine any changes in the organization of the biological community.

The time series data provide evidence of compensatory responses to heatwave perturbation. Although, the majority of species communities responded to perturbation independently of one another or exhibited evidence of positive covariance among species, increases in biomass within certain functional groups, indicated the presence of compensatory responses by macrofauna in the first year following perturbation impact, which was maintained in the second year following perturbation. In the year following perturbation, compensatory responses were observed, but were weakened relative to pre perturbation, indicating that community responses were essentially immediate. In the broadest terms, the patterns of species response are in line with expectation based on successional theory (Pearson and Rosenberg 1978, Sheley et al. 2006), where opportunistic species are the first responders and are replaced by a sequence of species over the longer term. As the findings here demonstrate, post-disturbance species responses are pronounced due to the presence of contrasting functional characteristics that are found within multitrophic communities (Rocha et al. 2011), providing a portfolio of response potential.

A consistent feature across many of the assemblages under study was the propensity of post-perturbation communities to undergo compositional reconfiguration. Species richness and evenness, key aspects of biodiversity that are important for ecosystem performance (Cardinale et al. 2012, Wittebolle et al. 2009, Wohlgemuth et al 2016) decreased initially in response to the effects of perturbation before increasing, similar to the response macrofauna biomass. Such shifts in the attributes of biodiversity, reflect classic community responses to environmental disturbance, in which more sensitive species decline or are lost from the system and alter relative evenness. This, in turn, changes circumstances such that surviving species may or may not be able to benefit and increase their proportional representation. Indeed, rates of directional community change during and after year of disturbance impact relative to that of pre-disturbance communities (Appendix F, Figure A.1) confirm evidence of community reorganization. While the most abundant functional groups were negatively affected by the perturbation impact, less abundant groups, such as biodifusers and free-moving species via burrow systems were able to benefit from the effects of the heatwave event. Overall, species turnover was relatively high and increased during the year of perturbation before decreasing again the first year following perturbation impact due to changes in the disappearance of species rather than the arrival of new ones.

Communities exposed to perturbation are more stable (Grman et al. 2010), but relatively modest changes in species evenness are known to cause variation in community stability (Brown et al. 2016). Our findings suggest that, in the short term, compensatory responses from certain functional groups may contribute to sustaining community stability. These findings are in agreement with strong species identity-effects of the compensating species, documented in other systems (Pan et al. 2016, Bai et al. 2004). Hence, alterations in community stability is not constrained to large compositional changes caused by the addition or deletion of species. In fact, communities that are regularly affected by environmental disturbance are likely to exhibit more stability than comparable undisturbed communities (Grman et al. 2010). The implications of these findings are that soft-bottom communities may be resilient to perturbation. However, Taylor’s power law responded with a proportional decrease in variance and increase the second year after perturbation impact, returning to pre perturbation conditions, indicating that community responses can vary and the outcomes can be very different from mean effects. Indeed, the rate of proportional increase observed here is congruent with expectation for less stable and more patchy distributed communities, as has been demonstrated elsewhere (Mellin et al. 2010). Overall, the data is suggestive of dynamic behaviour that is driven by a number of underlying physiological, behavioural and functional responses to perturbation which, in turn, are affected by the type, intensity and timing of the perturbation event (Milazzo et al. 2012, Pincebourde et al. 2012, Sanford 1999).Moreover, as the effect of compensation was strongest in the period that immediately followed the onset of perturbation, the consequences for community stability were not fully realised and did not manifest until the second year following perturbation impact.

5.6 Acknowledgements

I thank Jonne Kotta and colleagues at the University of Tartu for data availability. Supported by a scholarship (awarded to M.S.T., grant reference NE/L002531/1) co-funded by the Southampton Partnership for Innovative Training of Future Investigators Researching the Environment (SPITFIRE, a NERC Doctoral Training Partnership) and the Centre for Environment, Fisheries and Aquaculture Science (Cefas, reference DP371C), UK.

Chapter 6: General Discussion

Managing the consequences of biodiversity change (Barnosky et al. 2012) on ecosystem functions and related services of natural systems, whilst maintaining economic development and satisfying human demand for resources is becoming an increasing challenge for society in the Anthropocene (Naeem et al. 2012). Human activities are exerting pressures on certain biophysical subsystems and processes to the extent that they have already exceeded what some regard as the safe operating threshold for humanity (Rockström et al. 2009). Accepting that both extinction rate and species richness are weak metrics of a planetary biodiversity boundary (Mace et al. 2014), it is generally accepted that continuing loss of biodiversity is nevertheless likely to have unprecedented and profound consequences for ecosystem function and associated services (Cardinale et al. 2012, Balvanera et al. 2006). These can vary extensively, affecting the magnitude, direction and variation of functioning (Heilpern et al. 2018, Chapter 2), with anticipated outcomes ranging from dramatic functional deterioration (Solan et al. 2004, Bunker et al. 2005), through high levels of resistance (i.e. maintaining ecosystem functioning; Oliver et al. 2015), to amelioration or enhancement of functioning (i.e. overcompensation; McIntyre et al. 2007, Allgeir et al. 2015, Chapter 2).

Over the past two decades, in an attempt to improve predictions of the ecosystem consequences associated with changing biodiversity (Heilpern et al. 2018), significant progress has been made in incorporating various aspects of ecological context and realistic scenarios of species loss into experiments that examine the relationship between biodiversity and ecosystem functioning (Bracken et al. 2008, Godbold et al. 2009, Godbold et al. 2011, Donohue et al. 2017, Haggerty et al. 2018). Despite a wealth of early generation biodiversity-function experiments (reviewed in Cardinale et al. 2012) providing evidence for positive biodiversity-ecosystem function relationships across a variety of ecosystem functions (Balvanera et al. 2006, Cardinale et al. 2011, Tilman et al. 2014), they rarely explored how individual species populations (e.g. via compensatory responses; Thomsen et al. 2017, Heilpern et al. 2018) contribute to functioning in response to the changing circumstances following the release of resources (Yang et al. 2008), changes in predation (Heithaus et al. 2008) or facilitation (i.e. positive species interactions; Stachowicz 2001, Bruno et al. 2003, Donohue et al 2017) or following the emergence of other novel circumstances. This omission is important, because such mechanisms can lead to a fundamental reorganisation of species-environmental relationships that underpin the regulation of many ecosystem properties (Aizen et al. 2012, Valiente-Banuet et al. 2014). Whilst recent studies highlight the growing awareness of this knowledge gap (theory; Fung et al. 2015, Heilpern et al. 2018, Chapter 2 and empirical; Bai et al. 2004, Hoover et al. 2014, Pan et al. 2016, Chapter 3), the importance, and wider ecosystem consequences of, post-extinction compensatory responses (Ghedini et al. 2015, Chapter 2-3) have not been fully explored.

In this thesis, I explicitly demonstrate that compensatory responses following biodiversity change can dramatically alter the consequences on ecosystem functioning, and I emphasise the importance of incorporating compensation in a biodiversity-ecosystem function framework (

Figure 6. 1b, Chapter 2-4). While the magnitude and variability of compensatory responses on functioning depend on the type of compensation expressed (Ruesink and Srivastava 2001; *per capita* compensation, Ghedini et al. 2015; trophic compensation, Chapter 2; numeric or biomass compensation) and the sequence in which species go extinct (Chapters 2-4, Solan et al. 2004, Ives and Cardinale 2004, Zavaleta and Huvey 2004, Zavaleta et al. 2009)), the way in which compensation is sourced matters for the mediation of ecosystem process and function (e.g. Chapter 2; rare species, common species, between vs. within functional traits). My analyses confirm that compensatory responses (Chapter 2-4) are influenced by community composition and structure (Tilman et al. 1997), the net outcome of alterations to species interactions, and the distribution of functional traits within and between populations (Chapter 2-4; Wohlgemuth et al. 2016, Suding et al. 2008). In addition, the functional consequences of biodiversity change are also influenced by the prevalence or temporal frequency of compensatory species responses, which may change depending on the disturbance intensity (Chapter 4) Nevertheless, it is important to emphasise that the type of community attribute driving the compensatory responses (e.g. abundance or biomass, Chapter 2) can be critical in determining the ecological outcomes (Tilman 1997, Spehn et al. 2005 Mokany et al. 2008, Moretti et al. 2016, Roscher et al. 2018). Moreover, the implications for functioning may be subject to substantial variation depending on the type of mechanisms driving the compensatory species response (e.g. resource- or predator-release) as well as the level of interconnectivity of species that are declining or lost from the community.

It is important to also consider the consequences of local alterations in biodiversity over the longer term (Langenheder et al. 2010, Godbold and Solan, 2013) and, in this thesis, I highlighted the importance of how surviving species population dynamics fluctuate with external drivers (Hallett et al. 2014, Chapter 5) and, in turn, play a prominent role in determining the long-term legacy for ecosystems. Extrinsic and intrinsic factors act as a filter in determining the identity and sequence of ‘winners’ and ‘losers’ of the community, and such dynamics may be transient over time (Godbold and Solan. 2013) or within a spatial context (Godbold and Solan 2009; Godbold et al. 2017, Chapter 4), and affect the capacity for compensation at the landscape scale (Wilcox et al. 2017, Chapter 4). How external forces act simultaneously upon the community will ultimately determine the potential capacity for compensation within the community. However, whether this potential is realised and translated into a post-disturbance response that compensates for the loss of others does not necessarily hold (Gonzalez and Loreau 2009) and remains an open empirical question.

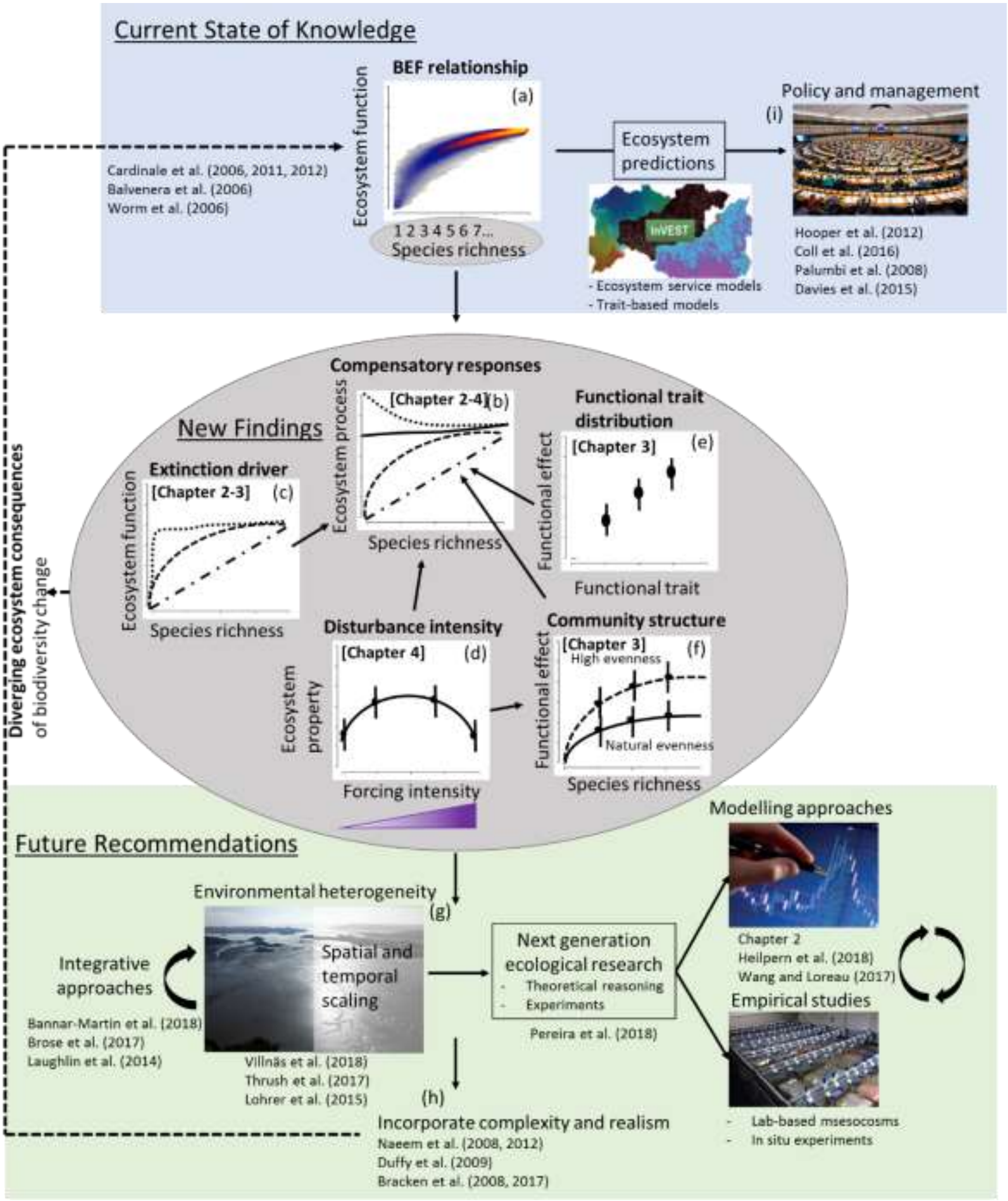


Figure 6. 1. Conceptual schematic summarising (a) currently accepted synthesis of biodiversity-ecosystem function relations based on the conclusions from several hundred experiments (*sensu* Cardinale et al. 2012, Gamfeldt et al. 2015). Note, however, that this relationship is subject to substantial variation, which can alter the trajectory of the biodiversity-functioning curve to the extent that the consequences of biodiversity loss diverge from expectation, resulting in accelerated loss, maintenance or overyielding (overcompensation) of ecosystem properties. Outcomes will depend on how biodiversity is altered (i.e. the way in which species are lost and respond to environmental change); (b) compensatory mechanisms can alter the consequences for ecosystem functioning, (c) irrespective of extinction driver (**Chapter 2**). However, (f) the functional effect of compensatory responses depend on community structure as well as (e) the distribution of functional traits within the surviving community (**Chapter 3-4**). In this context, (d) the disturbance intensity influence ecosystem property yield and the capacity for

species to respond through compensatory mechanisms (**Chapter 4**), which is, in turn, subject to variation at landscape scale (**Chapter 4**). There is now increasing awareness that biodiversity-function relations may substantively diverge from current expectation. In extension, there is (g) considerable uncertainty concerning how this relationship scale in space and time, which indeed is likely to yield different ecosystem responses when accounting for environmental and biological dynamics associated with spatio-temporal variation of natural ecosystems (Wang et al. 2017, Wang et al. 2015, Bracken et al. 2017, Brose and Hillebrand 2016, Zeppilli et al. 2016, O'Connor et al. 2017) and increasing ecological complexity (e.g. food web and trophic complexity; Wang and Brose 2018, Brose et al. 2017, Heilpern et al. 2018, O'Connor et al. 2017). Hence, next generation research foci should address how natural complexity at the landscape scale influence dynamics that govern a key role in the production of ecosystem properties. Doing so, will demand the development of a novel ecosystem framework that enhances the interplay between theory and empirical studies, combining their respective strengths as well as the empirical testing of theory to (h) improve the way in which ecological studies capture the complexity associated with biodiversity loss in natural systems. Such amendments and innovation is needed to (a) revise current understanding of biodiversity-function relations, if we are to (i) advance predictions of ecosystem consequences associated with changing biodiversity (e.g. Nelson et al. 2009), which is critical for effective ecosystem management (Gamfeldt et al. 2015).

A major implication of the findings from this thesis is that approaches that explore the ecosystem consequences of changing biodiversity without accounting for post-disturbance compensatory responses, are unlikely to be relevant (Srivastava and Velland, 2005; Ghedini et al. 2015) and lead to projections that differ to field observations (Chapter 2). There is an urgent need to recognise that different trajectories of ecosystem function can emerge from biodiversity change that cannot be anticipated by experimental manipulations (Cardinale et al. 2012). Indeed, it is already known that biodiversity-function relations, including the shape and form of the curve (Allgeier et al. 2015), can be modified by species rank dominance (Wohlgemut et al. 2016) due to species identity effects (Diaz and Cabido 2001, Wardle et al. 2011), but also morphological, behavioural or physiological traits can be important (Diaz et al. 2013, Gaucon et al. 2017, Maire et al. 2010), yet these complexities are rarely a feature of experiments and models (Leibold et al. 2017, Bannar-Martin et al. 2017) and call into question the relevance of these studies beyond academic curiosity.

The relationship between biodiversity and ecosystem functioning is a central feature of various approaches used as a theoretical basis for the management and conservation of ecosystems (i.e. ecosystem-based management), including the design of current and future environmental interventions and policy. Having established that compensatory responses can fundamentally alter the consequences for ecosystem functioning with changing biodiversity, the next step will be to integrate such responses across larger spatial scales in a cross-ecosystem framework. A difficulty in doing so, however, is that current model predictions of biodiversity-function relations often do not match the reality field observations (Snelgrove et al. 2014), as the parameterisation of the models is dependent on an experimental evidence base that is limited in terms of spatio-temporal scale and ecological complexity. Addressing uncertainties caused by divergent ecosystem consequences to biodiversity change (e.g. Heilpern et al. 2018, Allegier et al. 2015, Fung et al. 2015, Chapter 2), is, therefore, fundamental to refining understanding of biodiversity-ecosystem function relations. One way to integrate compensatory responses at the landscape scale is to recognise the importance of connectivity (Godbold et al. 2011) and adopt, for example, metacommunity theory (i.e. alpha, beta, gamma scale), as has been proposed for stability (Wang and Loreau, 2016) and, more recently, for synchrony (Wilcox et al. 2017). This would enable the focus to extend beyond the study of individual isolated communities and move towards understanding aggregate community responses across multiple communities at the habitat scale. This would allow for a more nuanced understanding of ecosystem responses to biodiversity change across heterogeneous landscapes.

A radical overhaul of thinking is required within biodiversity-functioning theory if next generation models and empirical frameworks are going to satisfactorily project the most likely consequences of biodiversity loss for ecosystem functioning (Chapter 3, Heilpern et al. 2018). Such approaches need to significantly extend along the temporal axis to incorporate post-disturbance community dynamics over multiple generations (Jones et al. 2017). Hence, novel approaches are needed that go beyond simple extrapolations from experimental findings to regional scenarios of the future (Pereira et al. 2018). Indeed, recent research concludes that the most appropriate way to address new questions is to use a diverse portfolio of approaches and methods (Eishenhauer et al. 2016, Hodgson and Halpern 2018) in tandem with the continual development of novel tools that can be used to strengthen and better address relevant ecological foci and complexities (Greig and Duinker 2011).

6.1 Summary of main conclusions and recommendations

The findings of this thesis demonstrate that compensatory responses, irrespective of the type of extinction driver, can fundamentally alter biodiversity-ecosystem function relations and, ultimately, the effect of compensation on ecosystem functioning is largely dependent on the functional traits of the surviving community. Specifically, my findings suggest that:

- Compensation matters for functioning, but its relative importance is dependent on intrinsic and extrinsic factors that are currently not well understood.
- There are various types of compensation responses, however certain types are poorly developed in the present literature (e.g. functional and behavioural switching; Chapter 2). Consequently, a strong bias exist in the literature. To date, research efforts have predominantly focussed on density compensation (biomass or abundance) and only touched upon *per capita* compensation (Ruesink and Srivastava 2001, Ghedini et al. 2015). Hence, there is a need to diversify the approaches used in the detection of compensatory responses to explore the prevalence of compensatory and other community responses.
- In order to gain generality, there is a need to extend experimental periods, and seek repeated experiments under different contexts rather than replication of identical experiments in the same locations and systems. Further, as multitrophic assemblages are likely to have different competition dynamics (Rocha et al. 2011) and functional trait structures, experimental systems would benefit from increasing trophic complexity and study the effects of compensatory responses in multitrophic communities.
- Compensation in the experimental systems used in this thesis has been demonstrated, but the prevalence and relative importance of compensatory processes in natural systems is inadequately constrained. Although theory on compensatory dynamics is relatively advanced, the occurrence and underlying compensatory mechanisms are largely unknown (Brown et al. 2016). In this context, evidence is needed on the type of community responses following different types of perturbation and the cumulative effects of multiple stressors. Such information is important for the development of next generation ecosystem models.
- To ensure future sustainability of ecosystem functions and services, it is fundamental that managers and policy-makers recognise the importance of

compensatory processes and their capacity to alter recovery trajectories in natural communities affected by anthropogenic activity. Accounting for compensatory processes can be an important step to reduce variability of model predictions, as current levels of variability compromise the capacity to project realistic ecosystem responses to environmental change (Snelgrove et al. 2018). Efforts to resolve discrepancies between field observation and model projections represent the next major challenge in moving towards improved ecosystem predictions in response to biodiversity change.

Appendices

Appendix A

Table A.1. Search terms used to compile data (total, marine, aquatic and freshwater, plant, soil and terrestrial systems) from a Web of Science (https://apps.webofknowledge.com; date of access: 28.02.2018) literature search. Search settings were conducted from “all databases”, “all years” (timespan), refined by “article” (document type) and by topic for; “marine”, “aquatic or freshwater” and “plant or soil or terrestrial”, respectively for each system(s) specificity. Search terms yielded no results (‡).

Study Focus	Search Term	Total	Marine	Aquatic, Freshwater	Plant, Soil, Terrestrial
Compensation	(("compensat* respons*" or "compensat* dynamic*" or "compensat*") and (extinct* or species or biodiversity or disturbance or perturbation))	40,235	2,330	3,136	3,136
Resistance	(("species resistance" or "ecological resistanc*" or "ecosystem resistance" or resistanc*) and (extinct* or species or biodiversity or disturbance or perturbation))	177,556	5,093	14,989	76,481
Resilience	(("species resilience" or "ecological resilience*" or "ecosystem resilience" or resilien*) and (extinct* or species or biodiversity or	13,826	3,146	3,076	7,543

	disturbance or perturbation))				
Stability	(("community stability*" or "ecological stability*" or "ecosystem stability" or stabil*) and (extinct* or species or biodiversity or disturbance or perturbation))	197,599	7,082	9,306	38,651
Disturbance	((disturbance* or perturbation* or stress*) and (species or community or ecolog* or environment* or ecosystem or natur* or anthropogenic))	787,936	52,250	72,375	279,497
Extinction	(extinct* or "species loss" or "biodiversity loss" or "species decline" or "biodiversity decline" or "biodiversity change" or "changing biodiversity")	159,516	10,519	9,307	40,216
Biodiversity-Ecosystem Functioning	((biodiversity or species or ecosystem) and funct*)	400,073	28,084	40,730	135,728
Functional Response Trait	("response trait*" and (funct* or species or organism* or community))	208	10	23	155

Functional Effect Trait	("effect trait*" and (funct* or species or organism* or community))	105	12	18	95
Character Displacement	("character displacement")	2,124	137	242	835
Competitive Release, Competition	(("competitive release*" or competit*) and (species or organism* or population* or communit* or ecologic* or ecosystem* or biotic))	167,642	12,857	17,951	73,659
Predator Release, Predator-Prey	(("predator* release*" or predator*) and (species or organism* or population* or communit* or ecologic* or ecosystem* or biotic or dynamic*))	140,103	29,286	31,024	72,649
Resource Release	(("resource release*" or resource*) and (species or organism* or population* or communit* or ecologic* or ecosystem* or biotic or dynamic*))	894,919	77,617	177,696	467,922
Trophic Structure	("trophic structure" or trophic)	78,939	21,375	25,508	35,449
Reproductive Displacement[‡]	(“reproductive displacement”)	NA	NA	NA	NA
Functional Trait	("functional trait*" and	5,673	375	568	4,812

	(organism* or species or communit* or population* or ecolog* or ecosystem*))				
Recovery	((recover*) and (species or communit* or ecosystem* or ecolog* or biodiversity or extinction))	187,160	21,324	29,777	80,086

Appendix B

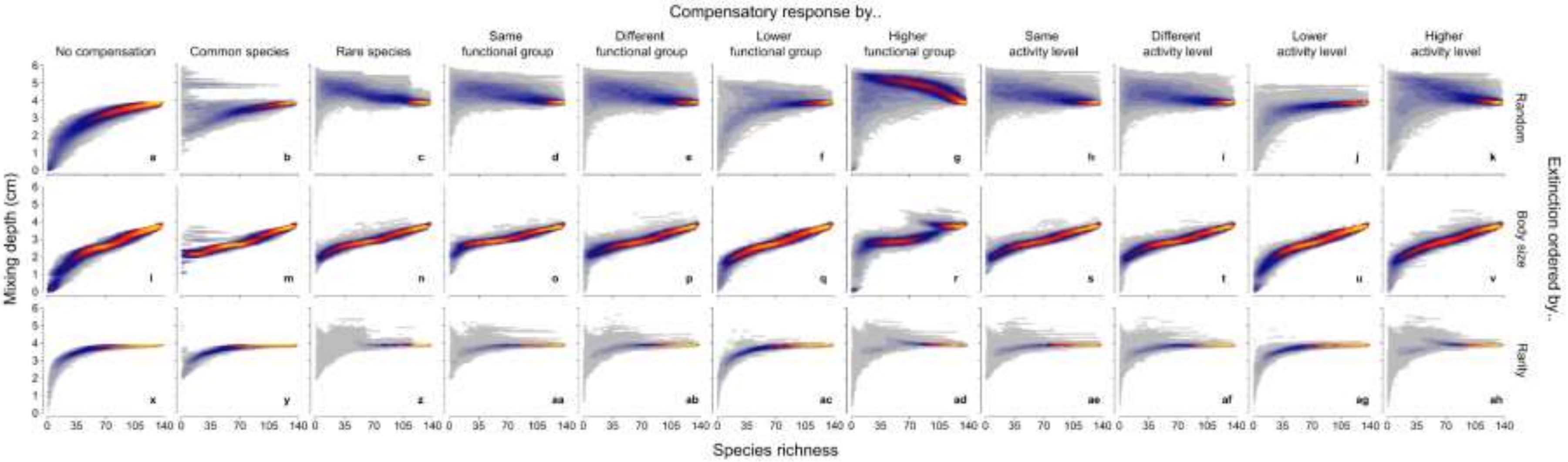


Figure A1. Predicted changes in sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction numeric compensation without Amphiura filiformis. Simulations (n = 1000 per panel) represent species losses that occur at random (panels a-k) or which reflect trait-based vulnerabilities to extinction governed by body size (panels l-v) or rarity (panels w-ag). I assumed that the surviving community shows either no compensatory response (a, l, w) or full numeric compensation by common (b, m, x) or rare (c, n, r) species, species from within (d, o, z), between (e, p, aa), lower (f,q,ab) or higher (g,r,ac) functional groups, or species with the same (h, s, ad), different (i,t,ae), lower (j,u,af) or higher (k,v,ag) level of activity to the species that have gone extinct. Colour intensity (cold to warm colouration; grey - blue – red - yellow) reflects an increasing density (low to high) of data points.

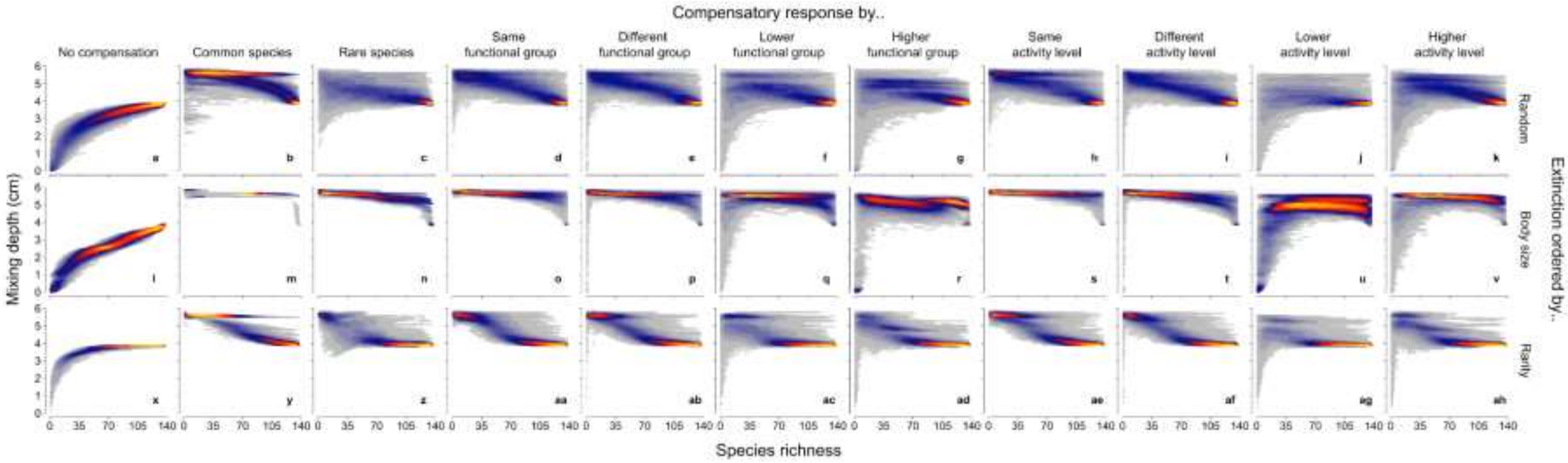


Figure A2. Predicted changes in sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction biomass compensation without Amphiura filiformis. Simulations (n = 1000 per panel) represent species losses that occur at random (panels a-k) or which reflect trait-based vulnerabilities to extinction governed by body size (panels l-v) or rarity (panels w-ag). I assumed that the surviving community shows either no compensatory response (a, l, w) or full biomass compensation by common (b, m, x) or rare (c, n, r) species, species from within (d, o, z), between (e, p, aa), lower (f,q,ab) or higher (g,r,ac) functional groups, or species with the same (h, s, ad), different (i,t,ae), lower (j,u,af) or higher (k,v,ag) level of activity to the species that have gone extinct. Colour intensity (cold to warm colouration; grey - blue – red - yellow) reflects an increasing density (low to high) of data points.

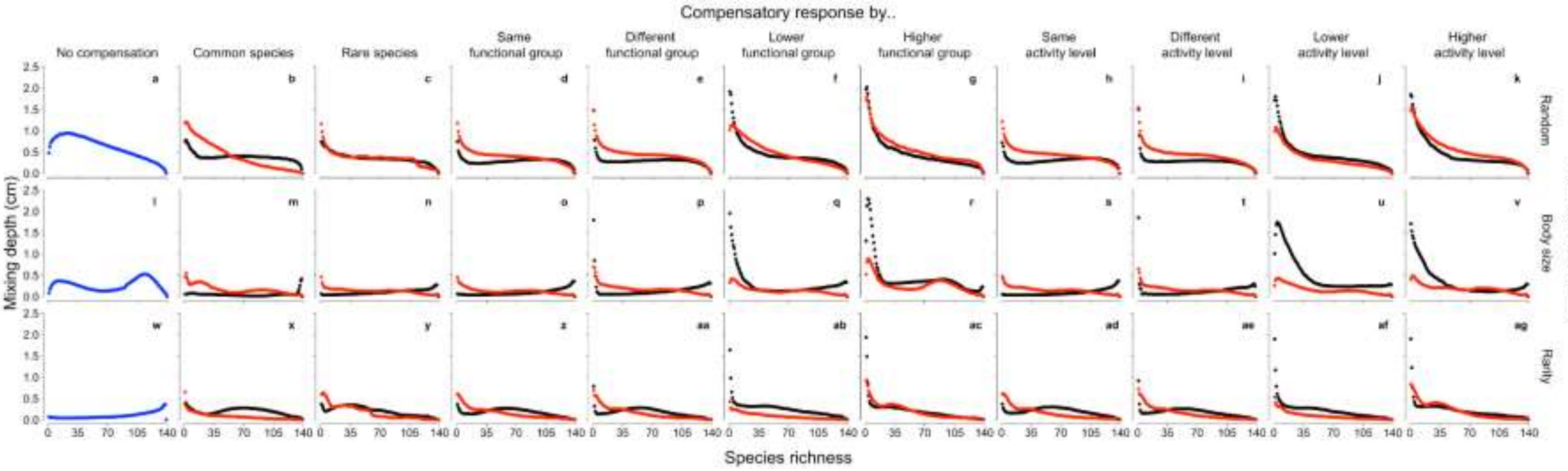


Figure A3. Variability of sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction compensation without Amphiura filiformis. Standard deviations are shown for the probabilistic distributions (n = 1000) at each level of species richness for the extinction scenarios depicted in Figures 1 and 2, assuming no compensatory response (blue), full numeric compensation (red) or full biomass compensation (black).

Equation A1. *Per capita* bioturbation potential, BP_i

$$BP_i = \overline{B_i}^{0.5} \times M_i \times R_i$$

B_i = mean species biomass (= total species biomass / total species abundance), in grams. Following Solan *et al.*[1], Bi is square root transformed to ensure species contributions conform to a linear scale.

R_i = a categorical scale to reflect increasing species effects on 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).

M_i = a categorical scale to reflect 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).

Equation A2. Population level bioturbation potential, BP_p

$$BP_p = BP_i \times A_i$$

A_i = Mean total species abundance

Equation A3. Community level bioturbation potential, BP_C

$$BP_c = \sum_{i=n}^{n} BP_P$$

Equation A4. Mixing depth (MD).

The relationship between BP_c and the MD is based on an empirical fit (Solan *et al.* 2004).

$$MD = \left(\frac{6 \times e^{0.719 \times \log(BP_C) - 4.55}}{1 + e^{0.719 \times \log(BP_C) - 4.55}}\right)$$

Equation A4 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[1]).

Code A1. R code for Compensation Models: Worked Example

Our post-extinction compensation models can be implemented in the open source software R (https://www.r-project.org). Here, I provide a fully worked step-by step example of how to run our models on a typical faunal dataset. Note that there are certain prerequisites in terms of species information, data and format required to calculate the community bioturbation potential (BP_c), including individual species biomass, species population abundance, bioturbation mode and level of activity (see Solan et al. 2004 for more details). The code provided has been tested up to R version 3.3.0.

```
## Step 1. Get data in the correct format

# Data columns:
# - Species names
# - Mean species biomass (Bi)
# - Mean total species abundance (Ai)
# - Bioturbation potential per individual (BPi)
# - Bioturbation potential per population (BPp)
# - Sediment reworking mode (Ri)
# - Activity level (Mi)

# Save data as a csv file.
## Step 2. Load data into R

# 1. Set working direktory

setwd("/Users/matthiasthomsen/Documents")

# 2. Load your data (csv) file

alldata <- read.csv("Data_CompModels.csv", header=T)

# 3. Check data structure and that data has been loaded correctly.

str(alldata)

## 'data.frame':    139 obs. of  7 variables:
##  $ Species: Factor w/ 139 levels "Abra alba","Abra nitida",..: 1 2 3
4 5 6 7 8 9 10 ...
##  $ Ai     : num  0.7273 0.5454 2.8182 0.8182 0.0909 ...
##  $ Bi     : num  0.00071 0.00637 0.00051 0.00224 1.31381 ...
##  $ BPi    : num  0.107 0.319 0.09 0.379 2.292 ...
##  $ BPp    : num  0.0776 0.1741 0.2536 0.31 0.2084 ...
##  $ Ri     : int  2 2 2 4 1 4 4 4 2 3 ...
##  $ Mi     : int  2 2 2 2 2 3 3 3 1 2 ...

## Step 3.  Run simulation model
# The worked example below is for random extinction with no compensatio
n.

# 1. For convenience store the number of species as a separate variable.

nsp <- nrow(alldata)

# 2. Set the number of simulations (in this case 100). This is the numbe
r of times you wish to simulate species removal of the entire community
(from the total number of species until 1 species in the community remai
```

```
n).

nsims <- 100

# 3. Define whether compensation is present (TRUE) or absent (FALSE).

CompFlag <- FALSE

# 4. Add new columns (AiSim and EPSim) in the data file  (alldata) to re
cord the abundances and extinction probabilities for each simulation, re
spectively.

alldata$AiSim <- NA
alldata$EPSim <- NA

# When compensation is driven by functional group or activity level, add
two new columns in the data file (alldata) to record functional group i.
e. reworking mode (Ri) and activity level (Mi), respectively.

alldata$RiSim <- NA # scenario: 5.C-D
alldata$MiSim <- NA # scenario: 5.E-F

# 5. Specify the probability of extinction, in this case random (all spe
cies have equal risk of extinction, 1/nsp).

alldata$ExtinctProb <- 1/nsp

# To modify the scenario of extinction redefine the risk of extinction
(i.e. 'alldata$ExtinctProb') by substituting '1/nsp' for the appropriate
probability of species extinction below.

# Extinction ordered by body size (largest to smallest):

# alldata$ExtinctProb <- alldata$Bi/sum(alldata$Bi)

# Extinction ordered by rarity (lowest to highest abundance):

# alldata$ExtinctProb <- (1/alldata$Ai)/sum(1/alldata$Ai)

# 6. Set up output data frame recording the simulated data. The columns
are:

 # - Simulation: the simulation number.
 # - Nsp: the number of species remaining in the community
 # - ExtinctSpecies: the species that went extinct for a given simulatio
n run.
 # - Measure: the community function that is being calculated, in this c
ase the mixing depth (MD).
 # - Value: the value of that community function.
 # - CompensatingSpecies: the name of the compensating species for a giv
en simulation run.
 # - Compensation: the amount of compensation (varies with compensation
type i.e. numeric or biomass).
```

```
# Note that the ExtinctSpecies column contains the name of the species t
hat will go extinct in the following run, i.e. the first row records the
mixing depth of the full, intact community, before any species has expir
ed.

output <- expand.grid(Simulation = 1:nsims, Nsp = nsp:1, ExtinctSpecies=
NA, Measure=c("MD"), Value=NA, CompensatingSpecies=NA, Compensation=NA)

# 7. For clarity, order the Simulation column in the output data frame.

output <- output[order(output$Simulation),]

# 8. Having set up the output data frame for the model results, we can n
ow run the simulations.

for (sim_count in 1:nsims){
cat("sim_count: ", sim_count, "\n")

# 9. Reset abundances and the probability of extinction for the next sim
ulation.

alldata$AiSim <- alldata$Ai
alldata$EPSim <- alldata$ExtinctProb

# If compensation is present (i.e. CompFlag <- TRUE), reset the new for
every simulation run columns recording functional group (reworking mode)
and activity level.

alldata$RiSim <- alldata$Ri # scenario: 5.C-D)
alldata$MiSim <- alldata$Mi # scenario: 5.E-F)

# 10. Species removal from the total number of species to 1, knocking ou
t species according to probability of extinction.

for (sp_count in nsp:1)
{

# 11. Calculate the total community bioturbation potential (BPc).

BPc <- sum(alldata$AiSim * alldata$BPi)

# 12.Calculate the mixing depth of sediment particles by the faunal comm
unity, based on an empirical fit (Solan et al. 2004) between BPc and the
measured sediment mixing depth (Equation S4).

MD <- (6*(exp((0.719*log(BPc))-4.55)))/(1+(exp((0.719*log(BPc))-4.55)))

# 13. Store these results in the output data frame.

output[output$Simulation == sim_count & output$Nsp==sp_count & output$Me
asure=="MD", "Value"] <- MD

# 14. Random deletition of species based on the probability specified ab
ove (see #8).
```

```
Extinct <- which(cumsum(alldata$EPSim)>=runif(1))[1]

# 15. If the capacity for compensation (i.e. “CompFlag”) is activated, t
he following two functions (19-20) will be executed prior to removal of
each species, implementing compensation.

if(CompFlag==TRUE)
{

# 16. Calculate, as appropriate, the amount of biomass or abundance that
will be lost with the extirpated species, depending on the type of compe
nsation considered.

# 'BiomassLost' for compensatory responses by biomass

BiomassLost <- alldata[Extinct,"AiSim"] * alldata[Extinct,"Bi"]

# OR 'abundanceLost' for numeric compensatory responses

AbundanceLost <- alldata[Extinct,"AiSim"]

# 17. Specify the compensatory response by inserting the code (above the
closing bracket) for the appropriate scenario of compensation from step
5.

}

# 18. Extinction happens! Set abundance and probability of extirpated sp
ecies to 0

alldata[Extinct,c("EPSim","AiSim")] <- 0

# 19. Normalise the exinction probabilities so that the sum = 1

alldata$EPSim <- alldata$EPSim / sum(alldata$EPSim)

# 20. Record the identity of the extipated species

output[output$Simulation == sim_count & output$Nsp==sp_count,
"ExtinctSpecies"] <- as.character(alldata[Extinct,"Species"])
  }
}

## sim_count:  1
## sim_count:  2

...
## sim_count:  100

# Note that, if you are running multiple model scenarios after one anoth
er you will have to adapt the code to accommodate for a unique id for ea
ch output file corresponding to each model scenario.
```

```
## Step 4. Post-extinction compensation responses

# First, define compensation as present (see Step 3.3).

CompFlag <- TRUE

# SampleVar and isEmpty are required for the functional group and activi
ty level compensation scenarios

# Function SampleVar allow the sampling of vectors of varying lengths (f
rom x components to 1).

SampleVar <- function(x) {
  if (length(x) <= 1) {
    return(x)
  } else {
    return(sample(x,1))
  }
}

# The function isEmpty is needed if there are no species left from the s
elected functional group or activity level, in these rare instances, com
pensation will instead be sustained by a species selected from a differe
nt functional group or activity level (depending on the appropriate comp
ensation scenario) than originally selected for.

isEmpty <- function(x) {
  return(length(x)==0)
}

## Compensatory responses by:
# 4.A: Common species
# 4.B: Rare species
# 4.C: Same functional group
# 4.D: Different functional group
# 4.E: Lower functional group
# 4.F: Higher functional group
# 4.G: Same activity level
# 4.H: Different activity level
# 4.I: Lower activity level
# 4.J: Higher activity level
# 4.K: Record amount of compensation

# Insert code for the appropriate compensatory response in step 3.20 (wi
thin the curly brackets!).

## 4.A Common species compensate

# Removes the species extirpated for a given simulation

temp<-alldata[-c(Extinct),]

# Removes all the species gone extinct previously in the simulation (AiS
im = 0)
```

```
temp<-temp[!temp$AiSim %in% 0,]

# Order species remaining in the community according to abundance (highe
st to lowest)

HighestAbn<-as.numeric(rownames(temp[order(temp$AiSim, decreasing=T),]
[1,]))

# The most abundant species compensates, as appropriate, by the biomass
or abundance lost with extirpated species.

# Biomass compensation

alldata$AiSim[HighestAbn] <- alldata$AiSim[HighestAbn] + BiomassLost/all
data$Bi[HighestAbn]

# OR numeric compensation

alldata$AiSim[HighestAbn] <- alldata[Extinct,"AiSim"] + alldata$AiSim[Hi
ghestAbn]

# Record the identity of the species with compensating capacity in the o
utput file

output[output$Simulation == sim_count & output$Nsp==sp_count,"Compensati
ngSpecies"] <- as.character(alldata$Species[HighestAbn])

## 4.B Rare species compensate

# The "-Extinct" is to tell R to take all abundance value but the one fr
om the extinct species and order them by their row number

# Removes the species extirpated for a given simulation

temp <- alldata[-c(Extinct),]

# Removes all the species gone extinct previously in the simulation (AiS
im = 0)

temp <- temp[!temp$AiSim %in% 0,]

# Order species remaining in the community at any given time of the simu
lation according to abundance (lowest to highest)

LowestAbn <- as.numeric(row.names(temp[order(temp$AiSim),][1,]))

# The species of lowest abundance compensates, as appropriate, by the bi
omass or abundance lost with the extirpated species.

# Biomass compensation

alldata$AiSim[LowestAbn] <- alldata$AiSim[LowestAbn] + BiomassLost/allda
ta$Bi[LowestAbn]
```

```
# OR

# Numeric compensation

alldata$AiSim[LowestAbn] <- alldata[Extinct,"AiSim"] + alldata$AiSim[Low
estAbn]

# Record the identity of the species with compensating capacity in the o
utput file

output[output$Simulation == sim_count & output$Nsp==sp_count,"Compensati
ngSpecies"] <- as.character(alldata$Species[LowestAbn])


## 4.C Same functional group compensation

# Calculate the numerical distance in terms of reworking mode for all re
maining species in the community in reference to species selected for ex
tinction

distance<-dist(alldata$RiSim, diag = TRUE, upper = TRUE)

# Create distance matrix

distance<-as.matrix(distance)

diag(distance) <- NA

# Define vector of species distances in reworking mode to the extinct sp
ecies, excluding the distance of the extirpated species with itself

d1D<-distance[,Extinct]

# Create vector d1D containing the distance for each species remaining i
n the community to the extinct species. Select species with most similar
reworking trait (i.e. shortest distance to extirpated species), omitting
species that have already gone extinction previously in the simulation
(i.e. NA’s).

d1D<-d1D[d1D==min(d1D, na.rm=TRUE)]

# Remove species that are already gone extinct previously in the simulat
ion (i.e. NA) from vector d1D.

d1D<-d1D[!is.na(d1D)]

# Select one species from vector d1D.

RdmRi<-SampleVar(names(d1D))

# Translate back into numeric.

RdmRi<-as.numeric(RdmRi)
```

```r
# Species of similar reworking trait compensates, as appropriate, by the biomass or abundance lost with the extirpated species.

#Biomass compensation.

alldata[RdmRi, "AiSim"] <- alldata[RdmRi, "AiSim"] + BiomassLost/alldata[RdmRi, "Bi"]

#Numeric compensation.

alldata[RdmRi, "AiSim"] <- alldata[Extinct,"AiSim"] + alldata[RdmRi, "AiSim"]

#Record the identity of the species with compensating capacity in the output file.

output[output$Simulation == sim_count & output$Nsp==sp_count,"CompensatingSpecies"] <- ifelse(!isEmpty(RdmRi), as.character(alldata$Species[RdmRi]), NA)


## 4.D Between functional group compensation

# Calculate the numerical distance in terms of reworking mode for all remaining species in the community in reference to species selected for extinction.

distance<-dist(alldata$RiSim, diag = TRUE, upper = TRUE)

# Create distance matrix

distance<-as.matrix(distance)

diag(distance) <- NA

# Define vector of species distances in reworking mode to the extinct species, excluding the distance of the extirpated species with itself.

d1D<-distance[,Extinct]

# Create vector d1D containing the species remaining in the community excluding all species with the same reworking trait to that of the extinct species. Select species with different activity level.

d1D<-d1D[!d1D %in% 0]

# Remove species that are already gone extinct (i.e. NA’s) from vector d1D.

d1D<-d1D[!is.na(d1D)]


# Select one species from vector d1D.
```

```
RdmRi<-SampleVar(names(d1D))

# Translate back into numeric.

RdmRi<-as.numeric(RdmRi)

# Species of dissimilar reworking trait compensates, as appropriate, by the biomass or abundance lost with the extirpated species.

# Biomass compensation.

alldata$AiSim[RdmRi] <- alldata$AiSim[RdmRi] + BiomassLost/alldata$Bi[RdmRi]

# OR

# Numeric compensation.

alldata$AiSim[RdmRi] <- alldata[Extinct,"AiSim"] + alldata$AiSim[RdmRi]

# Record the identity of the compensating species in the output file.

output[output$Simulation == sim_count & output$Nsp==sp_count,"CompensatingSpecies"] <- ifelse(!isEmpty(RdmRi), as.character(alldata$Species[RdmRi]), NA)

## 4.E Lower functional group

# Determine the functional (reworking, Ri) group of the extinct species.

RiExtinct <- alldata[Extinct,"Ri"]

# Create temporary data file (TEMPalldata) to avaoid NAs.

TEMPalldata<-alldata[complete.cases(alldata),]

# Select species with capacity for compensation by nesting two ifelse functions.

# Condition statement: Are there any species in alldata$RiSim from a lower functional group than the species that went extinct (i.e. RiExtinct).

LowRi<-ifelse(length(TEMPalldata$RiSim[TEMPalldata$RiSim < RiExtinct]) > 0,

# If yes, the SampleVar function selects one element from this group.

SampleVar(rownames(TEMPalldata[TEMPalldata$RiSim < RiExtinct,])),

# If no, are there any species in the remaining community (i.e. alldata$RiSim) from the same fucntional group to that of the species that went extinct (i.e. RiExtinct).
```

```
ifelse(length(TEMPalldata$RiSim[TEMPalldata$RiSim == RiExtinct]) > 0,

# If yes, the SampleVar function selects one element from this group.

SampleVar(rownames(TEMPalldata[TEMPalldata$RiSim == RiExtinct,])),

# If no, the SampleVar function selects one element from a functional gr
oup higher than that of the species that went extinct (i.e. RiExtinct).

SampleVar(rownames(TEMPalldata[TEMPalldata$RiSim > RiExtinct,]))))

# Translate back into numeric.

LowRi<-as.numeric(LowRi)

# Now add compensation by either biomass OR numeric!

# Add biomass of the species lost to the compensating species (from a lo
wer functional group).

alldata$AiSim[LowRi] <- alldata$AiSim[LowRi] + BiomassLost/alldata$Bi[Lo
wRi]

# Record ID of the compensating species.

outputB[outputB$Simulation == sim_count & outputB$Nsp==sp_count,"Compens
ateSpecies"] <- ifelse(!isEmpty(LowRi), as.character(alldata$Species[Low
Ri]), NA)


## 4.F Higher functional group

# Determine the functional (reworking, Ri) group of the extinct species.

RiExtinct <- alldata[Extinct,"Ri"]

# create temporary data file (TEMPalldata) to avaoid NAs.

TEMPalldata<-alldata[complete.cases(alldata),]

# Select species with capacity for compensation by nesting two ifelse fu
nctions.

# Condition statement: Are there any species in alldata$RiSim from a hig
her functional group than the species that went extinct (i.e. RiExtinc
t).

HighRi<-ifelse(length(TEMPalldata$RiSim[TEMPalldata$RiSim > RiExtinc
t]) > 0,

# If yes, the SampleVar function selects one element from this group

SampleVar(rownames(TEMPalldata[TEMPalldata$RiSim > RiExtinct,])),
```

```
# If no, are there any species in the remaining community (i.e. alldata
$RiSim) from the same fucntional group to that of the species that went
extinct (i.e. RiExtinct).

ifelse(length(TEMPalldata$RiSim[TEMPalldata$RiSim == RiExtinct]) > 0,

# If yes, the SampleVar function selects one element from this group
SampleVar(rownames(TEMPalldata[TEMPalldata$RiSim == RiExtinct,])),

# If no, the SampleVar function selects one element from species from a
functional group that is lower than that of the species that went extinc
t (i.e. RiExtinct).

SampleVar(rownames(TEMPalldata[TEMPalldata$RiSim < RiExtinct,]))))

# Translate back into numeric

HighRi<-as.numeric(HighRi)

# Now add compensation by either biomass OR numeric!

# Add biomass of the species lost to species from a higher functional gr
oup.

alldata$AiSim[HighRi] <- alldata$AiSim[HighRi] + BiomassLost/alldata$Bi
[HighRi]

# Record ID of the compensating species.

outputA[outputA$Simulation == sim_count & outputA$Nsp==sp_count,"Compens
ateSpecies"] <- ifelse(!isEmpty(HighRi), as.character(alldata$Species[Hi
ghRi]), NA)


## 4.G Same activity level compensate

Calculate the numerical distance in terms of activity level for all rema
ining species in the community in reference to species selected for exti
nction

distance<-dist(alldata$MiSim, diag = TRUE, upper = TRUE)

# Create distance matrix

distance<-as.matrix(distance)

diag(distance) <- NA

# Define vector of species distances in activity level to the extinct sp
ecies, excluding the distance of the extirpated species with itself.

d1D<-distance[Extinct,]

# Create vector d1D containing the distance for each species remaining i
```

```
n the community to the extinct species. Select species with most similar
activity level (i.e. shortest distance to extirpated species), omitting
species that have already gone extinction (i.e. NA’s).

d1D<-d1D[d1D==min(d1D, na.rm=TRUE)]

# Remove species that are already gone extinct (i.e. NA) from vector d1
D.

d1D<-d1D[!is.na(d1D)]

# Select one species from vector d1D.

RdmMi<-SampleVar(names(d1D))

# Translate back into numeric

RdmMi<-as.numeric(RdmMi)

# Species of same level of activity compensates, as appropriate, by the
biomass or abundance lost with the extirpated species.

# Biomass compensation

alldata[RdmMi, "AiSim"] <- alldata[RdmMi, "AiSim"] + BiomassLost/alldata
[RdmMi, "Bi"]

# OR numeric compensation

alldata[RdmMi, "AiSim"] <- alldata[Extinct,"AiSim"] + alldata[RdmMi, "Ai
Sim"]

# Record the identity of the species with compensating capacity in the o
utput file.

output[output$Simulation == sim_count & output$Nsp==sp_count,"Compensati
ngSpecies"] <- ifelse(!isEmpty(RdmRi), as.character(alldata$Species[RdmR
i]), NA)

## 4.H Different activity level compensate

# Calculate the numerical distance in terms of activity level for all re
maining species in the community in reference to species selected for ex
tinction

distance<-dist(alldata$MiSim, diag = TRUE, upper = TRUE)

# Create distance matrix

distance<-as.matrix(distance)

diag(distance) <- NA

# Define vector of species distances in activity level to the extinct sp
```

```
ecies, excluding the distance of the extirpated species with itself.

d1D<-distance[Extinct,]

# Create vector d1D containing the species remaining in the community ex
cluding all species from the same activity level of the extinct species.
Select species with different activity level.

d1D<-d1D[!d1D %in% 0]

# Remove species that are already gone extinct (i.e. NA’s) from vector d
1D.

d1D<-d1D[!is.na(d1D)]

# Select one species from the d1D vector.

RdmMi<-SampleVar(names(d1D))

# Translate back into numeric

RdmMi<-as.numeric(RdmMi)

# Species of different activity level compensates, as appropriate, by th
e biomass or abundance lost with the extirpated species.

# Biomass compensation

BiomassLost/alldata$Bi[RdmMi]
alldata[RdmMi, "AiSim"] <- alldata[RdmMi, "AiSim"] + BiomassLost/alldata
[RdmMi, "Bi"]

# OR numeric compensation

alldata$AiSim[RdmMi] <- alldata[Extinct,"AiSim"] + alldata$AiSim[RdmMi]

# Record the identity of the species with compensating capacity in the o
utput file

output[output$Simulation == sim_count & output$Nsp==sp_count,"Compensati
ngSpecies"] <- ifelse(!isEmpty(RdmRi), as.character(alldata$Species[RdmR
i]), NA)


## 4.I Lower activity level

# Determine the acitivity level (mobility mode, Mi) of the extinct speci
es

MiExtinct <- alldata[Extinct,"Mi"]

# create temporary data file to avaoid NAs

TEMPalldata<-alldata[complete.cases(alldata),]
```

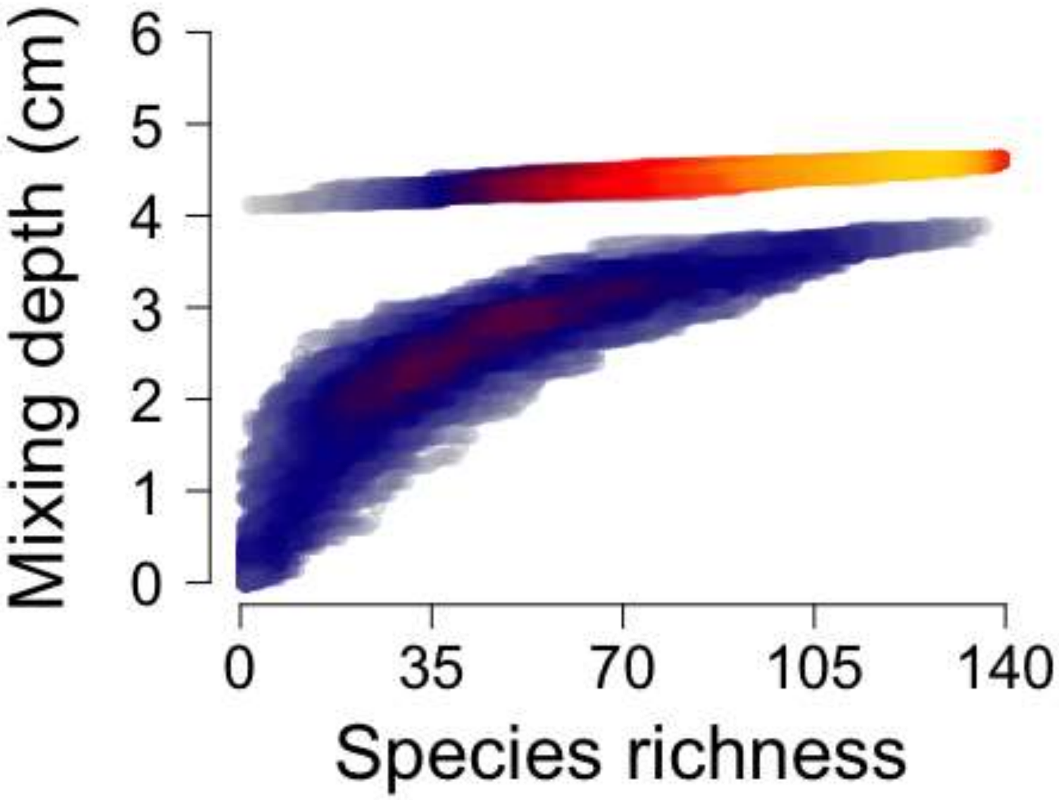
```
# Select species with capacity for compensation by nesting two ifelse functions.

# Condition statement: If there are any species in alldata$MiSim from a lower functional group to the species went extinct (i.e. MiExtinct).

LowMi<-ifelse(length(TEMPalldata$MiSim[TEMPalldata$MiSim < MiExtinct]) > 0,

# If yes, the SampleVar function selects one element from this group.

SampleVar(rownames(TEMPalldata[TEMPalldata$MiSim < MiExtinct,])),

#If no, are there any element of alldata$MiSim of the same activity level to that of the species that went extinct (i.e. MiExtinct).

ifelse(length(TEMPalldata$MiSim[TEMPalldata$MiSim == MiExtinct]) > 0,

# If yes, the SampleVar function selects one element from this group.

SampleVar(rownames(TEMPalldata[TEMPalldata$MiSim == MiExtinct,])),

# # If no, the SampleVar function selects one species from an activity level higher than the species that went extinct.

SampleVar(rownames(TEMPalldata[TEMPalldata$MiSim > MiExtinct,]))))

# Translate back into numeric.

LowMi<-as.numeric(LowMi)

# Now add compensation by either biomass or numeric!

# Add biomass from the species lost to compensating species (from a lower functional group).

alldata$AiSim[LowMi] <- alldata$AiSim[LowMi] + BiomassLost/alldata$Bi[LowMi]

# Record ID of who has compensated

outputD[outputD$Simulation == sim_count & outputD$Nsp==sp_count,"CompensateSpecies"] <-     ifelse(!isEmpty(LowMi), as.character(alldata$Species[LowMi]), NA)


## 4.J Higher activity level

# Determine the acitivity level (mobility mode, Mi) of the extinct species.

MiExtinct <- alldata[Extinct,"Mi"]
```

```
# create temporary data file to avaoid NAs.

TEMPalldata<-alldata[complete.cases(alldata),]

# Select species with capacity for compensation by nesting two ifelse fu
nctions.

# Condition statement: Are there any species in alldata$MiSim from a hig
her activity level (Mi)  than the species that went extinct (i.e. MiExti
nct).

HighMi<-ifelse(length(TEMPalldata$MiSim[TEMPalldata$MiSim > MiExtinc
t]) > 0,

# If yes, the SampleVar function selects one element from this group.

SampleVar(rownames(TEMPalldata[TEMPalldata$MiSim > MiExtinct,])),

# If no, are there any element of alldata$MiSim of the same activity lev
el to that of the species that went extinct (i.e. MiExtinct).

ifelse(length(TEMPalldata$MiSim[TEMPalldata$MiSim == MiExtinct]) > 0,

# If yes, the SampleVar function selects one element from this group.

SampleVar(rownames(TEMPalldata[TEMPalldata$MiSim == MiExtinct,])),

# If no, the SampleVar function selects one species from an activity lev
el lower than the species that went extinct.

SampleVar(rownames(TEMPalldata[TEMPalldata$MiSim < MiExtinct,]))))

# Translate into numeric.

HighMi<-as.numeric(HighMi)

# Now add compensation by either biomass OR numeric!

# Add biomass of the species lost to species with higher activity level.

alldata$AiSim[HighMi] <- alldata$AiSim[HighMi] + BiomassLost/alldata$Bi
[HighMi]

# Record ID of the compensating species.

outputC[outputC$Simulation == sim_count & outputC$Nsp==sp_count,"Compens
ateSpecies"] <- ifelse(!isEmpty(HighMi), as.character(alldata$Species[Hi
ghMi]), NA)


## 4.K Record amount of compensation

# Record the amount of biomass or numeric compensation, as appropriate,
in output file. Note that this line of code needs to be inserted after t
```

```
he command line recording the compensating species, but within the closing bracket in step 3.20.

# Record biomass compensation.

output[output$Simulation == sim_count & output$Nsp==sp_count,"BiomassCompensation"] <-BiomassLost

# OR

# Record numeric compensation.

output[output$Simulation == sim_count & output$Nsp==sp_count,"Compensation"] <- alldata[Extinct,"AiSim"]
```

You can also embed plots, for example:

```
## Step 5. Plot model results

# Plot model output using the heatscatter command. First, install the LSD package available at the CRAN repository. Once installed, load the LSD package into your library.

# Install LSD package by removing the hash for the line below, and run code.
#install.packages("LSD")

# Load LSD packaged
library(LSD)

par(mar = c(6,6,1,1))

heatscatter(output$Nsp,output$Value,
            bty="n",
            pch = 19,
            cexplot = 1,
            nrcol = 30,
            grid = 200,
            colpal = "heat",
            xlab = "",
            ylab = "",
            xaxt = "n",
            main = "",
            las = 1,
            cex.lab = 1.6,
            cex.axis = 1.6,
            ylim = c(0.0,6.0),
            xlim = c(0.0,139.5),
            alpha = 50)
axis(1, at = seq(0,140, by = 35), lab = c("0","35","70","105","140"),
     las = 1, cex.lab = 1.6, cex.axis = 1.6, mgp = c(0,1,0))
title(xlab = "Species richness", ylab = "Mixing depth (cm)", cex.lab = 2)
```



```
# Step 6. Save results to csv file.

# Use the write function to save data output as a csv file.

# Mac users:
write.csv(output, "~/Desktop/output.csv", row.names=T)

# Windows users:
write.csv(output, "C:/ Users/UserName/Desktop/output.csv", row.names=T)
```

Appendix C

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Consequences of biodiversity loss diverge from expectation due to post-extinction compensatory responses

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Consensus has been reached that global biodiversity loss impairs ecosystem functioning and the sustainability of services beneficial to humanity. However, the ecosystem consequences of extinction in natural communities are moderated by compensatory species dynamics, yet these processes are rarely accounted for in impact assessments and seldom considered in conservation programmes. Here, we use marine invertebrate communities to parameterise numerical models of sediment bioturbation – a key mediator of biogeochemical cycling – to determine whether post-extinction compensatory mechanisms alter biodiversity-ecosystem function relations following non-random extinctions. We find that compensatory dynamics lead to trajectories of sediment mixing that diverge from those without compensation, and that the form, magnitude and variance of each probabilistic distribution is highly influenced by the type of compensation and the functional composition of surviving species. Our findings indicate that the generalized biodiversity-function relation curve, as derived from multiple empirical investigations of random species loss, is unlikely to yield representative predictions for ecosystem properties in natural systems because the influence of post-extinction community dynamics are under-represented. Recognition of this problem is fundamental to management and conservation efforts, and will be necessary to ensure future plans and adaptation strategies minimize the adverse impacts of the biodiversity crisis.

Species extinction and the associated degradation of ecosystems are proceeding at an accelerating pace[1–3], but the consequences of the current decline in biodiversity for socio-ecological systems represent a critical knowledge gap for policy-makers[4]. Consensus reached from experiments that have manipulated biodiversity and measured various ecosystem functions, including primary productivity, nutrient cycling and decomposition, predict an accelerating decline in ecosystem properties with increasing biodiversity loss[5], yet it is not clear how appropriate it is to apply this general relationship at the landscape scale[6]. A major difficulty is that the complexities of natural communities[7,8], including the role of rare species[9] and the occurrence of co-extinctions[10], have been poorly articulated in controlled experiments, and very few studies have focussed on realistic trajectories of species loss that factor in a predisposition to community dynamics[11]. Indeed, the role of population dynamics in moderating the consequences of extinction have received little attention[12–14], despite direct evidence that communities undergo fundamental shifts in the relative abundance of taxa and the dominance of species in each successive assemblage that follows an extinction event[15,16]. Such community turnover resembles that of recovering post-disturbance communities[17], where a variety of compensatory interactions amongst surviving species[18] develop and offset, wholly or in part, the functional contributions made by species that have been extirpated[14].

Compensatory responses tend to be asynchronous within a perturbed community and can lead to to partial[19,20], complete[21–23], or over[24] compensation in ecosystem functioning. Species can also switch behaviour[25], make physiological regulation adjustments[26], exhibit elevated growth (biomass compensation[27]) or increase reproductive investment (numeric compensation[28]) in response to perturbation, especially following release from

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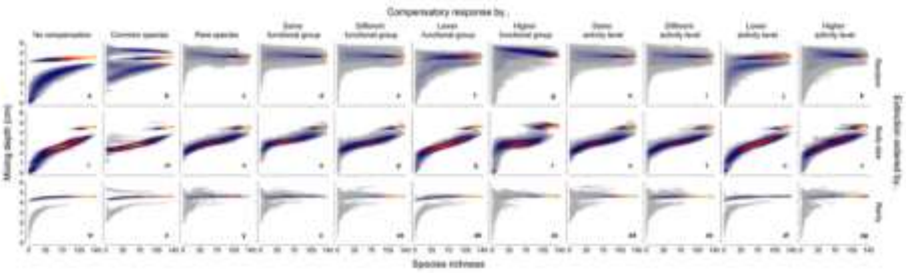

Figure 1. Predicted changes in sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction numeric compensation. Simulations (n = 1000 per panel) represent species losses that occur at random (panels a–k) or which reflect trait-based vulnerabilities to extinction governed by body size (panels l–v) or rarity (panels w–ag). We assumed that the surviving community shows either no compensatory response (a,l,w) or full numeric compensation by common (b,m,x) or rare (c,n,r) species, species from within (d,o,z), between (e,p,aa), lower (f,q,ab) or higher (g,r,ac) functional groups, or species with the same (h,s,ad), different (i,t,ae), lower (j,u,af) or higher (k,v,ag) level of activity to the species that have gone extinct. Colour intensity (cold to warm colouration; grey - blue – red - yellow) reflects an increasing density (low to high) of data points.

competition/predation[29] or during niche expansion[30]. These responses may not be immediate, in some instances taking months[31] to years[32] to develop, but once expressed they can be critical in influencing further species interactions[33] and can dramatically affect ecosystem properties[34–37]. Furthermore, where extinction events are localized and communities are interconnected[38], immigration and re-colonization from the surrounding area[39], as well as recruitment from the wider species pool[40], can play a pivotal role in stabilizing local population decline and ecological processes[41]. Ultimately, however, the degree of functional compensation will depend on the amount of functional redundancy in the surviving community, which, in turn, will reflect the spatial extent and consistency of the perturbation compromising biodiversity and the level of covariation between the extinction driver and the traits that mediate functioning[42].

Despite the range of compensatory mechanisms and variety of ways in which species interactions can affect the functional properties of natural communities[7,18], few studies have explored how surviving species moderate the consequences of extinction[42–45] and the relative role of different compensation mechanisms remain largely unexplored. Here, we use probabilistic numerical simulations to test how the loss of sediment dwelling marine invertebrates may affect the sediment mixing depth, an important mediator of biogeochemical cycling[46,47]. Our simulations assume that the sequence of species loss is either random or ordered by body size or rarity to reflect likely sources of extinction risk. We compare these probabilistic distributions to further simulations in which populations of surviving species maintain total abundance (numeric compensation) or total biomass (biomass compensation) sourced from different components (common or rare species, within or between bioturbation functional groupings, same or different/lower or higher level of activity) of the surviving community. In doing so, our objective is to establish the extent to which alternative compensatory dynamics alter biodiversity-function relationships.

Results

In the absence of compensatory dynamics, the form of the biodiversity function curve approximates expectations (accelerating loss of function with declining species richness, moderated by how extinctions are ordered), and our simulations include a previously documented[42] prominent bifurcation of the mixing depth that reflects whether a burrowing brittlestar, *Amphiura filiformis*, is present (deeper mixing depth) or absent (shallower mixing depth) in the surviving community (panels a,l,w in Figs 1 and 2). The disproportionate contribution of this species is evident throughout all of our simulations (Supplementary Figures S1 and S2), although it is clear that the loss of other species can also result in stepped changes (abrupt shifts in mixing depth, most prominently featured in Fig. 1) that show a tendency to only partially compensate for the loss of the extirpated species (Fig. 1).

When compensatory mechanisms of the surviving community are based on numerical responses, the mixing depth is largely maintained as species richness declines (Fig. 1), when extinctions are random (panels b–k) or ordered by rarity (panels x–ag). However, when extinctions are ordered by body size (panels m–v), compensatory responses, independent of how they are expressed, are unable to fully mitigate the functional consequences associated with species loss, yet notable differences exist depending on which species drive the compensatory response. However, when compensatory mechanisms of the surviving community are based on biomass, with a few exceptions, there is a tendency for overcompensation to take place along the main species-function trajectory (colour intensity in Fig. 2). Despite implementing these fundamentally different compensatory mechanisms, our simulations reveal that most probabilistic trajectories overlap one another to form a narrow band of likely ecosystem functioning (colour intensity in Figs 1 and 2). The variation of the outcome under numeric versus biomass compensation increases at low and high levels of species richness; this is particularly evident for compensatory responses driven by lower and higher functional groupings and activity level, but at intermediate levels of species

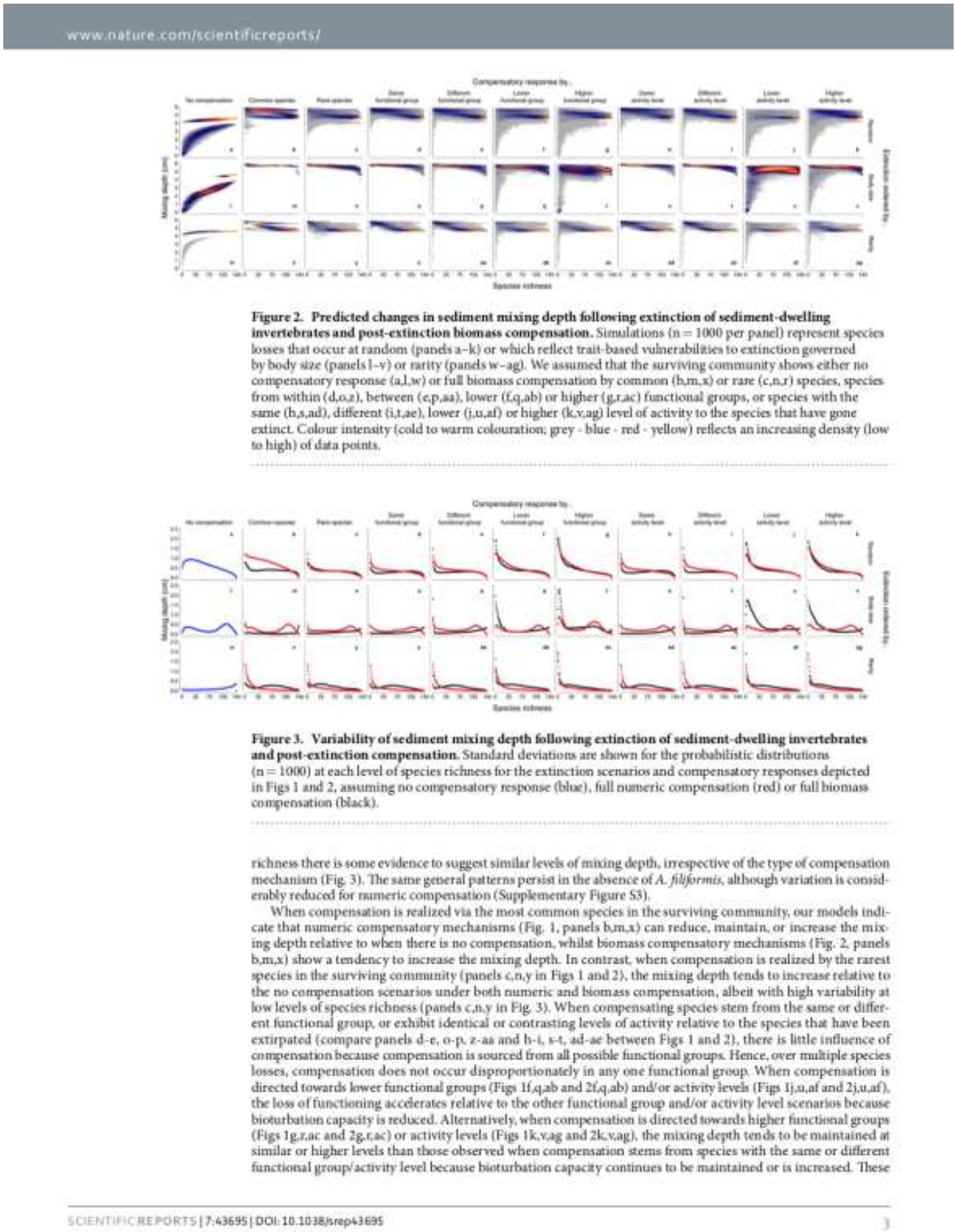

Figure 2. Predicted changes in sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction biomass compensation. Simulations (n = 1000 per panel) represent species losses that occur at random (panels a–k) or which reflect trait-based vulnerabilities to extinction governed by body size (panels l–v) or rarity (panels w–ag). We assumed that the surviving community shows either no compensatory response (a,l,w) or full biomass compensation by common (b,m,x) or rare (c,n,r) species, species from within (d,o,z), between (e,p,aa), lower (f,q,ab) or higher (g,r,ac) functional groups, or species with the same (h,s,ad), different (i,t,ae), lower (j,u,af) or higher (k,v,ag) level of activity to the species that have gone extinct. Colour intensity (cold to warm colouration; grey - blue - red - yellow) reflects an increasing density (low to high) of data points.

Figure 3. Variability of sediment mixing depth following extinction of sediment-dwelling invertebrates and post-extinction compensation. Standard deviations are shown for the probabilistic distributions (n = 1000) at each level of species richness for the extinction scenarios and compensatory responses depicted in Figs 1 and 2, assuming no compensatory response (blue), full numeric compensation (red) or full biomass compensation (black).

richness there is some evidence to suggest similar levels of mixing depth, irrespective of the type of compensation mechanism (Fig. 3). The same general patterns persist in the absence of *A. filiformis*, although variation is considerably reduced for numeric compensation (Supplementary Figure S3).

When compensation is realized via the most common species in the surviving community, our models indicate that numeric compensatory mechanisms (Fig. 1, panels b,m,x) can reduce, maintain, or increase the mixing depth relative to when there is no compensation, whilst biomass compensatory mechanisms (Fig. 2, panels b,m,x) show a tendency to increase the mixing depth. In contrast, when compensation is realized by the rarest species in the surviving community (panels c,n,y in Figs 1 and 2), the mixing depth tends to increase relative to the no compensation scenarios under both numeric and biomass compensation, albeit with high variability at low levels of species richness (panels c,n,y in Fig. 3). When compensating species stem from the same or different functional group, or exhibit identical or contrasting levels of activity relative to the species that have been extirpated (compare panels d-e, o-p, z-aa and h-i, s-t, ad-ae between Figs 1 and 2), there is little influence of compensation because compensation is sourced from all possible functional groups. Hence, over multiple species losses, compensation does not occur disproportionately in any one functional group. When compensation is directed towards lower functional groups (Figs 1f,q,ab and 2f,q,ab) and/or activity levels (Figs 1j,u,af and 2j,u,af), the loss of functioning accelerates relative to the other functional group and/or activity level scenarios because bioturbation capacity is reduced. Alternatively, when compensation is directed towards higher functional groups (Figs 1g,r,ac and 2g,r,ac) or activity levels (Figs 1k,v,ag and 2k,v,ag), the mixing depth tends to be maintained at similar or higher levels than those observed when compensation stems from species with the same or different functional group/activity level because bioturbation capacity continues to be maintained or is increased. These

observations suggest that certain traits may well be linked to the mediation of ecosystem functioning, but their role in determining observed levels of functioning will depend on how influential such traits are for underlying ecosystem processes[48].

Discussion

Using numerical models parameterised with data from a marine benthic community, we have demonstrated that incorporation of compensatory dynamics, irrespective of the mechanism of compensation (numeric or biomass) or how a species extinction risk is determined (random, ordered by rarity or body size), have the potential to lead to clear differences in aggregate community responses to species loss that do not always conform to expectations based on the generalised biodiversity-function relation curve[5]. Our models showed that the probabilistic distributions for sediment mixing depth were deeper when compensatory mechanisms were present relative to when they were absent, and when compensatory dynamics reflected post-extinction increases in biomass rather than abundance. Moreover, simulations indicate that the way in which numeric or biomass compensation is expressed within the surviving species pool is most influential. These observations highlight the importance of post-extinction compensatory mechanisms in determining how traits are expressed and mediate function, and suggest that the ecological status of soft-sediment benthic habitats is unlikely to conform to expectation as current visions of future scenarios of extinction lack the necessary sophistication.

Numerous studies investigating the consequences of environmental forcing for ecosystem functioning have focused on the decline of the number of species and their functional traits or attributes. Whilst the effect of various attributes of biodiversity on ecosystem functioning, including evenness[49], dominance[50], and functional traits[51] have been studied, the relative importance of compensatory mechanisms in natural ecosystems and the concept of compensation as a whole has largely been ignored despite evidence for the occurrence of compensation in natural systems[52]. Importantly, our simulations reveal that the mixing depth of sediment-dwelling invertebrate communities will depend on how compensatory behaviour is expressed, and the extent to which the functional attributes of compensating species affect bioturbation. A difficulty with determining the latter is that recent work has shown that differences in how species interact with sediment biogeochemistry and other aspects of the environment can converge in terms of absolute effects of ecosystem properties[48,51]. This may explain previous inconsistencies in linking particular species traits to ecosystem functioning[47] and why community compensation does not appear to be dominated by a limited number of species that host specific sets of traits; a conclusion consistent with recent studies that demonstrate the importance of common species in maintaining ecosystem functioning[53–55]. Whilst the differences between alternative compensatory scenarios may be subtle, they can form crucial differences. Consequently, the repercussions of species loss are more effectively offset by a subset of species that share the same functional group or level of activity, especially at low levels of species richness. Whether these mechanisms can be identified and operate in natural communities, however, remains an open empirical question[56].

It is important to acknowledge that our study is an abstraction of community dynamics and to recognize that the model assumptions we adopted represent an oversimplification of community interactions under environmental forcing. Our focus was not to predict the depth of sediment mixing for specific biodiversity futures, but rather to explore the relative importance of compensatory mechanisms in determining ecosystem properties. Whilst we were unable to incorporate the occurrence of co-extinctions[19], non-indigenous invasive species[57] or other cascading effects that can have further consequences for community structure and ecosystem functioning, we were able to establish divergent patterns in response for alternative extinction scenarios that hold promise for exploring new strategies of ecosystem management and governance. An important next step in predicting future biodiversity change, however, is to quantify the prevalence of local extinction drivers in the ecological landscape[58] and understand how these interact in natural systems[59,60] to influence the risk of extinction, altering community dynamics and ecosystem properties, both locally and across regional scales.

Extensive uncertainties exist in the responses of species and communities to environmental forcing, hence the use of empirically-based scenarios of the future to explore the potential consequences of species loss will continue to be a necessity for ecological advancements. We have shown, that the incorporation of important aspects of post-extinction community dynamics can lead to sharp contrasting forecasts of future ecosystem properties. Such information will help advance the predictability of community responses to change, provided that regionalised vulnerability assessments that determine the response of functionally important species under realistic future environmental conditions become available[61,62]. However, it is unlikely that all of these details will be available and incorporated into next generation models in the short-term, nor is this likely to be necessary. Consistency in community responses in the presence of compensation reveal patterns that may be general. Based on the available evidence, we should expect that the loss of species will be compensated by less efficient species over the long term[63], resulting in alterations to ecosystem properties.

However, the discrepancy in ecosystem consequences between biomass and numeric compensatory responses emphasise the need to identify which, or whether both, compensatory processes prevail in natural assemblages. Estimates of the functional consequences of biodiversity loss that incorporate the error associated with such variation are needed, and will allow more confidence in simulations of the future and provide improved levels of certainty on the consequences of future global change.

Methods

Sampling and study site. Field data were collected at station Margaretta (22 m water depth, 53° 13.50′N, 09° 6.50′W) in Inner Galway Bay on the central west coast of Ireland. Samples of macro-invertebrates (retained on a 500 μm sieve; n = 5, 0.1 m^2 van Veen grab) were collected approximately on a monthly basis over a one-year period (December 1996–November 1997, n = 11), returning a total of 139 invertebrate species[42]. Measurements of the sediment mixing depth were obtained using sediment profile imaging (SPI; n = 10) camera system[42].

Extinction simulations. Using a comprehensive study of the macrofaunal assemblages of Galway Bay, west coast of Ireland[42], we predict how species extinction is likely to affect the mixing depth, an indicator of invertebrate bioturbation. We established the relationship between an index of bioturbation potential that uses per capita bioturbation potential (BP_i, Supplementary Equation S1) to estimate population-level (BP_p, Equation Supplementary S2) and community-level bioturbation potential (BP_c, Supplementary Equation S3), which accounts for each species body size, abundance, activity level (4 levels, scored on a categorical scale reflecting increasing activity, 1 = in a fixed tube, 2 = limited movement, 3 = slow movement through sediment profile, 4 = free movement via burrow system[42]), and mode of sediment mixing (5 levels, scored on a categorical scale reflecting increasing impact on sediment turnover, 1 = epifauna, 2 = surfical modifiers, 3 = upward or downward conveyorbelt feeders, 4 = biodiffusers, 5 = regenerators[42]), and measurements of mixing depth obtained from sediment profile images. This relationship (Supplementary Equation S4) was used to parameterise probabilistic, numerical simulations that test how alternative extinction scenarios might affect sediment mixing depths. As environmental forcing in natural systems can target different components of the community[64], we consider simulations in which species go extinct at random ($\frac{1}{n}$, where n = the number of species) versus extirpations ordered by body size (largest expire first) or rarity (least abundant expire first). As the functional consequences of extinction also depend on the response of surviving species, we developed models in which species either do not exhibit compensatory responses or in which the abundance (numeric compensation) or biomass (biomass compensation) of the surviving community are held constant following extinction. In doing so, we recognized that compensating species are not randomly assigned, rather they represent different components of the species pool:

Compensation by common species. Compensatory responses by common species is arguably one of the most likely pathways of compensation in a community, both probabilistically in terms of their relative proportion of abundance, and ecologically as numeric success reflects their disproportionate share of resources and competitive advantage over less numerous species[19]. In addition, this type of compensation has been observed in natural communities[32].

Compensation by rare species. The majority of community species are rare, but some species are equipped with unique functional traits[65] and may become important if they increase in abundance[66,67].

Compensation by species from within/outwith or lower/higher functional grouping or which exhibit similar/distinct or lower/higher levels of activity. We assumed that species within the same functional group (e.g. sediment reworking mode[42]) will have similar functional traits and thus employ a similar ecological role, and that functional buffering can also be carried out by species from a different but adjacent functional group (e.g. grass versus forbs[19], local versus non-local distribution of sediment particles by bioturbators[42,68]), or species selected from any lower or higher functional group. Compensating species can also exhibit similar or contrasting levels of activity (mobility categorisation[42]) relative to the species that has been extirpated, such that functional buffering can also be carried out by species from a different but adjacent mobility group, or species selected from any lower or higher mobility group. In the absence of an adjacent functional group, compensation stems from the next available functional group of greater/lesser or equal standing.

Each of these model scenarios (i.e. 3 extinction orders, 2 compensation mechanisms and 11 compensation types, n = 66) was run for 1000 simulations (from 139–1 species). We provide the code for executing each of these simulations in Supplementary Material (Code S1).

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Author Contributions

M.S.T., M.S. and J.A.G. designed the study. C.G. and M.S.T. modified the R script from Solan *et al.*[42]. M.S.T., M.S., J.A.G., S.B. and R.P. contributed to the manuscript.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

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Appendix D

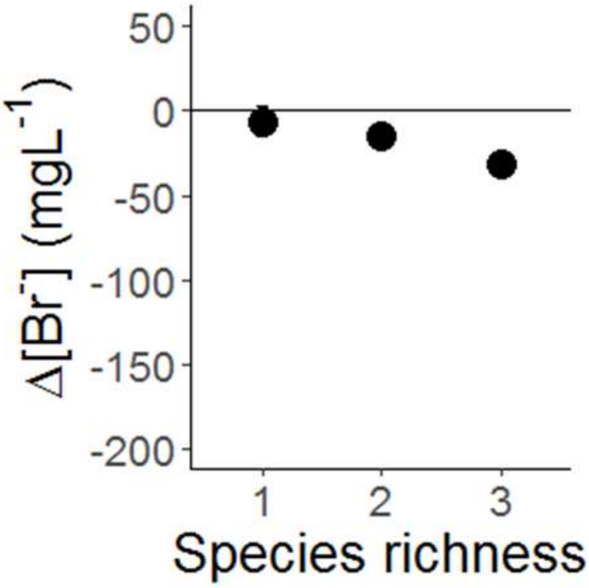

Figure A1. Burrow ventilation ([Br] ∆, mg L-1, mean ± s.e., n = 4) in even (J1.00) community assemblages across levels of species richness.

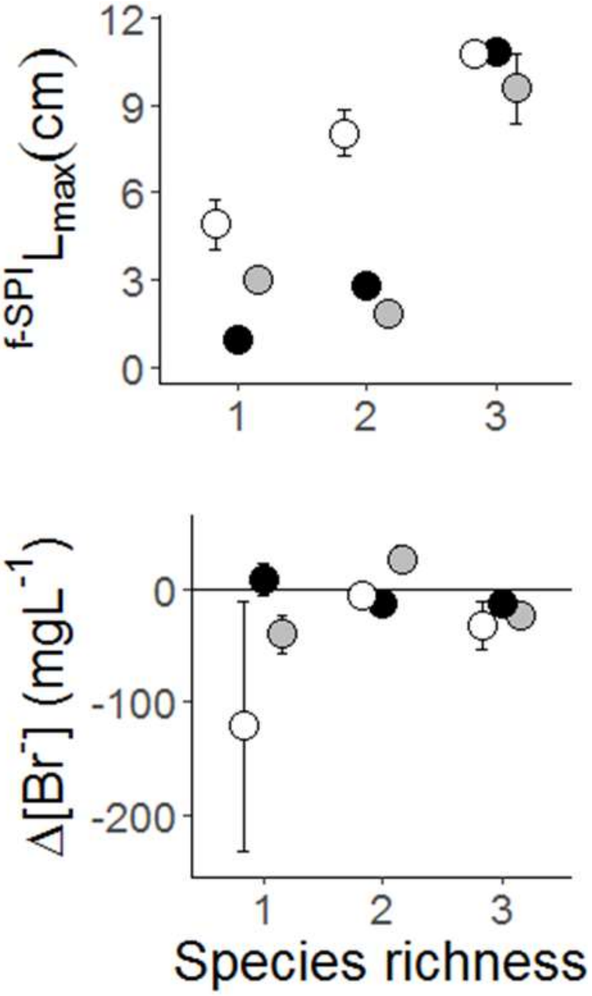

Figure A2. Effects of species richness and extinction scenario (random [white], body size [black], rarity [grey]) in natural ($J^{0.67}$) community assemblages on maximum mixing depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm, mean ± s.e., n = 4) and burrow ventilation ($\Delta[Br^-]$, mg L^{-1}, mean ± s.e., n = 4).

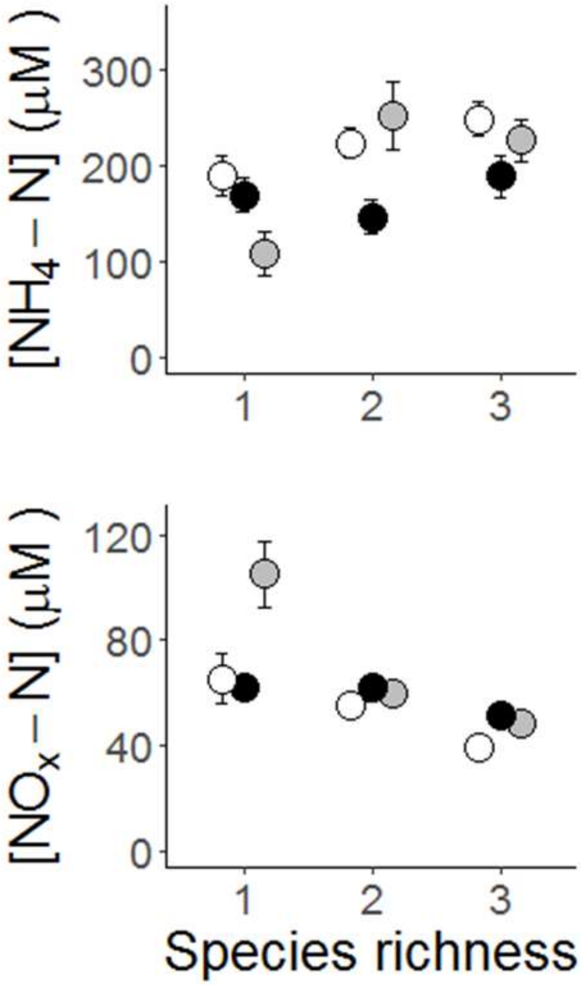

Figure A3. Effects of species richness and extinction scenario (random [white], body size [black], rarity [grey]) in natural ($J^{0.67}$) community assemblages on NH4-N and NOx-N concentrations ([NH_4-N],[NO_x-N], μM, mean ± s.e., n = 4).

Table A1. Experimental design for each scenario of extinction and compensatory response (n=4) and community assembly and biomass in even communities (J[1]). Controls (n=4) not included in this table.

Extinction scenario and response	**Community assembly**	**Total biomass**	***Peringia ulvae (P)***	***Corophium volutator (C)***	***Nereis diversicolor* (N)**
Random × NoComp	P	0.667	0.667	0.000	0.000
Random × NoComp	C	0.667	0.000	0.667	0.000
Random × NoComp	N	0.667	0.000	0.000	0.667
Random × NoComp	PC	1.333	0.667	0.667	0.000
Random × NoComp	PN	1.333	0.667	0.000	0.667
Random × NoComp	NC	1.333	0.000	0.667	0.667
Random × NoComp	PCN	2.000	0.667	0.667	0.667
Random × Comp	P	2.000	2.000	0.000	0.000
Random × Comp	C	2.000	0.000	2.000	0.000
Random × Comp	N	2.000	0.000	0.000	2.000
Random × Comp	PC	2.000	1.000	1.000	0.000
Random × Comp	PN	2.000	1.000	0.000	1.000
Random × Comp	NC	2.000	0.000	1.000	1.000
Random × Comp	PCN	2.000	0.667	0.667	0.667
Bodysize × NoComp	PCN	2.000	0.667	0.667	0.667
Bodysize × NoComp	PC	1.333	0.667	0.667	0.000
Bodysize × NoComp	P	0.667	0.667	0.000	0.000
Bodysize × Comp	PCN	2.000	0.667	0.667	0.667
Bodysize × Comp	PC	2.000	1.000	1.000	0.000
Bodysize × Comp	P	2.000	2.000	0.000	0.000
Rarity × NoComp	PCN	2.000	0.667	0.667	0.667
Rarity × NoComp	PC	1.333	0.667	0.667	0.000
Rarity × NoComp	C	0.667	0.000	0.667	0.000
Rarity × Comp	PCN	2.000	0.667	0.667	0.667
Rarity × Comp	PC	2.000	1.000	1.000	0.000
Rarity × Comp	C	2.000	0.000	2.000	0.000

Table A2. Experimental design for each scenario of extinction and compensatory response (n=4) and community assembly and biomass in communities representative of natural evenness ($J^{0.67}$). Controls (n=4) not included in this table.

Extinction scenario and response	**Community assembly**	**Total biomass**	***Peringia ulvae (P)***	***Corophium volutator (C)***	***Nereis diversicolor* (N)**
Random × NoComp	P	0.667	0.667	0.000	0.000
Random × NoComp	C	0.667	0.000	0.667	0.000
Random × NoComp	N	0.667	0.000	0.000	0.667
Random × NoComp	PC	1.333	0.667	0.667	0.000
Random × NoComp	PN	1.333	0.667	0.000	0.667
Random × NoComp	NC	1.333	0.000	0.667	0.667
Random × NoComp	PCN	2.000	0.667	0.667	0.667
Random × Comp	P	2.000	2.000	0.000	0.000
Random × Comp	C	2.000	0.000	2.000	0.000
Random × Comp	N	2.000	0.000	0.000	2.000
Random × Comp	PC	2.000	1.000	1.000	0.000
Random × Comp	PN	2.000	1.000	0.000	1.000
Random × Comp	NC	2.000	0.000	1.000	1.000
Random × Comp	PCN	2.000	0.667	0.667	0.667
Bodysize × NoComp	PCN	2.000	0.667	0.667	0.667
Bodysize × NoComp	PC	1.333	0.667	0.667	0.000
Bodysize × NoComp	P	0.667	0.667	0.000	0.000
Bodysize × Comp	PCN	2.000	0.667	0.667	0.667
Bodysize × Comp	PC	2.000	1.000	1.000	0.000
Bodysize × Comp	P	2.000	2.000	0.000	0.000
Rarity × NoComp	PCN	2.000	0.667	0.667	0.667
Rarity × NoComp	PC	1.333	0.667	0.667	0.000
Rarity × NoComp	C	0.667	0.000	0.667	0.000
Rarity × Comp	PCN	2.000	0.667	0.667	0.667
Rarity × Comp	PC	2.000	1.000	1.000	0.000
Rarity × Comp	C	2.000	0.000	2.000	0.000

Table A3. Statistics analysis for even communities (J1).

Response	Significant terms	d.f.	L-ratio	Compensation	Extinction	Species richness
SBR	3-way	4	12.4925			
$^{f\text{-}SPI}L_{med}$	3-way	4	32.2030			
$^{f\text{-}SPI}L_{max}$	3-way	4	18.9542			
$\Delta[Br^-]$	SR	2	6.4222			
$[NH_4\text{-}N]$	Comp*Ext +	2	23.3478			
	Comp*SR	2	25.4207			
$[NO_x\text{-}N]$	Comp*Ext +	2	7.4958			
	Comp*SR	2	26.2201			
$[PO_4\text{-}P]$	Comp*Ext	2	8.3114			

Table A4. Statistics analysis for communities with natural evenness ($J^{0.67}$).

Response	Significant terms	d.f.	L-ratio	Compensation	Extinction	Species richness
SBR	3-way	4	12.5304			
$^{f\text{-}SPI}L_{med}$	3-way	4	23.8706			
$^{f\text{-}SPI}L_{max}$	Ext*SR	4	52.8775			
$\Delta[Br^-]$	Ext*SR	4	16.2130			
$[NH_4\text{-}N]$	Ext*SR	4	24.6755			
$[NO_x\text{-}N]$	Ext*SR	2	9.78363			
$[PO_4\text{-}P]$	Comp*SR	2	6.51340			

Table A5. Relative importance of terms for even communities (J').

Response	**Compensation**	**Extinction**	**Species richness**
SBR	L-ratio = 26.1191, d.f. = 9, p = 0.002	L-ratio = 36.7977, d.f. = 12, p = 0.0002	L-ratio = 47.5698, d.f. = 12, $p < 0.0001$
$^{f\text{-}SPI}L_{med}$	L-ratio = 55.9446, d.f. = 9, $p < 0.0001$	L-ratio = 55.2916, d.f. = 12, $p < 0.0001$	L-ratio = 83.8107, d.f. = 12, $p < 0.0001$
$^{f\text{-}SPI}L_{max}$	L-ratio = 24.3810, d.f. = 9, p = 0.0037	L-ratio = 88.0374, d.f. = 12, $p < 0.0001$	L-ratio = 227.2205, d.f. = 12, $p < 0.0001$
$\Delta[Br^-]$	-	-	-
$[NH_4\text{-}N]$	L-ratio = 50.6567, d.f. = 5, $p < 0.0001$	L-ratio = 32.3382, d.f. = 4, $p < 0.0001$	L-ratio = 35.7138, d.f. = 4, $p < 0.0001$
$[NO_x\text{-}N]$	L-ratio = 34.3238, d.f. = 5, $p < 0.0001$	L-ratio = 29.3683, d.f. = 4, $p < 0.0001$	L-ratio = 19.2454, d.f. = 4, p = 0.0007

[PO_4-P]	L-ratio = 21.1508, d.f. = 3, p = 0.0001	L-ratio = 21.7833, d.f. = 4, p = 0.0002	L-ratio = 6.9382, d.f. = 2, p = 0.0311

Table A6. Relative importance of terms for communities with natural assemblages ($J^{0.67}$).

Response	**Compensation**	**Extinction**	**Species richness**
SBR	L-ratio = 17.1968, d.f. = 9, p = 0.0457	L-ratio = 53.6711, d.f. = 12, $p < 0.0001$	L-ratio = 58.5042, d.f. = 12, $p < 0.0001$
$^{f\text{-}SPI}L_{med}$	L-ratio = 67.9141, d.f. = 9, $p < 0.0001$	L-ratio = 73.8648, d.f. = 12, $p < 0.0001$	L-ratio = 57.3668, d.f. = 12, $p < 0.0001$
$^{f\text{-}SPI}L_{max}$	L-ratio = 0.8429, d.f. = 2, p = 0.3586	L-ratio = 88.1793, d.f. = 6, $p < 0.0001$	L-ratio = 127.1337, d.f. = 6, $p < 0.0001$
$\Delta[Br^-]$	L-ratio = 0.0004 d.f. = 2, p = 0.9847	L-ratio = 14.0217, d.f. = 6, p = 0.0294	L-ratio = 16.2842, d.f. = 6, p = 0.0123
$[NH_4\text{-}N]$	L-ratio = 0.9796 d.f. = 2, p = 0.3223	L-ratio = 22.3807, d.f. = 6, p = 0.001	L-ratio = 19.3411, d.f. = 6, p = 0.0036
$[NO_x\text{-}N]$	L-ratio = 0.0757	L-ratio = 20.6797,	L-ratio = 28.8959,

	d.f. = 2, p = 0.7832	d.f. = 6, p = 0.0021	d.f. = 6, p = 0.0001
s[PO_4-P]	L-ratio = 9.7858, d.f. = 3, p = 0.0205	L-ratio = 1.6417 d.f. = 2, p = 0.4401	L-ratio = 43.9928, d.f. = 4, $p < 0.0001$

Appendix E

Table A1. Equation and R^2 value of linear model for; TOC, TON, Phaeopigment, Chlorophyll-*a* and OPD versus BQP_c.

Model	Equation	R²
TOC ~BQPc	y = -6E-05x + 0.6768	0.1006
TON ~BQPc	y = -2E-05x + 0.0885	0.1782
Phaeo ~BQPc	y = -0.0011x + 3.885	0.3773
Chl ~BQPc	y = -9E-05x + 0.5556	0.0992
OPD ~BQPc	y = 0.0001x + 0.517	0.0279

Table A2. List of species and their respective activity level (Mi) reworking trait (Ri), ventilation rate of an individual species (aQi) and sediment volume passively influenced by ventilation (pQi). Values were assigned on a combination of the current literature (Queirós et al. 2013) and on the basis of expert opinion of species interaction with their environment. Contents of this dataset is being prepared for publication as: Hale et al. (in prep)

Taxa	M_i	R_i	$^{a}Q_i$	$^{p}Q_i$
Virgularia mirabilis	2	2	1	1
Cerianthus lloydii	1	2	2	1
Actiniaria	2	2	2	1
Edwardsia	2	2	2	1
Edwardsia claparedii	2	2	2	1
Turbellaria	2	2	1	1
Nemertea	3	4	2	3
Sipuncula	3	4	2	2
Phascolion strombus	2	2	2	1
Aspidosiphon muelleri	3	4	2	2
Golfingia elongata	3	4	2	2
Lumbrineris cingulata	3	4	2	3
Abyssoninoe hibernica	3	4	2	3
Malmgrenia mcintoshi	3	4	2	3
Leitoscoloplos mammosus	3	4	2	3
Aricidea suecica	3	2	2	3
Poecilochaetus serpens	2	2	2	3
Aonides paucibranchiata	2	3	2	3
Laonice bahusiensis	1	3	2	2
Laonice sarsi	1	3	2	3
Prionospio multibranchiata	2	3	2	2
Dipolydora coeca	3	3	2	2
Prionospio fallax	2	3	2	3

Scolelepis	2	3	2	3
Spio filicornis	2	3	2	2
Spiophanes bombyx	1	3	2	2
Spiophanes kroyeri	1	3	2	2
Magelona alleni	1	2	2	2
Magelona minuta	2	2	2	2
Chaetopterus variopedatus	1	3	3	3
Caulleriella zetlandica	2	2	2	3
Chaetozone setosa	2	2	2	3
Monticellina dorsobranchialis	2	2	2	3
Diplocirrus glaucus	2	3	2	3
Dasybranchus	2	3	2	3
Mediomastus fragilis	2	3	2	3
Notomastus	2	3	3	3
Peresiella clymenoides	2	3	2	2
Pseudonotomastus southerni	2	3	2	2
Euclymeninae	1	3	2	2
Euclymene	1	3	2	2
Praxillella affinis	1	3	3	2
Ophelina acuminata	2	4	3	3
Scalibregma inflatum	4	4	2	3
Galathowenia oculata	1	2	2	2
Owenia fusiformis	1	2	2	2
Amphictene auricoma	2	3	2	2
Lagis koreni	1	3	3	2
Sabellaria spinulosa	1	1	1	1
Sthenelais limicola	3	4	2	2
Ampharete falcata	2	3	2	2

Ampharete lindstroemi	2	3	2	2
Amphicteis gunneri	2	3	2	2
Terebellides stroemi	1	3	2	2
Eupolymnia nebulosa	1	1	2	2
Eteone barbata	3	4	2	2
Pista cristata	1	3	2	2
Polycirrus	1	3	2	3
Thelepus cincinnatus	1	3	2	2
Ditrupa arietina	1	1	2	2
Anaitides groenlandica	3	4	2	3
Glycera lapidum	3	4	2	3
Glycera rouxii	3	4	2	3
Glycera tridactyla	3	4	2	3
Glycinde nordmanni	3	4	2	3
Goniada maculata	3	4	2	3
Scoloplos armiger	3	4	2	3
Oxydromus flexuosus	3	4	2	3
Glyphohesione klatti	3	4	2	3
Nephtys hombergii	3	4	3	3
Nephtys kersivalensis	3	4	3	3
Nephtys hystricis	3	4	3	3
Nephtys incisa	3	4	3	3
Nephtys pente	3	4	3	3
Gattyana cirrhosa	3	4	2	3
Aponuphis bilineata	3	2	2	2
Hyalinoecia tubicola	3	2	2	2
Nothria	3	2	2	3
Harmothoe	3	4	2	2
Harmothoe antilopes	3	4	2	2
Marphysa kinbergi	3	4	2	2

Marphysa bellii	3	4	2	2
Helmutneris	3	4	2	2
Lumbrineridae	3	4	2	3
Copepoda	2	2	NA	NA
Cirolana borealis	3	2	2	3
Vaunthompsonia cristata	3	2	2	2
Iphinoe serrata	3	2	2	2
Leucon nasica	3	2	3	2
Alpheus glaber	4	4	4	2
Processa nouveli	4	2	2	1
Crangon allmanni	4	2	1	1
Nephrops norvegicus	4	4	4	3
Axius stirhynchus	4	4	4	3
Callianassa subterranea	4	4	4	3
Ebalia granulosa	3	1	1	1
Liocarcinus depurator	4	5	1	1
Goneplax rhomboides	4	4	1	1
Urothoe elegans	3	2	3	2
Harpinia antennaria	3	2	3	2
Ampelisca macrocephala	1	2	3	2
Ampelisca spinipes	1	2	3	2
Falcidens crossotus	2	2	2	3
Nucula nitidosa	3	2	3	2
Nucula nucleus	3	2	3	2
Nucula sulcata	3	2	3	2
Ennucula tenuis	3	2	3	2
Thyasira flexuosa	2	3	3	2
Cardiidae juvenile	2	2	3	2
Cerastoderma glaucum	2	5	3	2
Phaxas pellucidus	2	2	3	2

Gari fervensis	2	2	3	2
Chaetoderma nitidulum	2	2	2	3
Abra nitida	2	2	3	2
Abra prismatica	2	2	3	2
Azorinus chamasolen	2	2	2	2
Dosinia exoleta	2	2	3	3
Corbula gibba	2	2	3	2
Thracia	2	3	3	2
Thracia pubescens	2	3	3	2
Cuspidaria cuspidata	2	3	3	2
Euspira fusca	3	2	3	2
Cylichna cylindracea	3	1	2	2
Roxania utriculus	3	2	2	2
Phoronis	1	2	2	2
Amphiura juvenile	3	4	3	3
Amphiura chiajei	3	4	3	3
Amphiura filiformis	3	4	3	3
Amphipholis squamata	3	4	3	3
Ophiura ophiura	2	2	3	3
Echinocyamus pusillus	3	2	3	3
Astropecten irregularis	3	2	1	1
Holothuroidae	3	2	1	1
Leptosynapta	3	2	3	3
Leptosynapta inhaerens	3	2	3	3
Ascidiacea	1	1	2	2

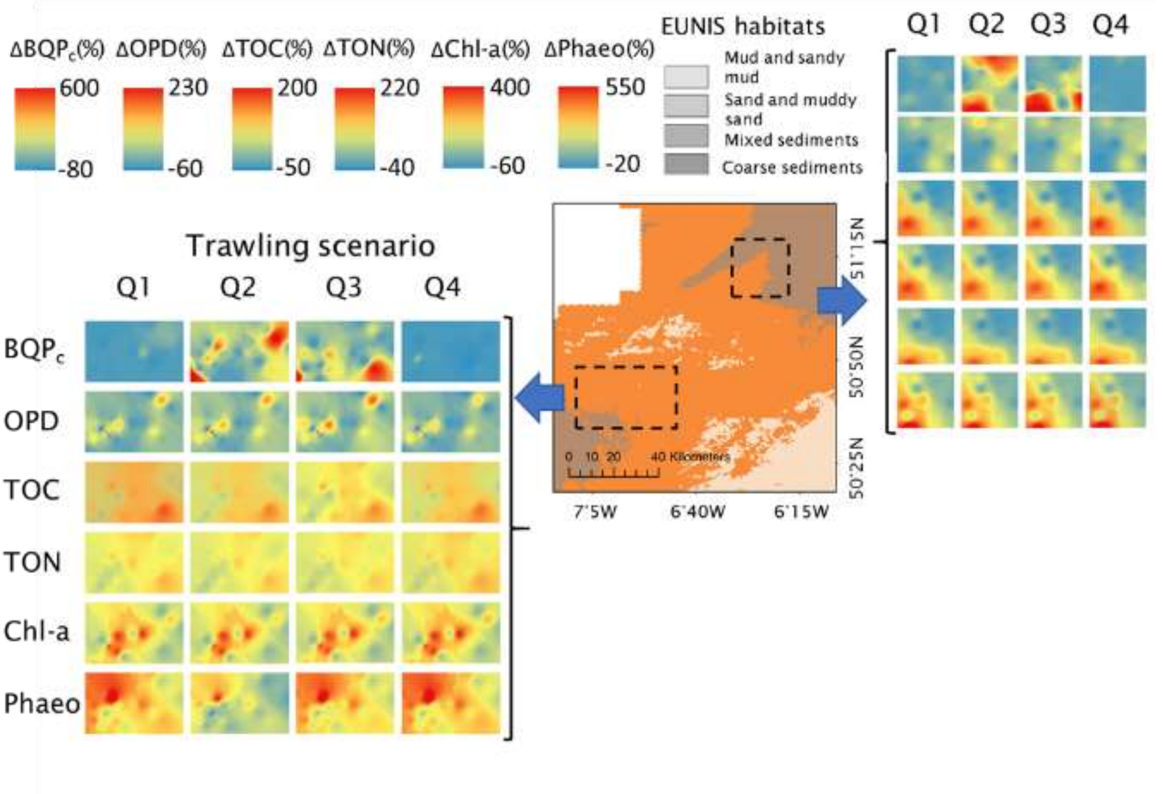

Figure A1. Spatial interpolation of ecosystem properties percentage change; (a) ΔBQPc, (b) ΔOPD, (c) ΔTOC, (d) ΔTON (e) Δchlorophyll *a*, (f) Δphaeopigment relative to the environmental circumstances of 2015 (%) for each of the four scenarios of trawling, increasing in fishing intensity from Q1 to Q4. The central map show predictions of sediment characteristics by EUNIS habitats.

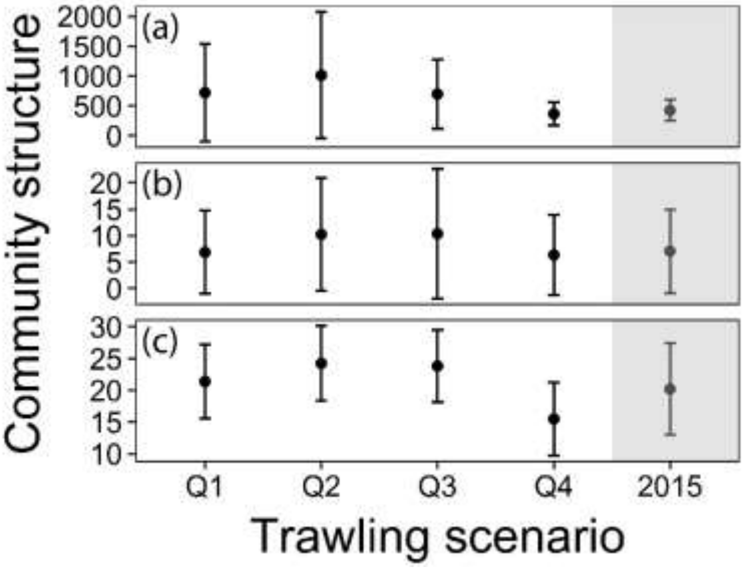

Figure A2. Community structure (a) mean station abundance, (b) mean station biomass, (c) mean station species richness (mean ± standard deviation, n = 35) for each scenario of trawling intensity (Q1-Q4) and 2015 circumstances within the shaded area.

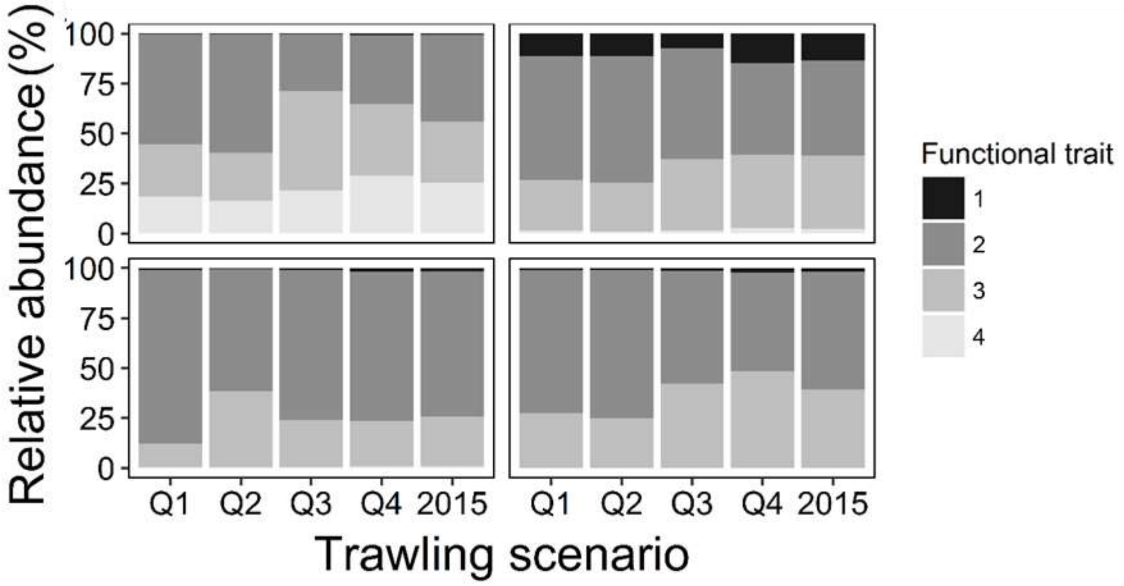

Figure A3. Relative abundance (%) of functional community trait; (a) reworking trait (R_i: 1; epifauna, 2; surficial modifiers, 3; head-down/head-up feeders, 4; biodiffusers), (b) activity level (M_i: 1; fixed tube, 2; limited movement or sessile, 3; slow movement through sediment, 4; free movement via burrow system), (c) ventilation rate (${}^{a}Q_i$: 1; no ventilation, 2; low ventilation rate [>0–<10 ml hr^{-1} $individual^{-1}$], 3; medium ventilation rate [10–1000 ml hr^{-1} $individual^{-1}$], high ventilation rate [>1000 ml hr^{-1} $individual^{-1}$]) and (d) sediment volume passively influenced (${}^{p}Q_i$: no flow directed towards or through the sediment, 2; flow is constrained through or over individuals body or within a tube that has an inlet or outlet connected to the sediment water interface, 4; Species generating advective flow through the sediment over a volume larger than that adjacent to the body) with increasing trawling intensity (scenario Q1-Q4, n = 35) and observations (2015; n = 35).

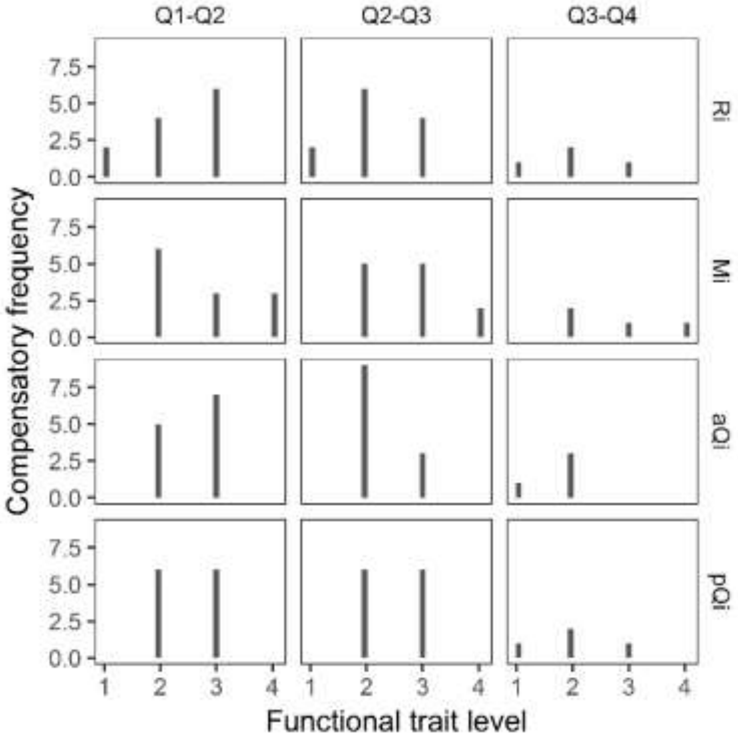

Figure A4. Functional trait compensatory capacity (i.e. frequency) for each transition in bottom trawling intensity for reworking trait (R_i), activity level (M_i), ventilation rate of an individual species (${}^{a}Q_i$) and sediment volume passively influenced by ventilation (${}^{p}Q_i$).

Appendix F

Table A.1. Locations of stations in the Eastern Baltic Sea where field data were collected**.**

Station	Area	Latitude	Longitude	Depth (m)
1Kl	Kõiguste lath	58.36776	22.96615355	3.6
16	Kõiguste lath	58.37043	22.98050093	1.2
24	Kõiguste lath	58.36226	22.97024152	3.4
28	Kõiguste lath	58.36679	22.95750529	1.3
28A	Kõiguste lath	58.36804	22.96385422	2.5
29	Kõiguste lath	58.38992	22.96034622	2.8
29A	Kõiguste lath	58.37035	22.95493367	1.5
30	Kõiguste lath	58.37516	22.9563624	1.6
31A	Kõiguste lath	58.36829	22.9667613	4.9
31B	Kõiguste lath	58.36898	22.96624041	3.4
5Kl	Kõiguste lath	58.37898	22.96542795	2
7	Kõiguste lath	58.37885	22.97059331	1.2
A3	Kõiguste lath	58.3675	22.96441167	2.5
A4	Kõiguste lath	58.36853	22.96727277	2.8
A5	Kõiguste lath	58.37186	22.97753451	1.4

Table A.2. List of species collected from Kõiguste lath, Estonia (Eastern Baltic Sea) and their respective activity level (Mi) and reworking trait (Ri). Values were assigned based on a combination of the current literature (Gogina et al. 2017 and Queirós et al. 2013) and on the basis of expert opinion, where such information was not available.

Taxa	**Activity level (M_i)**	**Reworking trait (R_i)**	**Group**
Alderia modesta	3	2	Macrofauna
Amphibalanus improvisus	1	1	Macrofauna
Argulus sp	NA	NA	NA
Asellus aquaticus	NA	NA	NA
Bathyporeia pilosa	3	2	Macrofauna
Battersia arctica	1	1	Plant
Bithynia tentaculata	3	2	Macrofauna
Bylgides sarsi	3	2	Macrofauna
Ceramium tenuicorne	NA	NA	Macroalgae
Ceramium virgatum	NA	NA	Macroalgae
Cerastoderma glaucum	2	5	Macrofauna
Ceratophyllum demersum	1	1	Plant
Chaetomorpha linum	NA	NA	Macroalgae
Chara aspera	NA	NA	Macroalgae
Chara baltica	NA	NA	Macroalgae
Chara canescens	NA	NA	Macroalgae
Chara connivens	NA	NA	Macroalgae
Chara horrida	NA	NA	Macroalgae
Chara sp	NA	NA	Macroalgae
Chironomidae	2	3	Macrofauna
Chorda filum	NA	NA	Macroalgae
Cladophora glomerata	NA	NA	Macroalgae
Cladophora rupestris	NA	NA	Macroalgae
Coccotylus truncatus	NA	NA	Macroalgae

Coleoptera	NA	NA	NA
Corophium volutator	4	2	Macrofauna
Cyanobacteria	NA	NA	NA
Cyanophthalma obscura	3	2	Macrofauna
Dictyosiphon foeniculaceus	NA	NA	Macroalgae
Diptera	NA	NA	NA
Donacia sp	NA	NA	NA
Dreissena polymorpha	3	3	Macrofauna
Ecrobia ventrosa	3	2	Macrofauna
Ectocarpus siliculosus	NA	NA	Macroalgae
Einhornia crustulenta	1	1	NA
Ephemeroptera	NA	NA	NA
Fontinalis sp	1	1	NA
Fucus vesiculosus	NA	NA	Macroalgae
Furcellaria lumbricalis	NA	NA	Macroalgae
Gammarus duebeni	2	1	Macrofauna
Gammarus juv	2	1	Macrofauna
Gammarus oceanicus	2	1	Macrofauna
Gammarus salinus	2	1	Macrofauna
Gammarus sp	2	1	Macrofauna
Gammarus tigrinus	2	1	Macrofauna
Gammarus zaddachi	2	1	Macrofauna
Gonothyraea loveni	1	1	Macrofauna
Halicryptus spinulosus	2	4	Macrofauna
Hediste diversicolor	4	4	Macrofauna
Hydracarina	NA	NA	NA
Hydrobia sp	3	2	
Idotea balthica	3	2	Macrofauna
Idotea chelipes	3	2	Macrofauna

Idotea granulosa	3	2	Macrofauna
Idotea juv	3	2	Macrofauna
Jaera albifrons	1	1	Macrofauna
Laomedea flexuosa	1	1	Macrofauna
Laonome armata	1	2	Macrofauna
Leathesia marina	NA	NA	Algae
Lepidoptera	NA	NA	NA
Leptocheirus pilosus	4	2	Macrofauna
Limapontia capitata	3	2	Macrofauna
Lymnaea stagnalis	3	2	Macrofauna
Macoma balthica	2	2	Macrofauna
Manayunkia aestuarina	1	3	Macrofauna
Marenzelleria neglecta	4	3	Macrofauna
Monoporeia affinis	3	2	Macrofauna
Monostroma balticum	NA	NA	Algae
Mya arenaria	2	2	Macrofauna
Myriophyllum spicatum	1	1	Plant
Mysis mixta	1	1	Macrofauna
Mysis salemaai	1	1	Macrofauna
Mytilus trossulus	1	1	Macrofauna
Najas marina	1	1	Plant
Neomysis integer	1	1	Macrofauna
Odonata	1	1	Plant
Oligochaeta	3	4	Macrofauna
Ostracoda	3	3	Macrofauna
Palaemon adspersus	4	1	Macrofauna
Peringia ulvae	3	2	Macrofauna
Physa fontinalis	3	2	Macrofauna
Pilayella/Ectocarpus	NA	NA	Algae
Piscicola geometra	1	1	Macrofauna
Planorbarius corneus	3	2	Macrofauna

Plecoptera	NA	NA	NA
Polysiphonia fibrillosa	NA	NA	Algae
Polysiphonia fucoides	NA	NA	Algae
Pontoporeia femorata	3	2	Macrofauna
Potamogeton perfoliatus	1	1	Plant
Potamopyrgus antipodarum	2	2	Macrofauna
Pygospio elegans	1	3	Macrofauna
Radix balthica	3	2	Macrofauna
Ranunculus baudotii	1	1	Plant
Rhithropanopeus harrisii	4	2	Macrofauna
Rhizoclonium riparium	NA	NA	Algae
Rhodomela confervoides	NA	NA	Algae
Ruppia maritima	1	1	Plant
Saduria entomon	3	2	Macrofauna
Stagnicola palustris	3	2	Macrofauna
Stictyosiphon tortilis	NA	NA	Algae
Stuckenia pectinata	1	1	Plant
Tenellia adspersa	3	2	Macrofauna
Theodoxus fluviatilis	1	1	Macrofauna
Tolypella nidifica	1	1	Plant
Trichoptera	NA	NA	NA
Ulothrix sp	NA	NA	Algae
Ulva intestinalis	NA	NA	Algae
Ulva prolifera	NA	NA	Algae
Urospora penicilliformis	NA	NA	Algae
Zannichellia palustris	1	1	Plant
Zostera marina	1	1	Plant

Model A1: Total biomass

lm(Mean total Biomass ~ Year)

Coefficient table: Intercept ± SE (when baseline is for pre perturbation impact): 283.54 ± 64.76, t = 4.378, p =.0.0000529

	Pre			
Impact	27.92 ± 91.59 0.305 (0.762)	**Impact**		
1 year post	76.32 ± 91.59 0.833 (0.408)	48.40 ± 91.59 0.528 (0.599)	**1 year post**	
2 year post	46.01 ± 91.59 0.502 (0.617)	18.09 ± 91.59 0.198 (0.844)	30.31 ± 91.59 0.331 (0.742)	**2 year post**

Model A2: Stability

lm(Log(Stability) ~ Year)

Coefficient table: Intercept ± SE (when baseline is for pre perturbation impact): 2.05 ± 0.20, t = 6.932, p = $4.49e^{-9}$.

	Pre			
Impact	0.01 ± 0.19 0.031 (0.975)	**Impact**		
1 year post	0.02 ± 0.19 0.081 (0.936)	0.01 ± 0.19 0.050 (0.960)	**1 year post**	
2 year post	0.23 ± 0.19 1.241 (0.220)	0.23 ± 0.19 1.209 (0.232)	0.22 ± 0.19 1.159 (0.251)	**2 year post**

Table A.3. Cohen's d effect size ± 95 % confidence interval (C.I.) for evenness in response to perturbation.

Year	Cohen's *d*	Lower C.I. (95 %)	Upper C.I. (95 %)
2005 vs. 2006	0.04	-0.36	0.44
2006 vs. 2007	-0.44	-0.84	-0.04
2007 vs. 2008	0.19	-0.19	0.58
2005 vs. 2007	-0.13	-0.54	0.27
2005 vs. 2008	0.06	-0.32	0.45
2006 vs. 2008	-0.23	-0.61	0.14

Table A.4. Effects of environmental disturbance on activity level (Mi) scaled by biomass (g m^{-2}) in shallow (< 5m depth) soft-bottom communities before, during and after impact of perturbation.

Time relative to perturbation	Activity level (M_i)	Biomass (g m^{-2})
Pre	1	49.38095
Pre	2	37.71727
Pre	3	8.365967
Pre	4	0.853306
Impact	1	31.50372
Impact	2	25.06739
Impact	3	4.663851
Impact	4	0.836357
1 yr post	1	45.9089
1 yr post	2	27.37719
1 yr post	3	3.964293
1 yr post	4	1.676803
2 yr post	1	45.9089
2 yr post	2	27.37719
2 yr post	3	3.964293
2 yr post	4	1.676803

Table A.5. Effects of environmental disturbance on reworking trait (Ri) scaled by biomass (g m^{-2}) in shallow (< 5m depth) soft-bottom communities before, during and after impact of perturbation.

Time relative to perturbation	**Reworking trait (R_i)**	**Biomass (g m^{-2})**
Pre	1	49.63707
Pre	2	24.40607
Pre	3	0.890267
Pre	4	0.9927
Pre	5	20.39138
Impact	1	31.81493
Impact	2	15.36972
Impact	3	0.976038
Impact	4	0.805726
Impact	5	13.1049
1 yr post	1	46.22693
1 yr post	2	20.26993
1 yr post	3	0.592827
1 yr post	4	1.633172
1 yr post	5	10.20433
2 yr post	1	46.22693
2 yr post	2	20.26993
2 yr post	3	0.592827
2 yr post	4	1.633172
2 yr post	5	10.20433

Table A.6. Variance ratio (null model mean variance ratio ± 95% confidence interval (C.I.); Hallett et al. 2014) in shallow (< 5m depth) soft-bottom communities for each station pre, during, 1 and 2 year post impact of perturbation.

Time relative to perturbation	Year	Station	Lower (2.5%) null model C.I.	Upper (97.5%) null model C.I.	Null model mean variance ratio	Variance ratio
Pre	2005	1 Kl	0.534387	1.455634	0.95767	0.793642
Pre	2005	16	0.189223	2.436158	0.981843	4.037708
Pre	2005	24	0.110022	2.433972	0.864746	0.50046
Pre	2005	28	0.615719	1.631745	1.006083	0.824128
Pre	2005	28A	0.036285	2.516169	0.883439	2.424385
Pre	2005	29	0.498975	1.482544	0.921883	1.039451
Pre	2005	29A	0.713934	1.344356	0.989071	0.92417
Pre	2005	30	0.06887	2.852357	1.117358	1.217529
Pre	2005	31A	0.048786	3.070495	1.092968	1.884671
Pre	2005	31B	0.151828	2.52803	1.056958	1.004981
Pre	2005	5 Kl	0.828502	1.271819	1.012431	1.146283
Pre	2005	7	0.044289	3.139278	0.991176	2.302709
Pre	2005	A3	0.10265	2.958119	1.118828	0.650108
Pre	2005	A4	0.114224	1.842503	1.024686	1.233681
Pre	2005	A5	0.830907	1.163094	0.999927	1.156445
Impact	2006	1 Kl	0.365155	2.174587	1.084721	2.165909
Impact	2006	16	0.514275	1.469483	1.021336	1.74326
Impact	2006	24	0.092678	1.872693	0.885794	0.756251
Impact	2006	28	0.858195	1.127947	0.987538	1.115671
Impact	2006	28A	0.054647	2.826806	1.000316	0.60439
Impact	2006	29	0.508281	1.408138	0.989635	1.467637
Impact	2006	29A	0.347486	1.970087	1.022322	0.481609
Impact	2006	30	0.317883	1.680527	1.04057	0.320601
Impact	2006	31A	0.007715	2.115432	1.107677	2.106611
Impact	2006	31B	0.283962	2.189097	0.911435	1.919458
Impact	2006	5 Kl	0.14246	2.342229	1.017598	0.793885
Impact	2006	7	0.176496	2.298027	0.964017	1.13293
Impact	2006	A3	0.342263	1.732139	1.089624	1.020538
Impact	2006	A4	0.069991	3.367564	0.982274	1.041648
Impact	2006	A5	0.64978	1.455688	1.023932	1.072847
1 yr post	2007	1 Kl	0.787102	1.433903	0.995127	1.056343
1 yr post	2007	16	0.272933	1.809125	1.002593	1.379838
1 yr post	2007	24	0.055763	2.451553	0.973062	1.651772
1 yr post	2007	28	0.672227	1.502906	1.017287	1.644855
1 yr post	2007	28A	0.308425	1.833534	0.879356	1.14615
1 yr post	2007	29	0.543663	1.814708	1.002572	0.743086
1 yr post	2007	29A	0.651596	1.400295	1.013699	0.850415
1 yr post	2007	30	0.032633	2.393491	0.916368	0.080995
1 yr post	2007	31A	0.078041	2.250981	0.947958	0.574414

1 yr post	2007	31B	0.203185	1.627106	1.017672	1.391267
1 yr post	2007	5 Kl	0.111212	2.634945	0.960159	0.771118
1 yr post	2007	7	0.161728	2.839049	1.038289	1.978989
1 yr post	2007	A3	0.240937	2.999871	1.135437	3.210085
1 yr post	2007	A4	0.399834	1.93949	0.984199	1.283382
1 yr post	2007	A5	0.49792	1.619246	1.042093	1.183364
2 yr post	2008	1 Kl	0.908729	1.110138	1.008415	1.047137
2 yr post	2008	16	0.534481	1.829533	1.004943	1.399542
2 yr post	2008	24	0.086561	2.249848	1.056522	0.31893
2 yr post	2008	28	0.675434	1.744881	0.992924	1.145293
2 yr post	2008	28A	0.101152	2.765181	1.102217	2.794074
2 yr post	2008	29	0.32955	2.030273	0.989842	1.801358
2 yr post	2008	29A	0.847432	1.292109	1.01841	1.3815
2 yr post	2008	30	0.802953	1.292247	0.988901	1.174123
2 yr post	2008	31A	0.303175	1.966666	1.061246	1.848335
2 yr post	2008	31B	0.149409	2.461709	1.049467	4.945957
2 yr post	2008	5 Kl	0.306595	2.32189	1.024271	0.905533
2 yr post	2008	7	0.569042	1.439054	0.98752	1.114214
2 yr post	2008	A3	0.457558	1.566295	1.018061	0.653871
2 yr post	2008	A4	0.259489	2.104507	0.979736	1.7192
2 yr post	2008	A5	0.302275	1.846726	0.977162	0.37591

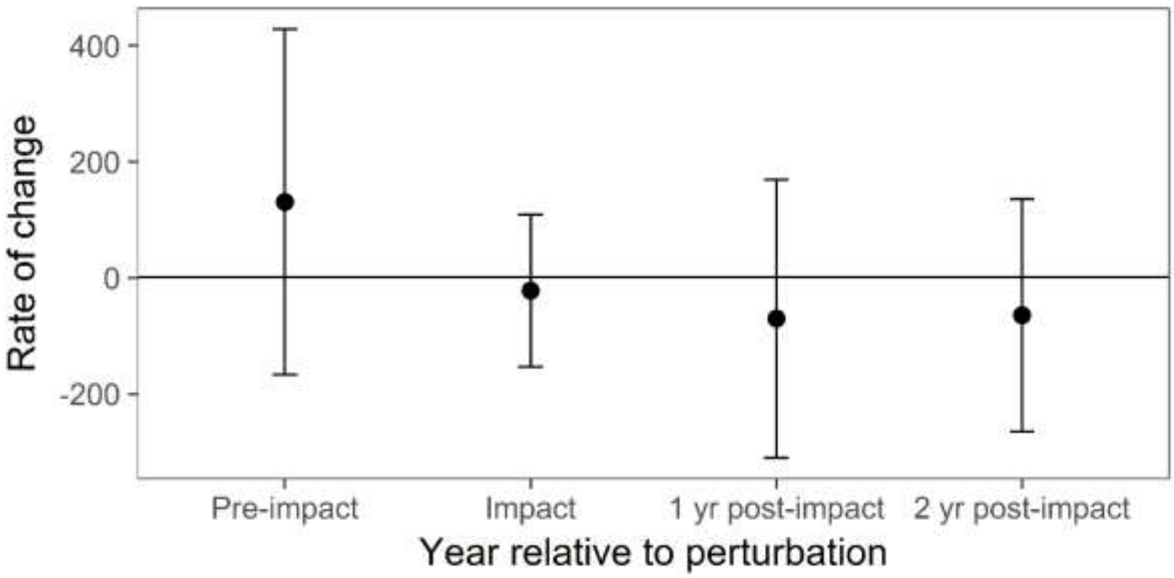

Figure A.1. Rate of community change (mean ± standard deviation, n = 15) for each year; pre-impact, impact, 1 year and 2 year post-impact of perturbation. Zero line indicates direction of change.

Table S1. T-test statistics for species total turnover between years; pre-impact, impact, 1 year and 2 year post-impact.

Year of comparison	t-value	d.f.	p-value
Pre vs. Impact	-0.544	53.450	0.589
Impact vs. 1 yr post	1.211	67.099	0.230
1 yr post vs. 2 yr post	-1.324	70.289	0.190
Pre vs. 1 yr post	0.404	55.543	0.688
Pre vs. 2 yr post	-0.625	53.334	0.535
Impact vs. 2 yr post	-0.103	79.937	0.918

Table S2. T-test statistics for species appearance between years; pre-impact, impact, 1 year and 2 year post-impact.

Year of comparison	t-value	d.f.	p-value
Pre vs. Impact	-0.024	66.695	0.981
Impact vs. 1 yr post	0.501	68.367	0.618
1 yr post vs. 2 yr post	-0.063	71.792	0.950
Pre vs. 1 yr post	0.465	62.881	0.644
Pre vs. 2 yr post	0.421	69.321	0.675
Impact vs. 2 yr post	0.458	79.337	0.649

Table S3. T-test statistics for species disappearance between years; pre-impact, impact, 1 year and 2 year post-impact.

Year of comparison	t-value	d.f.	p-value
Pre vs. Impact	-0.525	67.936	0.601
Impact vs. 1 yr post	0.336	65.036	0.738
1 yr post vs. 2 yr post	-0.797	74.329	0.428
Pre vs. 1 yr post	0.131	60.260	0.896
Pre vs. 2 yr post	-1.013	74.674	0.314
Impact vs. 2 yr post	-0.529	80.241	0.599

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