UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

Ocean and Earth Science

CONTEXT DEPENDENCY OF BIODIVERSITY-ECOSYSTEM PROCESS RELATIONS

by

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Abstract

Human domination of ecosystems has led to dramatic alterations of biodiversity, which has been shown to affect the functioning of ecosystems. However, much of what we know about the role of biodiversity in mediating ecosystem process and functioning stems from manipulative experiments that have mostly manipulated the number of species and largely been performed in isolated homogenous environments with artificially assembled communities that do not reflect natural observations. Yet, in natural systems, the restructuring of community composition, evenness and dominance occurs in response and alongside to multiple aspects of biotic and environmental change.

Here I address explicitly the disconnect that exists between the representation of biodiversity in experimental systems and the context in which biodiversity-ecosystem function relations are moderated in natural systems experiencing multiple sources of change, using laboratory based mesocosm experiments. The results show that more realistic changes in community evenness and species dominance identity are important mediators of ecosystem process and functions. Changes in evenness can affect ecosystem properties but the direction and magnitude of change depends on the dominant species identity, which can have disproportionate effects on ecosystem properties, especially at low evenness levels. While the general importance of species identity effects is a consistent feature across varying environmental context, the functional impacts of species are highly context dependent.

Collectively, my results indicate that context dependent functional variability within each level of species richness alters biodiversity-ecosystem functioning (BEF) relations, which means that the ecosystem consequences of natural and anthropogenic forcing will differ from current expectation. I conclude, that to overcome this limitation, BEF research should use integrative approaches based on dynamic trait expression in relation to the environment and introduce directional realistic biodiversity changes.

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Daniel Wohlgemuth

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Declaration of authorship

I, Daniel Wohlgemuth, 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.

Context dependency of biodiversity-ecosystem process relations.

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 my own work;

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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:

Wohlgemuth, D.; Solan, M.; Godbold, J.A. Specific arrangements of species dominance can be more influential than evenness in maintaining ecosystem process and function. Sci. Rep. 6, 39325; doi: 10.1038/srep39325 (2016).

Signed:.....

Date:.....

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Chapter 1: General introduction

Human domination of ecosystems has led to dramatic alterations of biodiversity from local (Johnson et al. 2009, Hejda et al. 2009, Vilà et al. 2011) to global (Lodge 1993, Barnosky et al. 2011) scales. The biota of ecosystems mediate many ecosystem processes and functions (e.g. decomposition, primary and secondary production) that regulate the stocks and fluxes of energy and matter, including nutrients or biomass, providing the basis for the delivery of ecosystem services (e.g. sustained production of plant and animal biomass, regulation of water quality, soil formation retention and fertility, climate regulation; Chapin et al. 2000, Díaz et al. 2006, White et al. 2010). Hence, alterations of biodiversity are a major concern for human well being and a sustainable future (Millenium Ecosystem Assessment 2005). While a plethora of experiments and observations have established that a loss of biodiversity can impair the functioning of ecosystems (Cardinale et al. 2012), conclusions are mostly based on empirical studies that have manipulated the number of species (species richness) as the single measure of biological diversity. However, biodiversity is a complex multivariate concept that includes variation across different hierarchical scales and the number and relative distribution (evenness) of genes, individuals, species or functional traits over space and time (Harper and Hawksworths 1994). Historically, it has been assumed that species richness and evenness correlate positively and that species richness accounts for the largest part of the variance in diversity (DeBenedictis 1973). However, more recent studies have found that species richness and evenness are not necessarily correlated positively, but can also be negatively or un-correlated (Wilsey et al. 2005, Soininen et al. 2012), depending on organism traits, such as trophic level or body size, as well as ecosystem type and study scale (Soininen et al. 2012). This suggests, that focussing on species richness alone may provide insufficient insight into biodiversity and ecosystem functioning relations, as evenness explains an additional part of variation in biodiversity that is largely independent of species richness (Wilsey et al. 2005, Soininen et al. 2012). Furthermore, the impact of major anthropogenic stressors, such as habitat change, climate change, species invasion or nutrient loading (Millenium Ecosystem Assessment 2005) on biotic communities is not restricted to species richness. In response to

changing environmental conditions, species initially respond with adjustments in physiology and behaviour, which can translate to population level shifts in species abundances and distributions (Doney et al. 2012). As such adjustments are often species-specific (Chen et al. 2011, Sunday et al. 2012) this leads to local alterations in community composition, the ordering of dominance rank and evenness (Bergström and Jansson 2006, Walker et al. 2006, Harpole and Tilman 2007, Hillebrand et al. 2007, Godbold et al. 2011). Importantly, such changes in the relative abundances of species can occur over short timescales without detectable changes in species richness, and can form the prelude to local species extinction (Collen et al. 2011, Turvey et al. 2015). Hence, changes in community evenness and the rank order of dominance may be a better representation of the impacts of directional forcing on biodiversity than species richness, and should be prioritized when exploring the ecosystem consequences of anthropogenic stressors (Hillebrand et al. 2008, Naeem 2009).

Despite the fact that community changes can modify the relative distribution of functional traits and the nature of species-environment interactions that are important in mediating ecosystem properties (Hillebrand et al. 2008, Godbold et al. 2011), few empirical studies have specifically assessed the effects of evenness and dominance structures on ecosystem functioning. Of those that have, most have focussed on primary production or decomposition (but see Wittebolle et al. 2009, Maestre et al. 2012, Orwin et al. 2014, Massaccesi et al. 2015) and therefore do not capture variability in divesity effects between functions or the multifunctionality of ecosystems (Hector and Bagchi 2007). Changes in evenness can have contrasting impacts on ecosystem functioning (positive, Wilsey and Potvin 2000, Stevens and Carson 2001, Kirwan et al. 2007; negative, Mulder et al. 2004, Dangles and Malmqvist 2004; neutral, King et al. 2002), which may be explained by the underlying mechanisms, such as complementarity and selection effects (Loreau and Hector 2001), driving diversity-ecosystem functioning relations and the facilitative effect of evenness on interspecific interactions (Hillebrand et al. 2008). If a given function is driven by complementarity between species, comprising synergistic interactions among species such as niche differentiation and facilitation (Loreau and Hector 2001), an increase in interspecific interactions with increased evenness is likely to increase functioning (Kirwan et al. 2007).

However, depending on the identity of the species and the function considered, increased interspecific interactions can also lead to a reduction in functioning, if the function is maximised by the traits of a single dominant species (Mulder et al. 2004). These mechanisms suggest that effects of evenness on ecosystem functioning can depend on species identity effects, as the traits of the dominant species can largely determine aggregate community processes (Norberg 2004). Hence, inconsistencies between the studies that explored evenness effects on ecosystem functioning may be related to concurrent alterations in community compositions (Avolio et al. 2014) and/or rearrangements in the order of species dominance (Mokany et al. 2008, Tolkkinen et al. 2013). However, experimental studies that specifically explore alterations in evenness alongside changes in community composition or dominance are rare (but see Orwin et al. 2014, Massaccesi et al. 2015) resulting in a significant gap in the understanding of the interactive effects and relative importance of evenness and dominance structure on ecosystem processes and functions.

Natural and anthropogenic environmental forcings do, however, not only alter the composition and structure of communities, but also the relative performance of individuals or populations, as organisms respond to the environmental conditions they experience (Albert et al. 2010a, Clark et al. 2011, Godbold et al. 2011, Langenheder et al. 2012, Godbold and Solan 2013). It is known that species can adjust the expression of physiological (Somero 2012), morphological (Pol et al. 2009, Hawlena et al. 2011) and/or behavioral (Ouellette et al. 2004, Maire et al. 2010) traits in response to their abiotic and biotic environment. If the traits of an organism that determine the response towards an abiotic or biotic factor (response traits) are linked to traits that determine the effect an organism has on its environment (effect traits, Suding et al. 2008), changes in context may disproportionately affect the relative performance of species in mediating ecosystem processes (Hodge 2004, Nogaro et al. 2007, Sassa and Watabe 2008), or lead to a shift in the functional role of species (Needham et al. 2010, Törnroos et al. 2015). These changes result in corresponding effects on biological-environment interactions and associated ecosystem properties (Levinton and Kelaher 2004, Ghazoul 2006, Godbold et al. 2011). Furthermore, context dependent variability in the

expression of functional traits may lead to intraspecific differences in the functional role of individuals or populations, especially if they experience varying environmental conditions. Approaches based on the analysis of functional traits, including physiological, morphological or phenological characteristics (Violle et al. 2007), can therefore be more accurate in predicting the ecosystem consequences of altered biodiversity than taxonomic approaches (Gagic et al. 2015), as they have the potential to capture intraspecific differences in organism environment interactions (e.g. Cianciaruso et al. 2009, Laughlin et al. 2012). However, most present approaches do not account for variation in trait values (Villéger et al. 2008, De Bello et al. 2011) and we know little about the relative importance of intraspecific variability for the faunal mediation of ecosystem properties (Albert et al. 2011, Albert 2015).

The responses of organisms to directional environmental change will not only alter individual species performances, but also the biodiversity ecosystem functioning relation (Balvanera et al. 2006, Rohr et al. 2016). As varying contexts are incorporated into experimental designs linking species richness and ecosystem properties, the magnitude and direction of biodiversity effects can change in response to abiotic factors, such as sea level rise (Yamanaka et al. 2013), eutrophication and organic enrichment (Godbold and Solan 2009, O'Connor and Donohue 2013), temperature (Hicks et al. 2011, Eklöf et al. 2012), elevated CO_2 levels (Hicks et al. 2011, Eklöf et al. 2012) or habitat structure (Godbold et al. 2011) and biotic factors, such as altered species interactions (Cardinale et al. 2007), or food web structure (Levinton and Kelaher 2004, Hillebrand et al. 2007, Bruno and Cardinale 2008). However, little is known about the importance of environmental context for the relation between other community attributes, such as evenness and identity of the dominant species, and ecosystem functioning (but see e.g. Wittebolle et al. 2009, Massaccesi et al. 2015). Furthermore, many experimental studies assessing the context dependency of biodiversity and ecosystem function relations have done so by manipulating environmental variables across fixed levels under constant experimental conditions (e.g. fixed levels of temperature and CO_2, Hicks et al. 2011; nutrient enrichment vs no enrichment, Fitch and Crowe 2011). But, in natural systems, regular cycles (e.g. diurnal, lunar or seasonal cycles), stochastic events (e.g. heat waves and cold spells, storms Meehl et al. 2007) and, superimposed on such variation, continuous directional

changes (e.g. global warming, ocean acidification, sea level rise, Meehl et al. 2007) mean that components of the environment are dynamic and vary over space and time. While there is evidence that such dynamics can largely control biological activities (Palmer 2002, Naylor 2010), the timing of lifecycle events (Brander 2010, Bellard et al. 2012) and/or spatio-temporal variation of organism environment interactions (Post and Forchhammer 2008, de Backer et al. 2010, Lindqvist et al. 2013), the relevance of such variation for the faunal mediation of ecosystem properties is not known. Moreover, multiple drivers of environmental change are likely to interact with another to affect the coupling between communities and ecosystem properties in ways that differ to those predicted from the consideration of individual drivers (Crain et al. 2008). Despite recognition of the likely importance of environmental dynamics, however, experiments that have manipulated assemblage structure have largely been performed in homogenous environments and failed to incorporate interactive effects of the multiple aspects of environmental variability in natural systems (but see e.g. Rodil et al. 2011, O'Connor and Donohue 2013).

Thesis aims and objectives

The overall aim of this Ph.D. thesis is to explicitly address the disconnect that exists between the representation of biodiversity in experimental systems and the context in which biodiversity-ecosystem function relations are moderated in natural systems experiencing multiple sources of change, using a marine benthic softsediment community as model system. Marine sedimentary benthic ecosystems cover most of the ocean seafloor and hence represent one of the spatially largest habitats (Snelgrove 1997). Particularly in the coastal regions up to the shelf edge benthic systems are socio-economically vital on a global scale, as they contribute a large amount to human welfare (Costanza et al. 1997) by providing essential ecosystem goods (e.g. food, raw materials) and services (e.g. nutrient cycling, regulation of carbon, climate regulation, detoxification, Snelgrove et al. 2014). In this context bioturbating infauna plays a key role by exerting a major control on fluxes of nutrients and organic matter between sediment and the water column, which in turn affects primary and consequently secondary production in coastal ecosystems (Laverock et al. 2011, Woodin et al. 2016). The species selected here represent the major taxonomic groups (polychaetes, bivalves, crustaceans, gastropods) of benthic ecosystems and do commonly co-occur in high abundances across European mudflats. Further, they differ in important functional traits related to bioturbation and bioirrigation, such as bioturbation or feeding mode (Wooding et al. 2016) and/or the architecture of biogenic features (mounds, pits, tubes and burrow galleries, Hale et al. 2014) and hence, have contrasting impacts on nutrient cycling (e.g. Godbold et a. 2011, Dyson et al. 2007).

The objectives of this Ph.D. are to reassess biodiversity-ecosystem functioning relations using more representative changes in community diversity by manipulating evenness and the rank order of dominance under controlled laboratory conditions (Chapter 1) and to test if community contributions to ecosystem properties (particle mixing and bioirrigation activity, sediment nutrient generation) are consistent across different biotic and abiotic contexts (Chapter 2 & 3), dynamic environments (Chapter 3) and between distinct populations (Chapter 4).

I hypothesise that:

1.) Ecosystem processes and functions are enhanced and less variable in communities in which species are more evenly distributed, but that differences in dominance rank order explain deviations from these predictions (Chapter 1).

2.) The functional impacts of the dominant species vary interactively with abiotic (resource quality and quantity) and biotic (presence of a predator) contexts (Chapter 2).

3.) The functional consequences of variations in community evenness and dominance identity change depending on environmental dynamics (tidal cycle) under different scenarios of sea level rise (Chapter 3).

4.) The functional role of species and communities varies between populations in response to local habitat conditions (Chapter 4).

Addressing these four hypotheses will allow the reassessment of biodiversity ecosystem functioning relations that occur when changes in community composition and multiple aspects of environmental variability are linked with and follow directional environmental forcing.

Chapter 2: Specific arrangements of species dominance are more influential than evenness in maintaining ecosystem properties

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2.1 Abstract

The ecological consequences of species loss are widely studied, but represent an end point of environmental forcing that is not always realised. Changes in species evenness and the rank order of dominant species are more widespread responses to directional forcing. However, despite the repercussions for ecosystem functioning such changes have received little attention. Here, the effects of the rearrangement of species dominance structure within specific levels of evenness, rather than changes in species richness and composition, on invertebrate particle reworking and burrow ventilation behaviour - important moderators of microbial-mediated remineralisation processes in benthic environments - and associated levels of sediment nutrient release are assessed. The results show that the most dominant species exert a disproportionate influence on functioning at low levels of evenness, but that changes in biomass distribution and a change in emphasis in species-environmental interactions become more important in governing system functionality as evenness increases. The study highlights the need to consider the functional significance of alterations to community attributes, rather than to solely focus on the attainment of particular levels of diversity when safeguarding biodiversity and ecosystems that provide essential services to society.

2.2 Introduction

Alterations to biodiversity influence the functioning of ecosystems and, by extension, the services that benefit human society, as evidenced by a plethora of experiments that have altered the number of genes, species or functional groups within a community and observed associated changes in various ecosystem properties (Cardinale et al. 2012). However, the effects of natural or human-induced factors on biological communities are not solely limited to the adjustment of species richness, they also affect other important aspects of biodiversity, in particular species evenness (Walker et al. 2006, Hillebrand et al. 2007, Hejda et al. 2009), the identity and rank order of dominant species (Dangles and Malmqvist 2004, Langenheder et al. 2012, Zelikova et al. 2014), and the spatial arrangement of individuals within a community (Arenas et al. 2009, Godbold et al. 2011, Maestre et al. 2012, Lohbeck et al. 2016). Changes in such community attributes tend to be context dependent, occur over extended timescales and are often a prelude to local species extinction (Collen et al. 2011, Turvey et al. 2015). Moreover, they modify the relative distribution of functional traits and the nature of species-environment interactions that are important for mediating ecosystem processes and functioning (Hillebrand et al. 2008, Godbold et al. 2011).

Whilst theory predicts that increases in evenness will enhance synergistic interspecific interactions that intensify species contributions to ecosystem functioning (Hillebrand et al. 2008), empirical studies that have examined the effects of changes in evenness on ecosystem properties report mixed results (positive; Wilsey and Potvin 2000, Stevens and Carson 2001, Kirwan et al. 2007; negative; Mulder et al. 2004, Dangles and Malmqvist 2004; neutral; King et al. 2002). Recent work, however, has shown that the functional outcome of a change in evenness can be attributed to substitutions in species composition (Avolio et al. 2014) and rearrangements in the order of species dominance (Mokany et al. 2008, Tolkkinen et al. 2013) rather than changes in evenness *per se*. Hence, when a community is dominated by a species that disproportionately contributes to functioning, a shift towards a more even community is more likely to promote species that are functionally inferior and lead to a decline in function (Li et al. 2013). Conversely, when a community is dominated by a species that contributes least to functioning, better performing species will increase in relative abundance as communities become more even

and elevate the level of functioning (Ward et al. 2010). Hence, it is the interplay between species dominance and the relative distribution of traits within a community that can be important in moderating ecosystem properties (Loreau and Hector 2001, Massaccesi et al. 2015), because multiple permutations of dominance structure are possible within each level of evenness.

Here, it was determined whether alterations in the identity and rank order of dominant species across contrasting levels of community evenness affect benthic community contributions to ecosystem processes (particle reworking and bioirrigation = bioturbation) and functioning (nutrient cycling). The *a priori* expectation was that ecosystem properties would be higher and less variable in communities in which species are more evenly distributed, because the functional expression of species traits is more likely to balance and the probability of positive synergistic interactions would increase (Daly et al. 2015). Furthermore, differences in dominance order are expected to explain deviations from these predictions because the identity of the most dominant species will exert a disproportionate influence on net trait contributions to functioning.

I specifically tested the hypothesis that (H1) evenness has a direct impact on functioning by facilitating interspecific interactions, which could be positive (as disruptions of borrow structures may lead to increased reconstruction and consequently particle mixing activities) or negative (as disruptions based on overlapping habitat use may reduce organism activities) and (H2) changes in the dominance structure will modify functioning due to differences in species traits and their contribution to functioning. Specifically, I hypothesise that communities dominated by *Hediste diversicolor* will show increased particle mixing depth as well as bioirrigation activity, which in turn is likely to stimulate microbial nutrient cycling, as it builds the deepest borrow structures of the study species and is a strong bioirrigator (Hale et al. 2014). Further, communities dominated by *Corophium volutator* will show increased particle mixing depths compared to communities dominated by *Hydrobia* (Bulling et al. 2010). If the expectations are met, it raises the possibility that the use of diversity metrics to represent complex communities may form an insufficient vehicle for determining the functional integrity of an ecosystem (Mace et al. 2014).

2.3 Methods

2.3.1 Experimental design and setup

Surficial sediment (less than 3 cm depth) and individuals of the gastropod *Hydrobia ulvae* and the mud shrimp *Corophium volutator* were collected by sieving from the Hamble Estuary, Southampton (50˚53'20.2"N 1˚17'35.3"W), whilst individuals of the polychaete *Hediste diversicolor* were collected by hand from Langstone Harbour, Portsmouth (50˚50'46.5"N 1˚00'05.3"W) during April 2014. Sediment was sieved (500 µm mesh) in a seawater bath to remove macrofauna, allowed to settle for 48 h (to retain the fine fraction, <63 µm) and homogenised.

Replicate (n = 5) macrofaunal communities across four evenness levels (Pielou's evenness index, J; Pielou 1966) that span the spectrum of dominance curves possible in natural communities (J = 0.47 – 0.78, Biles et al. 2003, Yamanaka et al. 2013) were assembled by altering the distribution of biomass (constrained to 2.0g aquarium^{-1}). Specifically, communities were established in which species either had identical biomass ($J^{1.00}$), the biomass of each species decreased sequentially in equal proportions ($J^{0.92}$), or a single species dominates and the remaining biomass levels decrease either linearly ($J^{0.64}$) or are held constant ($J^{0.42}$, Figure 2.1). To allow the generality of any evenness effects to be evaluated, whilst enabling the identification of any effects caused by differences in the relative distribution of individual species, all possible permutations of species dominance order ($J^{1.00}$, 1 permutation; $J^{0.92}$, 6 permutations; $J^{0.64}$, 6 permutations; $J^{0.42}$, 3 permutations) were assembled (Appendix 1 Table A1.1). As nutrient cycling is primarily a microbial process, aquaria containing no macrofauna (n = 5) were included to distinguish the extent of macrofaunal mediation. As the focus was to determine the effect of altered levels of evenness and dominance, rather than presence versus absence effects, these aquaria were not included in the statistical analysis. The experimental design required a total of 85 aquaria (16 permutations of species dominance + aquaria containing no macrofauna x 5 replicates).

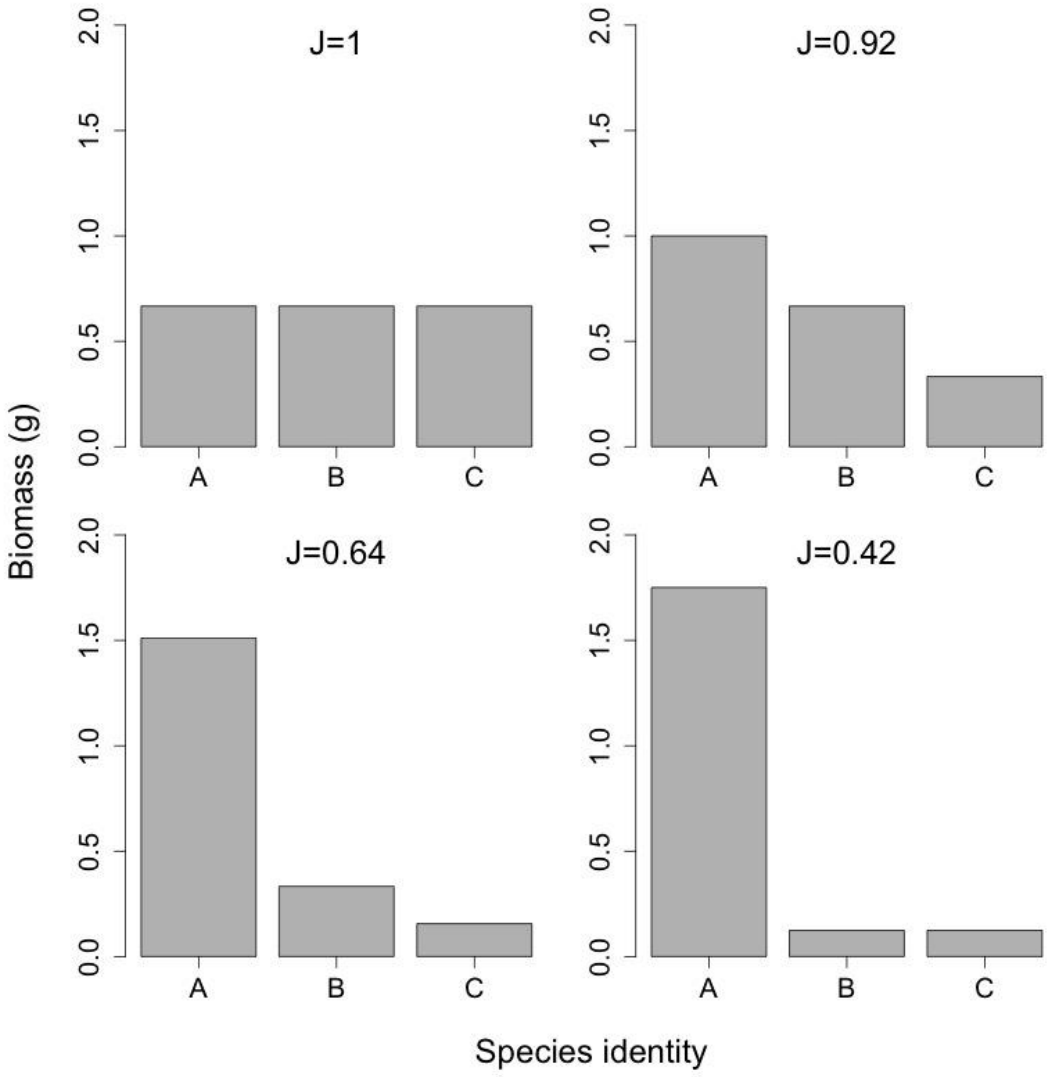

Figure 2.1: Experimental design: Four arrangements of evenness were selected that span the full spectrum of dominance structures that are possible in natural communities. Each contained three species and each bar represents the biomass of one of the three species: *Hediste diversicolor, Hydrobia ulvae* and *Corophium volutator*. All possible permutations of species dominance rank order where utilised ($J^{1.00}$, 1 permutation; $J^{0.92}$, 6 permutations; $J^{0.64}$, 6 permutations; $J^{0.42}$, 3 permutations).

Transparent square acrylic aquaria (internal dimensions, LWH; 12 x 12 x 35 cm), filled to 10 cm with mud and overlain by 20 cm of seawater (UV sterilised, 10 μm filtered, salinity 33) were used. Seawater was replaced after 24 h to remove excess nutrients associated with assembly. Aquaria were randomly positioned in a recirculating seawater bath (Figure 2.2 at 10 ± 1 ˚C under a

12:12 h light regime (Aqualine T5 Reef White 10K fluorescent light tubes, Aqua Medic) and continually aerated for 12 days.

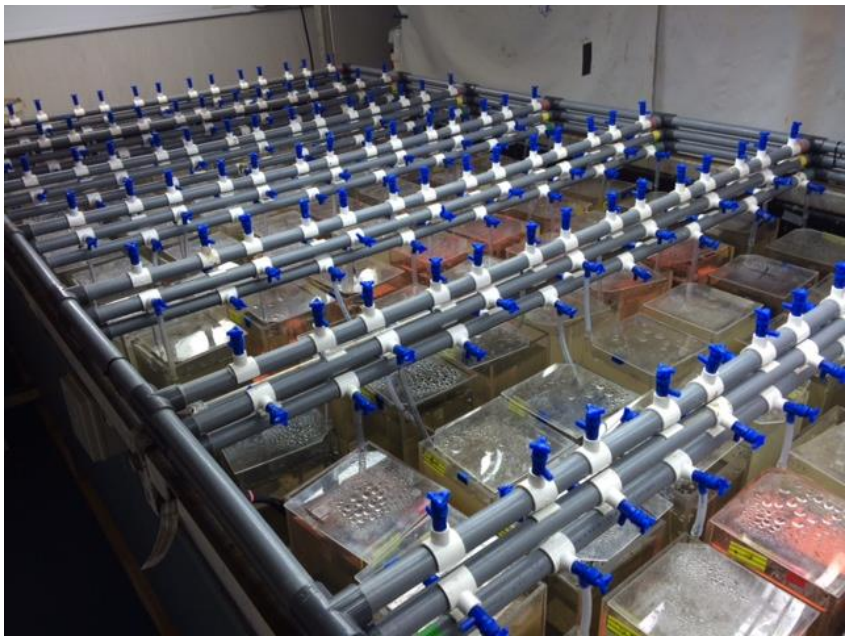

Figure 2.2: Randomly arranged mesocosms in recirculating seawater bath at 10 ± 1 ˚C.

2.3.2 Quantification of ecosystem process and functioning

Faunal mediated sediment particle reworking was estimated non-invasively using a sediment profile imaging camera (Canon 400D, set to 30 s exposure, aperture f4.5 and ISO 400; 3888 x 2592 pixels, effective resolution at aquarium side = 57 x 57 μm per pixel), optically modified to allow preferential imaging of fluorescently labelled particulate tracers (luminophores, red colour, size class less than 125 μm; Brianclegg Ltd., UK) under UV light (f-SPI, (Solan et al. 2004a)) that were introduced on the first day of the experiment (25g aquarium^{-1}). Vertical luminophore particle re-distribution was determined from stitched composite images (RGB colour, JPEG compression, GNU Image Manipulation Program, Version 2.8.4, http://www.gimp.org/, Kimball, S., Mattis, P., GIMP (1995), Date of access 01/07/2014) of all four sides of each aquarium obtained in a UV illuminated imaging box (Schiffers et al. 2011) using a custom-made semi-automated macro that runs within ImageJ (Version 1.47), a java-based public domain program developed at the US National Institutes of Health (http://rsb.info.nih.gov/ij/index.html, Rasband, W.,

ImageJ., (1997), Date of access 01/07/2014). From these data, the mean ($^{f\text{-}SPI}L_{mean}$, time dependent indication of mixing), median ($^{f\text{-}SPI}L_{median}$, typical short-term depth of mixing) and maximum ($^{f\text{-}SPI}L_{max}$, maximum extent of mixing over the long-term) mixed depth of particle redistribution were calculated. In addition, the vertical deviation of the sediment-water interface (upper – lower limit; surface boundary roughness, SBR) provided an indication of surficial activity (Hale et al. 2014).

Following the addition of 2.74 g of the inert tracer sodium bromide (NaBr, dissolved in 10 ml seawater, = ~9 mM aquaria^{-1}), bioirrigation was estimated from absolute changes in the concentration of bromide ($\Delta[Br^-]$, mg L^{-1}; negative values indicate increased bioirrigation activity) over a 4h period (Forster et al. 1999) on day 12, determined from pre-filtered (Fisherbrand, QL100, ⌀ 70 mm) water samples (5 ml, taken centrally and ~ 5 cm above the sediment-water interface) using a flow injection auto-analyser (FIAstar 5000 series, Foss-Tecator).

Nutrient concentrations ($[NH_4\text{-}N]$, $[NO_x\text{-}N]$ and $[PO_4\text{-}P]$) were determined from pre-filtered (Fisherbrand, nylon 0.45 µm, ⌀ 25 mm) water samples (10ml, taken centrally and ~2cm below the air-water interface) taken on day 12 by flow injection auto-analysis (FIA Star 5010 series) using an artificial seawater carrier solution.

2.3.3 Statistical analyses

Two separate statistical models for each of the dependent variables (ecosystem processes: $^{f\text{-}SPI}L_{mean}$, $^{f\text{-}SPI}L_{median}$, $^{f\text{-}SPI}L_{max}$, SBR, $\Delta[Br^-]$; ecosystem functioning: $[NH_4\text{-}N]$, $[NO_x\text{-}N]$, $[PO_4\text{-}P]$) were developed, to establish the independent effect of evenness per se and the effect of alterations in the arrangement of species dominance. Evenness was treated as a continuous explanatory variable to establish generic effects of evenness and, in an alternative analysis, as a single nominal explanatory variable (to establish specific effects of the 4 treatment levels: $J^{1.00}$, $J^{0.92}$, $J^{0.64}$, $J^{0.42}$). Species dominance was treated as a single nominal explanatory variable (16 levels, Appendix 1 Table A1.2).

The initial linear regression models were assessed for normality (Q-Q-plot), heterogeneity of variance (plotted residual vs. fitted values) and influential data

points (cook's distance) (Zuur et al. 2007). Where data exploration indicated heterogeneity of variances, the residual spread was allowed to vary with individual explanatory variables using generalized least squares (GLS) estimation. This procedure uses appropriate variance functions (here *varIdent* for nominal and *varPower* or *varExp* for continuous explanatory variables) to model the variance structure (Pinheiro and Bates 2000). The optimal variance covariate structure was determined by comparing the initial regression model without variance structure to the equivalent GLS model incorporating specific variance structures using AIC and visualisation of model residuals following restricted maximum likelihood (REML) estimation. The optimal fixed structure was determined by applying backward selection using the likelihood ratio test obtained by maximum likelihood (ML) estimation (Zuur et al. 2007). The coefficient tables are presented (Appendix 1, statistical model summary) without correction for the alpha-error, as Bonferroni correction increases the beta error and has further objections (Moran 2003). All statistical analysis were performed using the 'R' statistical and programming environment (R Core Team 2014) and the "nlme" package (Pinheiro et al. 2014).

2.4 Results

Overall, there was only a weak support for hypothesis one as there were only weak effects of evenness *per se*, suggesting that the facilitation of interspecific interactions only plays a minor role for bioturbation and bioirrigation activities as well as sediment nutrient generation. While the results show a strong effect of species dominance order on most ecosystem responses for low evenness levels, generally supporting hypothesis two, the species specific impacts differ slightly from the expectations, as communities dominated by *Corophium volutator* show highest particle mixing depths and sediment NO_X-N release.

2.4.1 Effects of evenness on ecosystem process and functioning

There was no evidence that evenness, when treated as a continuous explanatory variable, affected the mean mixed depth of particle reworking, maximum mixed depth of particle reworking, surface boundary roughness or bioirrigation activity (Table 2.1). However, there was a marginal effect of evenness on the median mixed depth of particle reworking (Figure 2.3), ranging from (mean ± s.d.) 1.23 ± 1.09 cm for $J^{0.42}$ to 2.15 ± 0.34 cm for $J^{1.00}$. For nutrient concentrations, the analyses reveal that changes in species evenness did not influence [NH_4-N] or [PO_4-P], but [NO_x-N] did decrease (mean ± s.d., from 0.78 ± 0.26 mg L^{-1} for $J^{0.42}$ to 0.56 ± 0.08 mg L^{-1} for $J^{1.00}$) with increased evenness (Table 2.1, Figure 2.4), giving only weak support for facilitation of synergistic interspecific interactions by increased evenness (hypothesis one).

Interestingly, the data also suggests that a shift towards greater evenness ($J \rightarrow 1$) reduces variability (standard deviation) in the response variables ($^{f\text{-}SPI}L_{mean}$: $J^{0.42} = 0.88 \rightarrow J^{1.00} = 0.60$; $^{f\text{-}SPI}L_{median}$: $J^{0.42} = 1.09 \rightarrow J^{1.00} = 0.34$; $^{f\text{-}SPI}L_{max}$: $J^{0.42} = 0.58 \rightarrow J^{1.00} = 0.29$; SBR: $J^{0.42} = 0.36 \rightarrow J^{1.00} = 0.36$; [$NH_4$-N]: $J^{0.42} = 1.02 \rightarrow J^{1.00} = 0.58$; [$NO_x$-N]: $J^{0.42} = 0.26 \rightarrow J^{1.00} = 0.08$). A reanalysis of the data using evenness as a nominal explanatory variable confirms these results (Appendix1 Model S9-S16).

Table 2-1: Summary of statistical analyses for the effects of evenness (J). The test statistic indicates F value or L-ratio depending on the statistical model (see statistical model summary Appendix 1, model S1-S8)

response variable	d.f.	test statistic	p
$^{f\text{-}SPI}L_{mean}$	1	2.23	0.14
$^{f\text{-}SPI}L_{median}$	1	4.37	**0.04**
$^{f\text{-}SPI}L_{max}$	1	0.04	0.84
SBR	1	0.003	0.96
$\Delta[Br^-]$	1	0.17	0.68
$[NH_4\text{-}N]$	1	0.17	0.68
$[NO_x\text{-}N]$	1	8.25	**0.004**
$[PO_4\text{-}P]$	1	2.90	0.09

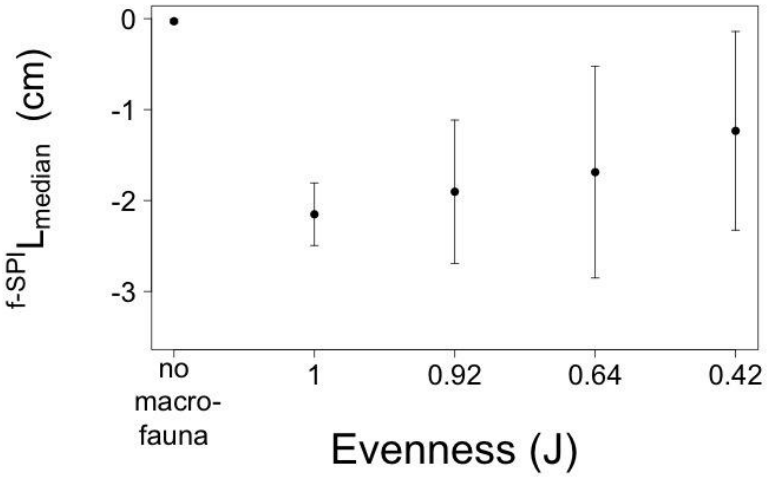

Figure 2.3: The effects of community evenness (J) on the mean depth of sediment particle reworking ($^{f\text{-}SPI}L_{mean}$, cm, mean ± s.d., n = 5) calculated from the vertical distribution of luminophore tracers (Appendix1 Figure A1.2). Observations in the absence of macrofauna are shown for comparison, but were not included in the statistical analyses.

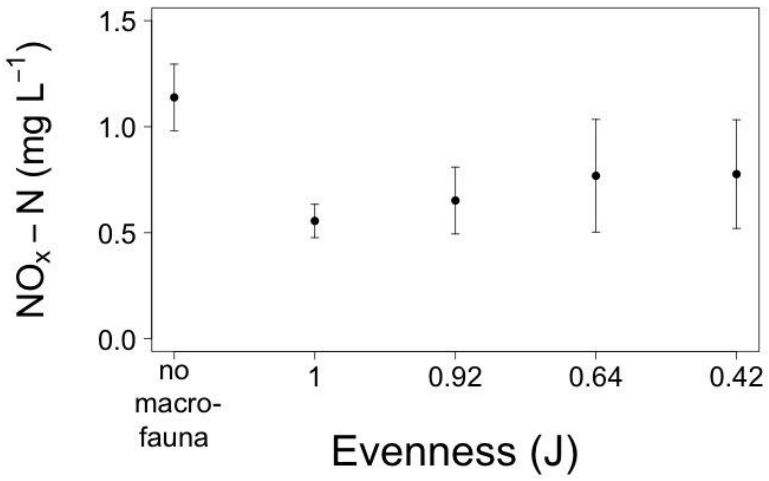

Figure 2.4: The effects of community evenness (J) on NO_x-N concentrations (mg L^{-1}, mean ± s.d., n = 5). Nutrient concentrations observed in the absence of macrofauna are shown for comparison, but were not included in the statistical analyses.

2.4.2 Effects of changes in the arrangement of dominance structure on ecosystem process and functioning

There were strong effects of changes in the arrangement of dominance structure on ecosystem process supporting hypothesis two (Appendix1 Model S17-S21) that were driven by the activities of *Corophium volutator*, followed by those of *Hediste diversicolor* and those of *Hydrobia ulvae*. The mean and median mixed depth of particle reworking differed between alternative dominance structures, with the largest differences occurring at lower evenness levels ($J^{0.64}$ and $J^{0.42}$; Table 2.2,

Figure 2.5). Treatments dominated by *Corophium volutator* (CV) and *Hediste diversicolor* (HD) tended to result in a greater degree of particle mixing relative to treatments where *Hydrobia ulvae* (HU) was dominant (

Figure 2.5). Surficial sediment reworking activities were affected by alterations to dominance structure (

Figure 2.5), but the maximum depth of mixing was unaffected. Bioirrigation activity ($\Delta[Br^-]$) was also affected, albeit marginally, by alternative arrangements of dominance structure, but the sequence of species-specific effects was not as pronounced as the patterns observed for particle reworking (

Figure 2.5).

Alterations in the arrangement of species dominance also led to changes in nitrogen cycling for [NH_4-N] and [NO_x-N], but not for [PO_4-P] (Table 2.2, Figure 2.6). At the lowest levels of evenness, [NH_4-N] was low when *Corophium volutator* was dominant, intermediate when treatments were dominated by *Hydrobia ulvae* and highest when *Hediste diversicolor* was dominant. The [NO_x-N] were reciprocal to those of [NH_4-N], suggesting a predominance of denitrification, with lowest concentrations for treatments dominated by *Hediste diversicolor* followed by *Hydrobia ulvae* and *Corophium volutator*. This pattern was largely maintained at intermediate levels of dominance ($J^{0.64}$), but was less prominent at higher levels of dominance ($J^{0.92}$ and $J^{1.00}$) (Figure 2.6). All data used in the statistical analyses are provided in Appendix 1, Table A1.2.

Table 2-2: Summary of statistical analyses for the effects of the arrangement of species dominance. The test statistic indicates F value or L-ratio depending on the statistical model (see statistical model summary Appendix 1, model S17-S21)

response variable	d.f.	test statistic	p
$^{f\text{-}SPI}L_{mean}$	15	78.76	**<0.0001**
$^{f\text{-}SPI}L_{median}$	15	4.17	**<0.0001**
$^{f\text{-}SPI}L_{max}$	15	1.29	0.24
SBR	15	36.98	**0.001**
$\Delta[Br^-]$	15	26.06	**0.04**
[NH_4-N]	15	79.21	**<0.0001**
[NO_x-N]	15	8.53	**<0.0001**
[PO_4-P]	15	0.57	0.89

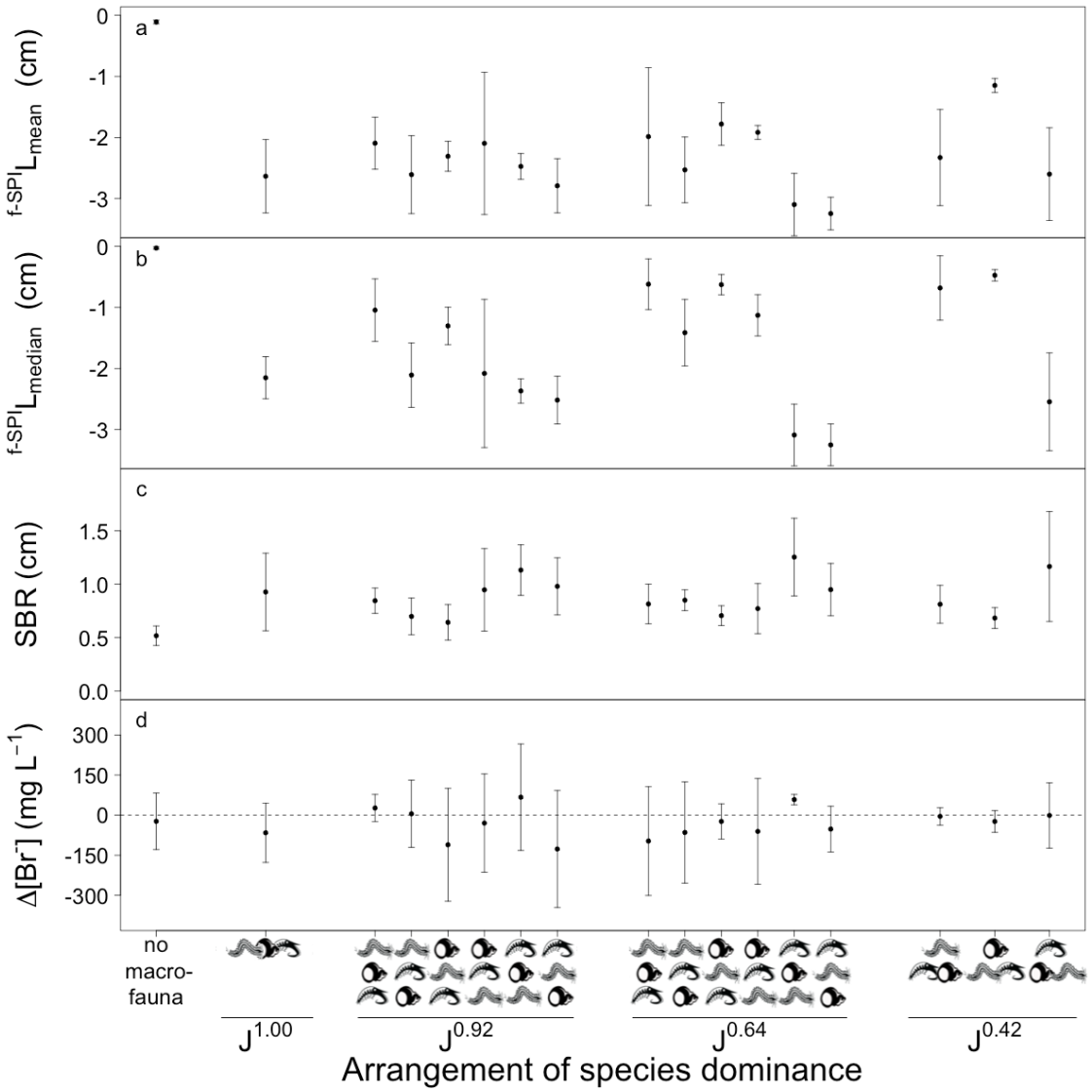

Figure 2.5: The effects of changes in the arrangement of species dominance within different evenness levels ($J^{1.00}$, $J^{0.92}$, $J^{0.64}$, $J^{0.42}$; Figure 2.1) on (a) the mean depth of sediment particle reworking ($^{f\text{-}SPI}L_{mean}$, cm, mean ± s.d., n = 5) and (b) the median depth of sediment particle reworking ($^{f\text{-}SPI}L_{median}$, cm, mean ± s.d., n = 5) calculated from the vertical distribution of luminophore tracers (Appendix1 Figure A1.2), (c) the surface boundary roughness (SBR, cm, mean ± s.d., n = 5) and, (d) bioirrigation activity ($\Delta[Br^-]$ mg L^{-1}, mean ± s.d., n = 5). For mean and median depth of sediment particle reworking and bioirrigation activity negative values indicate increased activity. Observations in the absence of macrofauna are shown for comparison, but were not included in the statistical analyses. The sequence of species dominance (vertically, from most to least; horizontally, equal dominance) is indicated in the inset of each panel: = *Corophium volutator*, = *Hydrobia ulvae*, = *Hediste diversicolor.*

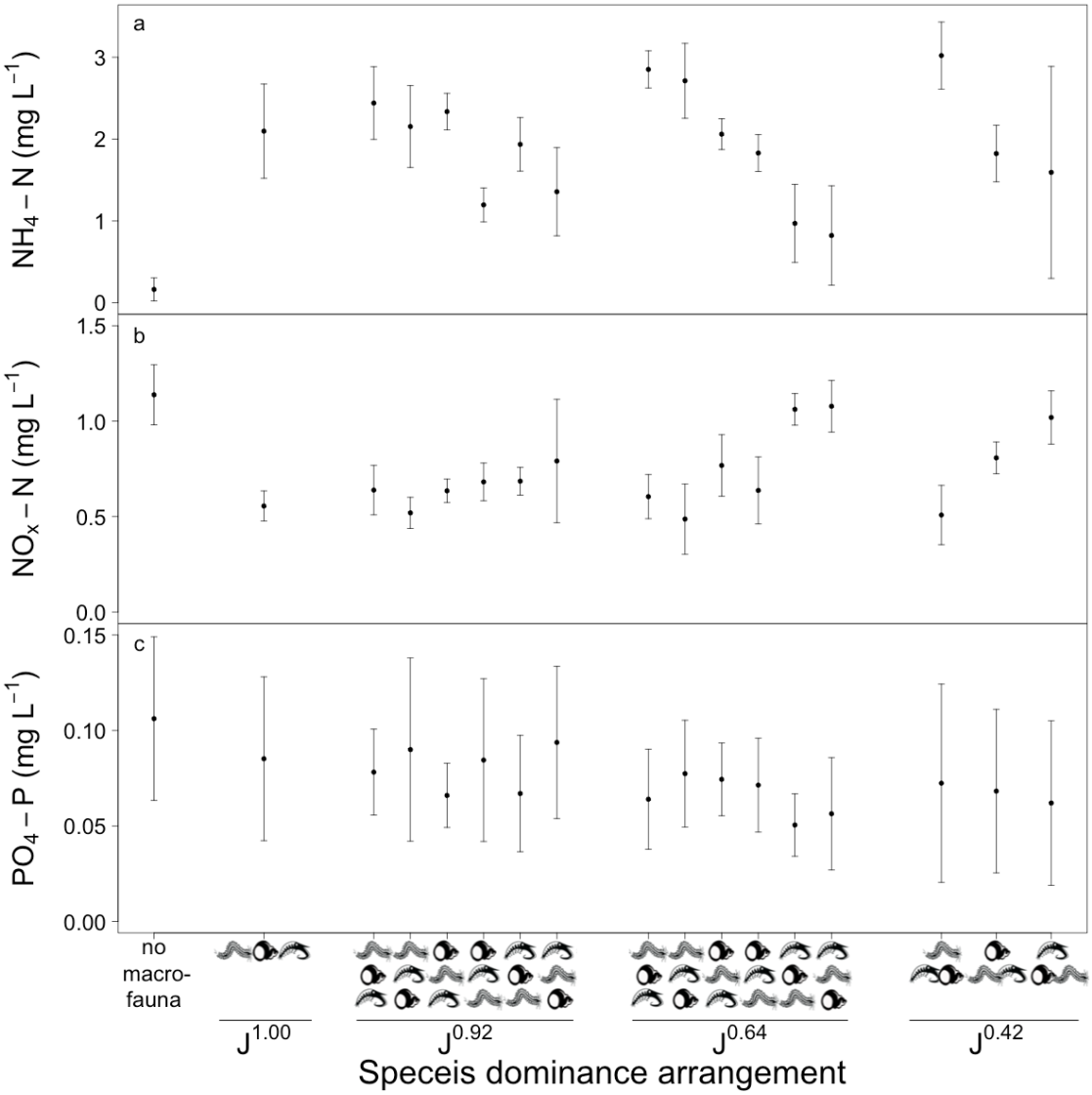

Figure 2.6: The effects of changes in the arrangement of species dominance within different evenness levels ($J^{1.00}$, $J^{0.92}$, $J^{0.64}$, $J^{0.42}$; Figure 2.1) on water column nutrient concentration (mg L^{-1}, mean ± s.d., n = 5) for (a) [NH_4-N], (b) [NO_x-N] and (c) [PO_4-P] (no significant effect). Nutrient concentrations observed in the absence of macrofauna are shown for comparison, but were not included in the statistical analyses. The sequence of species dominance (vertically, from most to least; horizontally, equal dominance) is indicated in the inset of each panel: = *Corophium volutator*, = *Hydrobia ulvae*, = *Hediste diversicolor.*

2.5 Discussion

The results demonstrate that, irrespective of evenness level, rearrangements in the rank order of species dominance can lead to distinct changes in ecosystem properties that, in turn, depend on the functional identity of the most dominant species. This implies that differences in species dominance might best explain apparent inconsistent community responses to directional changes in evenness (Wilsey and Potvin 2000, Stevens and Carson 2001, King et al. 2002, Mulder et al. 2004, Dangles and Malmqvist 2004, Kirwan et al. 2007), although the observed levels of nutrient concentrations here were not always coherent with bioturbation (Murray et al. 2014). Such discrepancies are maximised at low levels of evenness where the most dominant species exert a disproportionate influence on functioning, but increasingly reflect changes in biomass distribution as evenness increases. These effects can be augmented, as species contributions to ecosystem properties can reflect a range of simultaneously operating mechanisms that are not necessarily proportional to species biomass (Woodin et al. 2016). Changes in species behaviour (Ouellette et al. 2004), density (Winfree et al. 2015), excretion (Villéger et al. 2012) and/or the architecture of biogenic features (mounds, pits, tubes and burrow galleries, Hale et al. 2014), for example, can disproportionately influence microbial community structure and associated biochemical transformations (Gilbertson et al. 2012). Indeed, for nitrogen, divergence in the relative contributions of particle reworking, bioirrigation and nutrient generation observed here do suggest that alterations in the nature of species interactions and/or the expression of traits accompanied changes in evenness. Interestingly, this was not the case for phosphate, where changes in the arrangement of species dominance had little influence. Complex chemical retention systems can decouple species traits from aspects of nutrient release and may, under certain circumstances, overwhelm biotic control (Hupfer and Lewandowski 2008, Teal et al. 2013). Nevertheless, the findings of this study generally indicate that the functional outcome of a change in evenness is dependent not only on the arrangement of dominance structure and the realised density of individual species, but also on the propensity of species to adjust their functional role under novel biotic and/or abiotic circumstances (Ouellette et al. 2004, Godbold et al. 2011, 2013).

A second prominent outcome from this study is that there was little evidence to support the view that changing levels of evenness facilitate synergistic interspecific interactions (Orwin et al. 2014, Daly et al. 2015). Instead, an increase in evenness led to a reduction in variance and a convergence in ecosystem performance that reflected interspecific alterations in biomass. Previous experimental work emphasised that ecosystem properties tend to be maximised by the traits of individual species (Mermillod-Blondin et al. 2005, Ieno et al. 2006, Godbold et al. 2009a, Langenheder et al. 2012) and that interspecific synergistic interactions are unlikely, at least initially, as complex interactions between combinations of species and resources underlie mechanisms of complementarity and take time to develop (Langenheder et al. 2010, Godbold et al. 2013). However, the relative importance and nature (synergistic versus antagonistic) of interspecific interactions depends on the identity of the interacting species (Ghazoul 2006) and is further complicated by alterations in context, including resource availability (Langenheder et al. 2010), habitat configuration (Godbold et al. 2011) and changing environmental conditions (Bulling et al. 2010, Hicks et al. 2011, Godbold et al. 2013). It follows therefore, that complementarity mechanisms are unlikely to be documented in short-term experiments, but will be more prominent in naturally assembled systems where there is a multi-generational history of species interaction.

It is important to consider the findings of this study within the context of natural ecosystems. Skewed species-abundance distributions, where only a few species dominate amongst many rare species, are a universal feature of biological communities (McGill et al. 2007, Winfree et al. 2015), and can constrain any effect of biodiversity on ecosystem functioning to a subset of dominant species. Consequently, a shift in the identity of the most dominant species can lead to considerable changes in net community contribution to ecosystem properties (Loreau and Hector 2001, Lohbeck et al. 2016). However, communities in natural systems are not isolated and interact with other communities within the regional species pool, leading to complex meta-community dynamics (Thompson and Gonzalez 2016). When meta-communities are dominated by a single species, substitution of the most dominant species is likely to have a strong local impact on ecosystem

functioning. In contrast, when meta-community populations are dominated by a range of different species, regional evenness is correspondingly elevated (Hillebrand et al. 2008), leading to reduced variability in ecosystem properties that, in turn, acts to stabilise functioning against shifts in dominance arrangement (Loreau et al. 2003). It may be anticipated, therefore, that evenness will be especially important at larger scales when environmental fluctuations (Wittebolle et al. 2009, Langenheder et al. 2012) and the multifunctionality of ecosystems are considered (Pasari et al. 2013), a view that places emphasis on the reciprocal relationship between biodiversity and the environment (Godbold and Solan 2009).

Overall, the findings of the present study are consistent with current consensus that both the identity and the diversity of organisms jointly control the functioning of ecosystems (Cardinale et al. 2012) and that species identity effects and community composition are most important at small scales, whilst species richness and community biomass are most important at large scales (Brose and Hillebrand 2016). However, this study highlights the need to consider the functional significance of changes in the properties of biodiversity, rather than solely focus on the attainment or maintenance of biodiversity *per se*. In particular, more emphasis is required on the distribution of functional traits across different spatial scales, temporal variation in species contributions to ecosystem properties, and variability in trait expression, including compensatory responses, in changing environments. Such information will be essential if we are to guide efforts to protect species and ecosystem services or generate ecosystem models that accurately predict the ecological consequences of environmental change.

2.6 Acknowledgements

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Chapter 3: Faunal mediation of ecosystem properties is dependent on differences in trait expression that relate to interactions with the abiotic and biotic environment

3.1 Abstract

The distribution of functional traits within communities plays a key role in mediating ecosystem properties. Natural communities are mostly dominated by only few common species. Hence, net community functional trait expression and consequently ecosystem functioning in ecosystems is likely to be driven by the dominating species. However, changes in the environmental context may further modify community trait expression and ecosystem properties. Here I quantify the effects of community dominance of single species, constrained within a fixed level of total community biomass, across alternative abiotic (resource quantity and quality) and biotic (predator presence/absence) conditions on ecosystem processes (bioturbation, bioirrigation) and functioning (nutrient release) in a model benthic ecosystem. The results show that the relative performance of the community is largely dependent on the identity of the dominant species, but, depending on their traits, less abundant species can contribute unique aspects of ecosystem functioning. Community performance can further be modified by species interactions, which may be facilitated or dampened under certain environmental conditions. These findings indicate that the faunal mediation of important ecosystem properties is not only dependent on the presence of particular functional effect traits, but also subject to differences in trait expression that relate to how individuals interact with their abiotic and biotic environment. I conclude that re-distribution of functional traits, and how traits are expressed in natural systems, will need to be prioritised when considering the ecological consequences of altered biodiversity.

3.2 Introduction

Current understanding of the ecosystem consequences of changing biodiversity is largely based on highly-controlled experiments that seldom take factors into account that lead to variations in the relative distribution of organisms (Cardinale et al. 2012, Gamfeldt et al. 2015), such as resource availability, predator/consumer pressure or physical and climatic conditions. Yet, natural communities universally exhibit strong dominance patterns (McGill et al. 2007, Winfree et al. 2015) in response to changing local biotic and/or abiotic conditions (Therriault and Kolasa 1999, Hillebrand et al. 2007, Zelikova et al. 2014). In addition, as species respond and adapt to local conditions (Nogaro et al. 2007, Hereford 2009, Godbold et al. 2011, Rudman et al. 2015), the functional performance and behaviour of individuals can be modified and has the potential to significantly alter species contributions to ecosystem functioning (Fitch and Crowe 2011, Godbold et al. 2011, Pratt et al. 2014). This is important, because the ecosystem consequences of incorporating more realistic species distributions alongside varying environmental conditions in empirical investigations are likely to lead to outcomes that are very different to those based on contemporary single or multi-species experiments that adopt even species distribution (Winfree et al. 2015, Wohlgemuth et al. 2016).

The relevance of biodiversity-ecosystem function experiments to natural systems undergoing directional change have previously been criticised (Srivastava and Vellend 2005) because experimental assemblages do not resemble natural observations (Bracken et al. 2008, Naeem 2008). Furthermore, the magnitude and direction of the effects of changing biodiversity are highly variable and often depend on the direct or indirect influence of other biotic or abiotic drivers (O'Connor and Donohue 2013, Alsterberg et al. 2014), including predator-prey interactions (Duffy et al. 2007, Bruno and Cardinale 2008) and resource distribution or availability (Hillebrand 2003, Isbell et al. 2013, O'Connor et al. 2015). Under certain circumstances, however, functional consequences of biodiversity loss may occur, but their relative importance is diminished when more prominent environmental factors that can directly affect ecosystem functioning are present (Baerlocher and Corkum 2003, Godbold and Solan 2009, Bracken et al. 2011). Nevertheless, irrespective of the mechanism of variability, organisms continually modify their behaviour and activity patterns in response to changing circumstance (e.g.

temperature, Ouellette et al. 2004, Przeslawski et al. 2009; oxygen availability, Long et al. 2008; hydrodynamic conditions, Yamanaka et al. 2013, Törnroos et al. 2015; sediment conditions, Needham et al. 2010, Chapter 4) and such adjustments to how traits are expressed will alter the functional performance of organisms (Nogaro et al. 2007, Needham et al. 2011, Godbold et al. 2011, Canal et al. 2015, Chapter 3 & 4).

The importance of local resource availability and distribution in mediating functionally important aspects of species behaviour, activity levels and species interactions are well-established across multiple ecosystems (Worm et al. 2002, Przeslawski et al. 2009, Ashton et al. 2010, Godbold et al. 2011, Vos et al. 2013, O'Connor et al. 2015), as are the effects of predator/consumer-presence or identity (Bruno and O'Connor 2005, Griffin et al. 2008, Bruno et al. 2008, Bruno and Cardinale 2008, Maire et al. 2010). Here, using intertidal soft-sediment invertebrate communities that contrast in the relative distribution and dominance of co-occurring species, these perspectives are combined to investigate the functional consequences of concurrent changes in biotic (predator presence/absence; *Crangon crangon*) and environmental (organic enrichment using ground algae of varying palatability) context, as biotic and abiotic factors vary simultaneously in natural systems and may interactively modify community mediation of ecosystem properties (Crain et al. 2008, O'Connor and Donohue 2013). I hypothesis (H1) that the addition of the predator (*Crangon crangon*) reduces the particle mixing depths and bioirrigation activities, resulting in reduced sediment nutrient release, mediated by the infaunal communities. As the study species differ in their borrowing depth (*Hediste diversicolor* > *Macoma balthica* > *Hydrobia ulvae*) I expect the impact of *C. crangon* to be stronger on communities dominated by *H. ulvae* resulting in an interactive effect of dominant species identity and predator presence/absence. Further, I hypothesis (H2) that algal enrichment will increase or decrease faunal bioturbation and bioirrigation activity and consequently sediment nutrient generation, depending on the palatability of the used algae, as the organisms adjust their feeding activities to the increased resource availability and quality. As the study species differ in their feeding strategies (Barnes 2006, Maltagliati et al. 2006, Toernroos et al. 2015), this effect is likely to be interactive with the identity of the dominant species.

3.3 Methods

3.3.1 Experimental design and setup

All sediment and macrofaunal invertebrates were collected along the south coast of the United Kingdom in June 2014. Surface sediment, the gastropod *Hydrobia ulvae* and the bivalve *Macoma balthica* were collected from the Hamble Estuary (50˚52'23.5"N 1˚18'48.4"W) by sieving (500 µm mesh, <5cm depth). Individuals of the polychaete *Hediste diversicolor* were collected by hand from Langstone Harbour, Portsmouth (50˚50'46.5"N 1˚00'05.3"W), whilst individuals of the mud shrimp *Crangon crangon* (max. wet weight 1g) were collected from Hayling Island (50˚47'05.6"N 1˚00'57.5"W), using a push net (1 cm mesh size, 55 cm wide). Surface sediment (<3 cm depth) was sieved (500 µm mesh) in a seawater bath to remove macrofauna, allowed to settle for 48 h (to retain the fine fraction, <63 µm) and homogenised. In order to minimise the effects of consumption by *C. crangon*, individuals of *H. ulvae*, *M. balthica* and *H. diversicolor* were selected that were larger than the prey-handling size of *C. crangon* (Pihl and Rosenberg 1984, Oh 2001, Campos and Van Der Veer 2008). The macro algae *Ulva lactuca* (Chlorophyta, green algae) and *Fucus serratus* (Heterokontophyta, brown algae) were collected from Swanage bay (50˚36'27.4"N 1˚56'38.1"W). Algae were rinsed with filtered seawater to remove debris and fauna, dried over 24 hours at 50˚C and then ground to a fine powder.

Macrofaunal communities were assembled in transparent square acrylic aquaria (12 ×12 cm, 35 cm high). Given the ubiquitous occurrence of skewed species distributions in natural communities (McGill et al. 2007) and that ecosystem properties can be largely determined by the functional traits of the dominant species (Cardinale et al. 2012, Winfree et al. 2015, Wohlgemuth et al. 2016), the dominance identity of individual species in communities with an overall evenness level of J = 0.64 (Pielou's eveness index, Pielou 1966), which is within the evenness range commonly observed in natural communities (Whitlatch 1977, Van Colen et al. 2008, Dossena et al. 2012), was modified. Either *H. ulvae*, *M. balthica* or *H. diversicolor* dominated the community (n = 4 replicates per species) in terms of biomass (mean ± s.d., 1.55 ± 0.02 g). The biomass of the remaining species was lower (mean ± s.d., 0.23 ± 0.02 g) and

held constant between species (Appendix 2 Table A2.1). The impacts of organic enrichment and resource quality (four levels: no enrichment, *F. serratus* only, *U. lactuca* only and a 50:50 mixture of *F. serratus* and *U. lactuca*) and the presence/absence of the predator *C. crangon* were included in a fully crossed design. Different resource qualities were achieved by adding and homogenising 3g DW of *U. lactuca,* (high palatability, Buchsbaum et al. 1991), *F. serratus,* (low palatability, Buchsbaum et al. 1991), or a mixture of both (intermediate palatability) into the sieved sediment. In those treatments in which the predator was present, 1 individual of *C. crangon* (0.78 ± 0.16 g wet weight) was added to each aquarium. As nutrient cycling is primarily a microbial process, aquaria containing no macrofauna were also included to distinguish the extent of macrofaunal mediation. As the focus was to determine the effect of altered community dominance in relation to the biotic and abiotic context, rather than presence versus absence effects, these aquaria were not included in the statistical analysis. This experimental design contained a total of 128 aquaria: 4 macrofaunal treatments (no fauna, *H. ulvae*, *M. balthica* or *H. diversicolor* dominant) × 4 algal enrichment treatments (no algae, *F. serratus* only, *U. lactuca* only and 50:50 mixture) × 2 predator treatments (presence/absence of *C. crangon*) × 4 replicates per treatment.

Each aquarium contained 10 cm of sieved sediment and 20 cm of filtered seawater. Following Godbold et al. (2011) the ground algae was added and mixed homogenously into the sediment during assembly. After 24 hours the overlying seawater was exchanged to remove excess nutrients associated with assembly and the infaunal organisms were added. *C. crangon* were added after 12 hours to give the other macrofauna sufficient time to settle and/or burrow into the sediments. Aquaria were randomly placed in a seawater bath at 14 ± 1 ˚C, under a 12:12h light regime (Aqualine T5 Reef White 10K fluorescent light tubes, Aqua Medic) and continually aerated for 12 days.

3.3.2 Quantification of ecosystem process and functioning

Twenty-four hours after adding the organisms, 25 g of fluorescent tracer particles (coloured sand that fluoresces under ultraviolet light, red colour, Brianclegg Ltd, Uk) were equally distributed on the sediment surface of each aquarium. After 12 days, bioturbation was quantified by imaging (Canon EOS set to 15 s exposure, aperture f5.6 and ISO 400; 3888 × 2592 pixels, effective

resolution at aquarium side = 49 × 49 µm per pixel) all sides of each aquarium under UV light. Vertical particle distribution (mean ($^{f\text{-}SPI}L_{mean}$) and maximum ($^{f\text{-}SPI}L_{max}$) particle depth, surface boundary roughness (SBR)) was quantified using GNU Image Manipulation Program (GIMP, Version 2.8.4, http://www.gimp.org/, Kimball, S., Mattis, P., GIMP (1995), Date of access 01/09/2014) and a custom made, semi-automated macro for ImageJ (Version 1.47) (following Solan et al. 2004, Godbold and Solan 2013, Hale et al. 2014).

To estimate bioirrigation (burrow ventilation) the redistribution of the inert tracer sodium bromide (NaBr) was measured on the final day of the experiment. 2.97 g of NaBr dissolved in 10 ml seawater was added to each core (~ 10 mM [NaBr] aquarium^{-1}) and carefully homogenised into the water column without disturbing the sediment surface. Water samples of 5 ml volume were taken immediately after addition of NaBr from the centre of each aquarium approximately 5 cm above the sediment surface and again after 4 hours. During this time, aeration was stopped to prevent additional water movement not caused by bioirrigation activity. The samples were filtered (Fisherbrand, QL100, ø 70 mm) and frozen at -20°C until analysis. [Br^-] was determined using a flow injection auto-analyser (FIAstar 5000 series, Foss-Tecator) and the change in concentration over a 4-hour period ($\Delta[Br^-]$) was calculated (negative values indicate increased bioirrigation activity, Forster et al. 1999).

To quantify water column nutrient concentrations 10 ml water samples were taken on day 12 from the centre of each aquarium approximately 5 cm above the sediment surface, filtered using nylon syringe filters (Fisherbrand, nylon 0.45 µm, ø 25 mm) and immediately frozen until analyses. NH_4-N (ammonium), NO_x-N (nitrate+nitrite) and PO_4-P (phosphate) concentrations were measured using a flow injection auto-analyser (FIAstar 5010 series, Foss-Tecator) and an artificial seawater carrier solution.

3.3.3 Statistical analyses

Statistical models to investigate the impacts of the nominal explanatory variables dominant species identity (3 levels, with either *H.ulvae*, *H. diversicolor* or *M. balthica* dominant), organic enrichment/resource quality

(enrichment, 4 levels) and presence/absence of *C. crangon* (2 levels) on each of the depended variables ($^{f\text{-}SPI}L_{mean}$, $^{f\text{-}SPI}L_{max}$, SBR, [ΔBr^-], [NH_4-N], [NO_x-N] and [PO_4-P]) were developed. Treatments that did not include macrofauna were excluded from the statistical analysis, as the primary interest was to assess the effects of community performance under varying biotic and abiotic context rather than the effects of the presence versus absence of macrofauna. Initial linear models were visually assessed for normality (Q-Q-plot), heterogeneity of variance (residual vs. fitted values) and influential data points (cook's distance) (Zuur et al. 2007). When the graphical analysis indicated variance heterogeneity, generalised least squares (GLS) analysis was conducted to model the variance structure using the *varIdent* variance function for nominal explanatory variables (Pinheiro and Bates 2000). To find the optimal variance-covariate structure the GLS model including a variance-covariate structure was compared with the initial regression model using Akaike Information Criteria (AIC) and graphical assessment of the model residuals plotted versus the fitted values following restricted maximum likelihood estimation (REML). To find the optimal fixed effects structure a manual backward selection was applied using the likelihood ratio test obtained by maximum likelihood (ML) estimation (Pinheiro and Bates 2000). The minimal adequate models and model coefficient tables, indicating the relative performance of each treatment level relative to the relevelled baseline, are summarized in Appendix 2 statistical model summary. The coefficient tables are presented without correction for the alpha-error, as Bonferroni correction increases the beta error and tends to obscure multiple significant results if p-values are moderate and the statistical power is low (Moran 2003). All statistical analyses were conducted using the 'R' statistical and programming environment (R Core Team 2014) and the 'nlme' package (Pinheiro et al. 2014). All data are provided in Appendix 2 (Appendix 2, table A2.2).

3.4 Results

The results show independent effects of dominant species identity, algal enrichment and predator presence/absence on ecosystem processes (bioturbation and bioirrigation) only partly supporting hypothesis one and two. While there was a reduction in particle mixing depth in the presence of *C. crangon*, as expected (H1), this effect was not dependent on dominant species identity, indicating that the borrowing behaviour of the infaunal species did not influence the impact of the predator. There also was a reduction in particle mixing depth with algal enrichment, weakly depending on resource quality as expected (H2).

There were strong interactive effects between dominant species identity and algal enrichment on ecosystem functioning (water column nutrient concentration), however this effect was independent of resource quality, partly supporting hypothesis two. Algal enrichment dampened or enhanced the species-specific impacts on ecosystem functioning, depending on nutrient identity.

3.4.1 Effects of dominant species identity, abiotic and biotic context on ecosystem process

Mean particle mixing depth ($^{f\text{-}SPI}L_{mean}$) was influenced by the independent effects of dominant species identity, algal enrichment and predator presence/absence, whilst maximum particle mixing depth ($^{f\text{-}SPI}L_{max}$) was influenced only by dominant species identity (table 3.1). Sediment mixing in communities dominated by *H. ulvae* was shallower compared to communities dominated by *H.* and *M. balthica*. However, there was no difference in $^{f\text{-}SPI}L_{mean}$ between communities dominated by *H. diversicolor* or *M. balthica* (figure 3.1). The deepest maximum mixing depth was found for communities dominated by *H. diversicolor*, compared to *M. balthica* and *H. ulvae* (figure 3.2). Algal enrichment and predator presence reduced $^{f\text{-}SPI}L_{mean}$ by up to 0.21 cm (figure 3.1). In addition, the results show that there was a small, but significant difference in $^{f\text{-}SPI}L_{mean}$ in treatments enriched with *U. lactuca* and *F.* (figure 3.1, Appendix 2 Model S1). Surface boundary roughness (SBR) was significantly higher in the presence of *C. crangon* (table 3.1, figure 3.3).

Bioirrigation was influenced by the interactive effects of algal enrichment × predator presence/absence (table 3.1), but not by dominant species identity (L-ratio = 2.99, df = 2, p = 0.224). The results show that bioirrigation reduced in the presence of *C. crangon* in sediments enriched with *U. lactuca* (figure 3.4).

Table 3-1: Summary of statistical analyses for the effects of dominant species identity (DSI), predator presence/absence and algal enrichment. The test statistic indicates F value or L-ratio depending on the statistical model (see statistical model summary Appendix 2, model S1-S7)

response variable	explanatory variable	d.f.	test statistic	p
$^{f\text{-}SPI}L_{mean}$	DSI	2	17.13	**<0.001**
$^{f\text{-}SPI}L_{mean}$	enrichment	1	36.70	**<0.0001**
$^{f\text{-}SPI}L_{mean}$	predator	3	17.06	**<0.001**
$^{f\text{-}SPI}L_{max}$	DSI	2	18.87	**<0.0001**
SBR	predator	1	14.93	**0.005**
$\Delta[Br^-]$	predator-enrichment-interaction	3	9.65	**0.02**
$[NH_4\text{-}N]$	DSI	2	3.23	**0.04**
$[NO_x\text{-}N]$	DSI-enrichment-interaction	6	15.11	**0.02**
$[NO_x\text{-}N]$	predator	1	12.58	**<0.001**
$[PO_4\text{-}P]$	DSI-enrichment-interaction	6	22.17	**0.001**

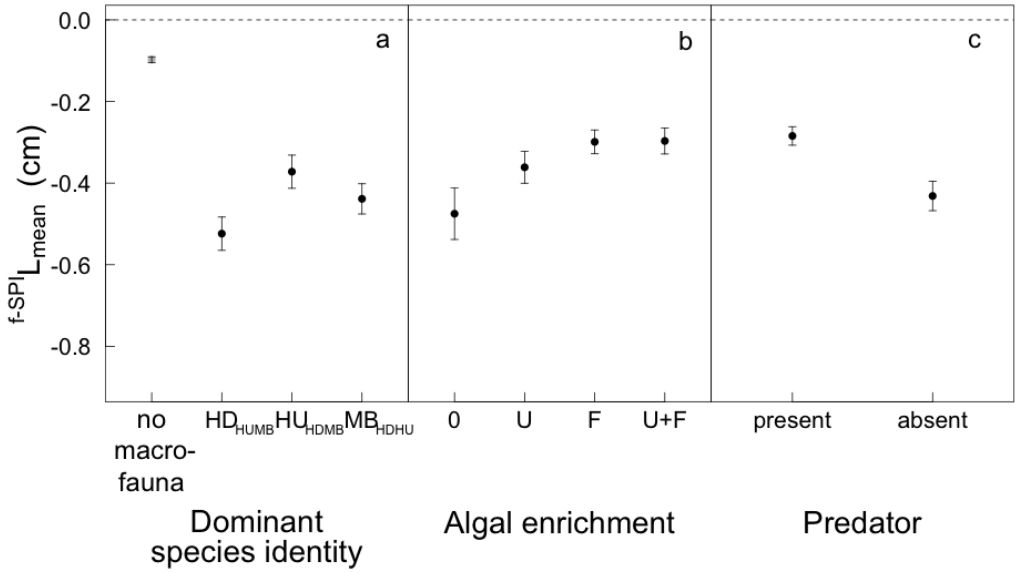


Figure 3.1: The independent effects of a) dominant species identity (HD = *Hediste diversicolor*, HU = *Hydorbia ulvae*, MB = *Macoma balthica*), b) algal enrichment (U = *Ulva lactuca*, F = *Fucus serratus*, U+F = 50:50 mixture of *Ulva lactuca* and *Fucus serratus*) and c) presence/absence of the predator *Crangon crangon* on the mean depth of sediment particle reworking ($^{f\text{-}SPI}L_{mean}$, cm, mean ± s.e., n = 4) calculated from the vertical distribution of luminophore tracers (Appendix 2 figure A2.1-A2.3). The dashed line indicates the sediment surface. In a) $^{f\text{-}SPI}L_{mean}$ in the control aquaria without macrofauna (grey) is shown for comparison, but not included in the statistical analysis or interpretation.

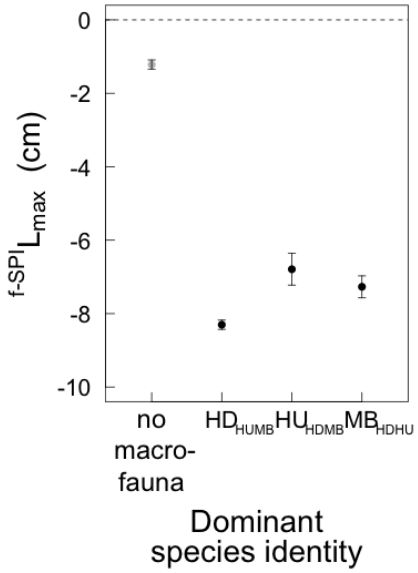


Figure 3.2: The effects of dominant species identity on the maximum depth of sediment particle reworking ($^{f\text{-}SPI}L_{mean}$, cm, mean ± s.e., n = 4) calculated from the vertical distribution of luminophore tracers (Appendix 2 figure A2.1-A2.3). The dashed line indicates the sediment surface. Observations in the absence of

macrofauna (grey) are shown for comparison, but not included in the statistical analysis or interpretation.

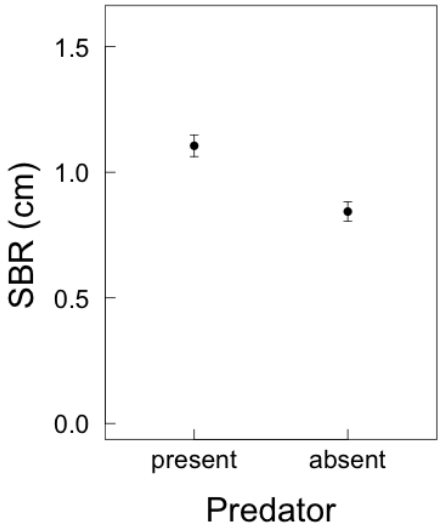


Figure 3.3: The effects of the presence/absence of the predator *Crangon crangon* on the surface boundary roughness (SBR, cm, mean ± s.e., n = 4).

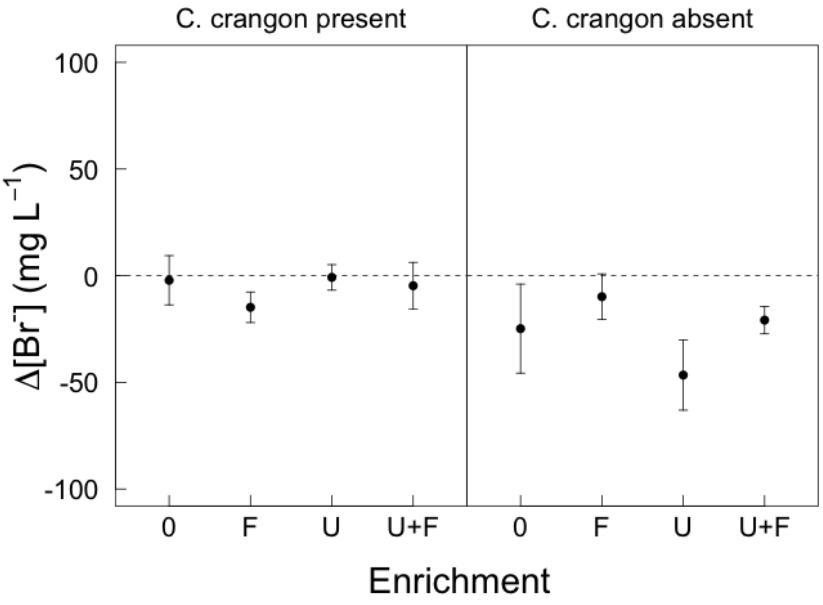


Figure 3.4: The interactive effects of algal enrichment (U = *Ulva lactuca*, F = *Fucus serratus*, U+F = a mixture of *Ulva lactuca* and *Fucus serratus*) and presence/absence of *Crangon crangon* on bioirrigation activity ($\Delta[Br^-]$ mg L^{-1}, mean ± s.e., n = 4). Negative values indicate increased activity.

3.4.2 Effects of dominant species identity, abiotic and biotic context on ecosystem functioning

The identity of the dominant species was important for all nutrients (table 3.1), but the mediating role of algal enrichment and predator presence varied with nutrient identity ([NH_4-N]: algal enrichment or predator presence, figure 3.5; [NO_x-N]: independent effect of *C. crangon* and interactive effect with algal enrichment, figure 3.6; [PO_4-P] interactive effect with algal enrichment, figure 3.7).

[NH_4-N] was mediated by the independent effect of dominant species identity. [NH_4-N] was highest (mean ± s.d.) in communities dominated by *H. diversicolor* (11.75 ± 4.27) compared to *H. ulvae* (9.11 ± 4.20), but there was no significant difference in [NH_4-N] between communities dominated by *H. diversicolor* and *M. balthica* or *H. ulvae* and *M. balthica* (figure 3.5, Appendix 2 Model S5).

[NO_x-N] and [PO_4-P] was mediated by the interactive effects of dominant species identity × algal enrichment. Whilst differences in [NO_x-N] between communities dominated by different species were dampened under enriched conditions per se, there was no difference in [NO_x-N] between the individual algal treatments (figure 3.6, Appendix 2 Model S6). In addition, the presence of *C. crangon* increased [NO_x-N] by 0.11 mg L^{-1} (figure 3.6). Differences in [PO_4-P] between dominant species identities only manifested under enriched conditions, where [PO_4-P] was increased by 0.27 ± 0.009 mg L^{-1} (figure 3.7, Appendix 2 Model S7).

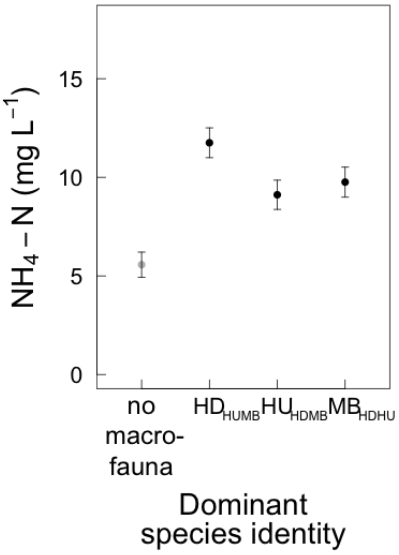
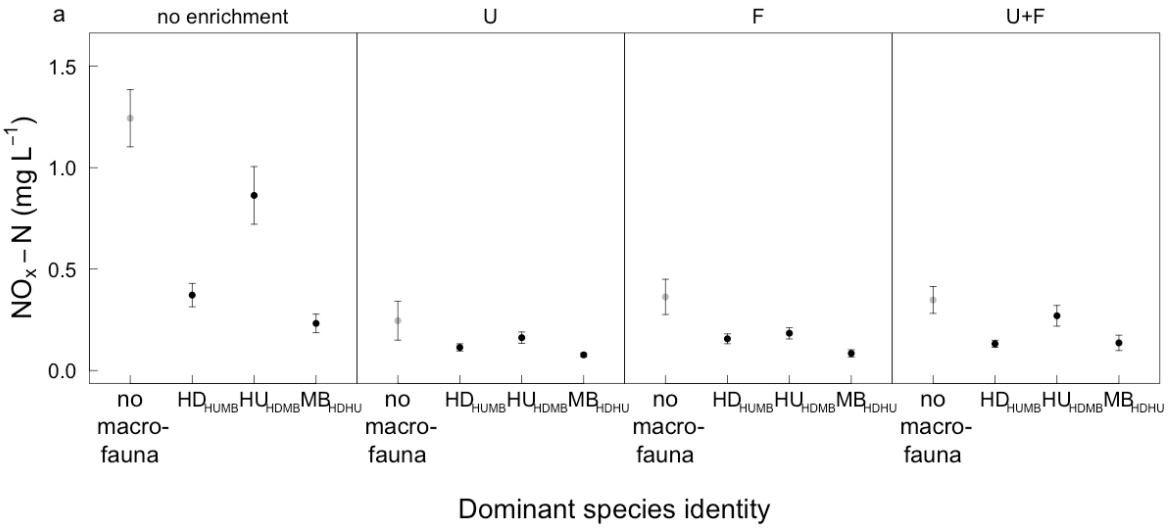


Figure 3.5: The effect of dominant species identity on water column NH_4-N concentration (mg L^{-1}, mean ± s.e., n = 4). Observations in the absence of macrofauna (grey) are shown for comparison, but not included in the statistical analysis or interpretation.



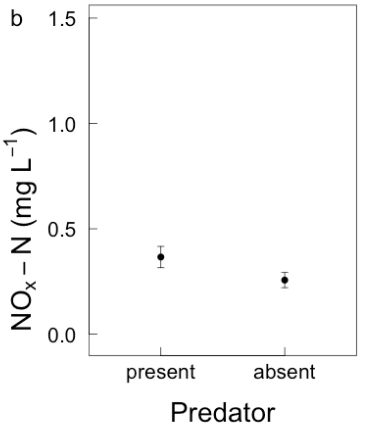


Figure 3.6: The effect of (a) dominant species identity and algal enrichment (U = *Ulva lactuca*, F = *Fucus serratus*, U+F = a mixture of *Ulva lactuca* and *Fucus serratus*) and (b) the absence/presence of the predator *Crangon crangon* on water column NO_X-N concentrations (mg L^{-1}, mean ± s.e., n = 4). For (a) nutrient concentrations observed in the absence of macrofauna (grey) are shown for comparison, but were not included in the statistical analyses.

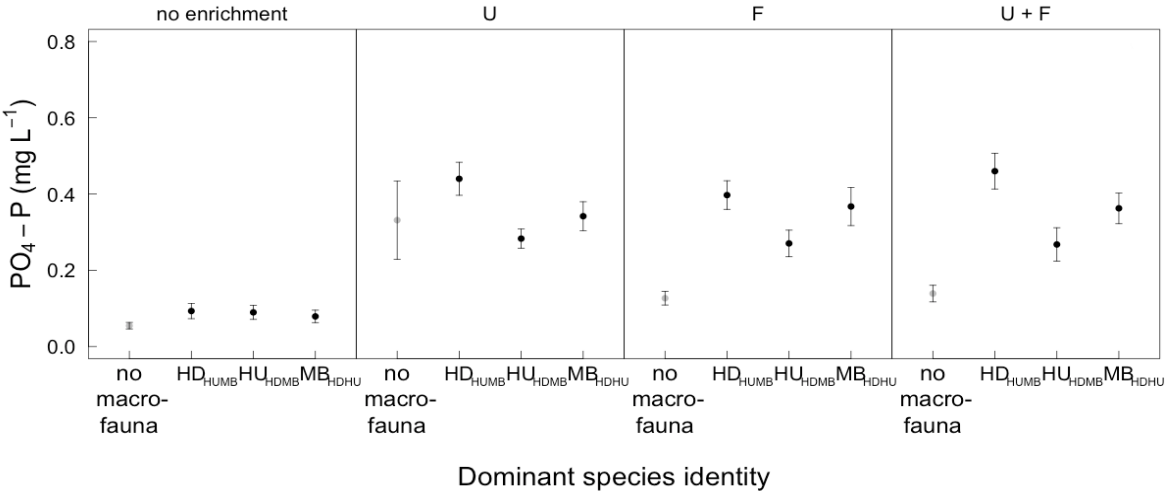


Figure 3.7: The effects of dominant species identity and algal enrichment (U = *Ulva lactuca*, F = *Fucus serratus*, U+F = a mixture of *Ulva lactuca* and *Fucus serratus*) on water column PO_4-P concentrations (mg L^{-1}, mean ± s.e., n = 4). Nutrient concentrations observed in the absence of macrofauna (grey) are shown for comparison, but were not included in the statistical analyses.

3.5 Discussion

In natural systems organisms continually respond to changing biotic and abiotic conditions by modifying their behaviour, activity and spatial distribution, which can alter the functional performance of organisms (Fitch and Crowe 2011, Godbold et al. 2011, Pratt et al. 2014, Chapter 3 & 4). The results have demonstrated that these effects can be either independent or interactive depending on the ecosystem properties under consideration. With the exception of surface boundary roughness and bioirrigation, levels of ecosystem process and functioning predominantly reflected the relative distribution of species and the identity of the dominant species. This supports general theory (Grime 1998) and empirical evidence (Winfree et al. 2015, Lohbeck et al. 2016, Wohlgemuth et al. 2016) that net community contribution to ecosystem properties is largely determined by the functional traits of the dominant species. For example, here communities dominated by *Hediste diversicolor* show increased particle mixing depths and PO_4-P release compared to communities dominated by *Macoma balthica* or *Hydrobia ulvae*, as it builds deeper borrow structures contributing to particle mixing and is a strong bioirrigator facilitating PO_4-P release from the sediment (Hale et al. 2014).

However, this is not necessarily always the case, as there was no difference between all communities dominated by functionally contrasting species (Hale et al. 2014). Negative interspecific interactions can modify the functional effect (Mermillod-Blondin et al. 2005, Li et al. 2013) or density (Clare et al. 2016) of the dominating species, reducing the disproportionate impact of the dominating species on aggregate community properties. This implies that rare species, which might not have a strong direct impact on ecosystem functioning because of their low relative biomass within the community and consequently weak functional contribution (Grime 1998, Dangles and Malmqvist 2004, Winfree et al. 2015), can influence ecosystem functioning by modulating the behaviour of the dominant species. Furthermore, the addition or loss of a predator can have direct cascading effects on species abundance and community structure, with significant implications for the structure of food webs (Estes et al. 2011), which may be further compounded by non-consumptive impacts on prey trait expression (Maire et al. 2010, Schaum et al. 2013). Specifically, the cue or physical presence of a predator can mediate prey activity and food uptake patterns (Maire et al. 2010, Premo and Tyler 2013, De

Smet et al. 2016), which can have implications for prey species fitness (Krause and Liesenjohann 2012) and species-environment interactions (Maire et al. 2010). In the present study, the presence of *Crangon crangon* reduced both mean particle mixing depth and bioirrigation, suggesting that, irrespective of the relative distribution of species, their overall activity was reduced. Furthermore, *C. crangon* had a direct enhancing effect on an ecosystem process related to sediment mixing (SBR), suggesting that *C. crangon* adds a unique contribution to community trait expression (strong surficial mixing activity, Pinn and Ansell 1993, Campos and Van Der Veer 2008). Overall, these findings demonstrate that the expression of functional traits within communities can be strongly modified by inter-specific interactions and affect the magnitude and variety of ecosystem processes and functions supported by communities (Mouillot et al. 2011, 2013, Gagic et al. 2015). The latter is particularly important, as it highlights the importance of enhanced biodiversity for the maintenance of multi-functional ecosystems (Lefcheck et al. 2015).

Furthermore, I demonstrate that environmental conditions have the potential to strongly mediate community contribution to ecosystem properties, but that the magnitude and direction of impact varies between the processes and functions considered. Whilst organic enrichment *per se* reduced the magnitude of overall community bioturbation performance irrespective of the relative distribution of species and the identity of the dominating species, resource quality only had a minor effect. Thus, there was a generic reduction of species mixing activities with increased resource availability, which may be a consequence of reduced foraging and food searching activities in response to plentiful food availability (Levinton and Kelaher 2004, Nogaro et al. 2007, Godbold et al. 2011) and/or a result of adverse sediment oxygen conditions related to organic enrichment (Long et al. 2008). Although no evidence was found of enhanced ecosystem properties in the presence of higher food quality, previous studies have shown that resource quality can have strong impacts on other ecosystem processes, such as decomposition (Godbold et al. 2009b, Fugère et al. 2012), or community composition (Bishop et al. 2010).

While faunal mediated impacts of the abiotic and biotic context on ecosystem processes showed generic alterations in magnitude, the degree of change in ecosystem functioning, here nutrient concentration, depended on the identity

of the dominant species. This is likely a consequence of differences in the context dependent adjustments of functional traits related to bioturbation and feeding activities (Dyson et al. 2007, Hale et al. 2014), which are known to modify the physicochemical conditions in sediments and consequently nutrient release and/or microbial driven nutrient cycling (Gilbertson et al. 2012). The results further suggest that the effects of abiotic context on differences in trait expression and subsequently ecosystem functioning also depend on the specific function investigated; Differences in NO_x-N concentration between dominant species identities are increased under non-enriched conditions, whereas the converse is the case for PO_4-P concentration. This suggests that the functioning-specific biogeochemical processes underpinning nutrient release (NO_x-N: i.a. macrofauna-microbial transformations, Laverock et al. 2011, Gilbertson et al. 2012; PO_4-P: i.a. macrofauna-redox conditions-Fe oxidation state, Hupfer and Lewandowski 2008, Chen et al. 2015) are differentially affected by context-dependent changes in species behaviour. The dampening effect of enriched conditions on NO_x-N concentrations between communities was largely driven by a stronger reduction in NO_x-N concentrations when *Hydrobia ulvae* was dominant compared to dominance of *Hediste diversicolor* or *Corophium volutator*. This is likely the consequence of the adjustments of *H. ulvae* in behavioural traits in response to resource supply (Orvain and Sauriau 2002). Such changes in behaviour mainly affect the upper sediment layers (Orvain and Sauriau 2002, Hale et al. 2014), where nitrogen is largely available in the form of NO_x-N (Laverock et al. 2011). This suggests that changes in the behaviour of *H. ulvae* may strongly affect NO_x-N release, even though the underlying biochemical processes cannot clearly be identified here. Under certain conditions, environmental controls may overwhelm biotic controls of ecosystem functioning (Baerlocher and Corkum 2003, Godbold and Solan 2009). Here, in non-enriched conditions, chemical processes that lead to PO_4-P precipitation and binding in the sediment may have blocked PO_4-P release from the sediment into the water column (Hupfer and Lewandowski 2008, Teal et al. 2013), decoupling faunal bioturbation behaviour from sediment PO_4-P release. However, under enriched conditions when PO_4-P release into the water column was largely enhanced, which may be related to faunal and/or context related changes in sediment redox conditions (Hupfer and Lewandowski 2008, Teal et al. 2013, Chen et al. 2016), the magnitude of PO_4-P release reflected the traits of the dominant species in

terms of their overall bioturbation/bioirrigation behaviour. Collectively, these findings indicate that the mechanistic basis for interactive effects of environmental context and the faunal mediation of ecosystem properties can be specific for the species and functions considered. This highlights the importance of the links between species traits that are important for the response and the effect of an organism in relation to its environment for aggregate community processes (Suding et al. 2008).

I conclude that the relative distribution of functional traits and how they are expressed across variable contexts in natural systems will need to be prioritised when considering the ecological consequences of altered biodiversity. The results support theory (Grime 1998) and further evidence (Winfree et al. 2015, Wohlgemuth et al. 2016) that individual dominating species can largely control community contributions to ecosystem properties. However, rare or less abundant species can contribute unique aspects of functioning (Mouillot et al. 2013) or modify trait expression (Li et al. 2013) or density (Clare et al. 2016) of dominant species and thereby indirectly affect ecosystem functioning. Furthermore, the results suggest, that we also need to account for how predicted changes in the environmental conditions affect ecosystem properties directly (Godbold and Solan 2009), and how species will respond and adapt trait expression to new local conditions in their habitats (Suding et al. 2008, Godbold et al. 2011, Orwin et al. 2015) and within food webs (O'Connor and Donohue 2013), as this can fundamentally change species functional roles and the mechanisms underpinning biodiversity and ecosystem functioning relations. Ultimately, if we are to manage ecosystems in a manner to sustain ecosystem functionality and ensure human well being for future generations (Rands et al. 2010, Mace et al. 2014), it is necessary to integrate the interactive effects of changes in the environmental context, the redistribution of species within communities and associated changes in net community trait expression on ecosystem properties into biodiversity and ecosystem functioning relations.

3.6 Acknowledgements

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Chapter 4: Dynamic environmental variation and the rearrangement of species dominance independently modify ecosystem process and functioning

4.1 Abstract

Environmental variability is an inherent and dynamic feature of natural systems that can affect the distribution of species and amend the nature of species-environment interactions that are important in mediating ecosystem functioning. Yet, dynamic abiotic conditions and changes in species dominance patterns have received little attention in experiments that examine the relationships between biodiversity and ecosystem function, limiting the ability to scale findings to natural ecosystems. Here I specifically incorporate environmental dynamics (tidal regimes) alongside community changes in an experimental study, to evaluate the impacts of environmental variability on aggregate community contributions to ecosystem process (particle reworking and bioirrigation = bioturbation) and functioning (nutrient cycling). The results show that environmental dynamics do not necessarily alter the effects of community changes on ecosystem properties, but can affect the magnitude of community performance. Hence, controlling environmental dynamics may not largely hamper the generality of findings in experimental studies, although the present study cannot account for effects of time or disruptive stochastic events that may further modify community specific effects on ecosystem properties.

4.2 Introduction

Current knowledge on the role and importance of biodiversity for the mediation of ecosystem process and function, is largely based on experimental studies that strictly control environmental variability (Gamfeldt et al. 2015), or if environmental variables are included, then often as fixed factor levels under constant experimental conditions (e.g. fixed levels of temperature and CO_2, Hicks et al. 2011; nutrient enrichment vs. no enrichment, Fitch and Crowe 2011). Yet, natural systems are characterised by continuous environmental dynamics throughout regular cycles (e.g. diurnal, lunar or seasonal cycles), stochastic events (e.g. heat waves and cold spells, storms Meehl et al. 2007) and, superimposed on such fluctuations, continuous directional changes (e.g. global warming, ocean acidification, sea level rise, Meehl et al. 2007). It is known that natural dynamics can largely control biological activities (Palmer 2002, Naylor 2010), which in turn leads to temporal variation in organism-environment interactions across daily (Last et al. 2009, de Backer et al. 2010, Bertolo et al. 2011, Lindqvist et al. 2013) or seasonal (Esselink and Zwarts 1989, Godbold and Solan 2013, Baldock et al. 2016) cycles. Furthermore, superimposed directional forcings may additionally modify organism environment interactions for future scenarios of global change (Ouellette et al. 2004, Bulling et al. 2010, O'Connor and Donohue 2013). Importantly, as organism environment interactions also determine the effect of an organism on its environment, variation in such will affect the faunal mediation of ecosystem processes and functions (Dyson et al. 2007, Needham et al. 2011, Sassa et al. 2011, Törnroos et al. 2015). However, as variability in species trait expression is not necessarily directly proportionate to the source of environmental variation (Last et al. 2009, de Backer et al. 2010) it is unclear how environmental dynamics will affect aggregated community contributions to ecosystem properties.

A second important consequence of environmental dynamics is the alteration of species abundance distributions and community structure across varying spatial and temporal scales (Van Der Wal et al. 2008, Kraan et al. 2015, Morley et al. 2016). On local scales, environmental dynamics can lead to temporally shifting mosaics of environmental variables, such as temperature (Baldock et al. 2016), microclimatic conditions (Karr and Freemark 1983), (Malard et al. 2002, Levinton and Kelaher 2004) or sediment characteristics (Paterson and

Black 1999) and organisms can move between patches in response to adverse or favourable conditions (Levinton and Kelaher 2004, Baldock et al. 2016). This leads to spatio-temporal variation in local species density distributions and dominance patterns (Hewitt et al. 2008, Godbold et al. 2011, Kraan et al. 2015, Morley et al. 2016). On larger scales alterations in climatic conditions can affect species geographical distribution ranges (Chen et al. 2011, Sunday et al. 2012) and shifts in the timing of lifecycle events (Brander 2010, Bellard et al. 2012), which can cause disruptions of biological interactions (Post and Forchhammer 2008) and affect community composition and dominance patterns (Walker et al. 2006, Williams and Jackson 2007, Zelikova et al. 2014). While there is evidence that both, small and large-scale changes in community structure, affect community mediation of ecosystem properties (Hewitt et al. 2008, Rodil et al. 2011, Godbold et al. 2011, Pratt et al. 2014, Wohlgemuth et al. 2016), we know little about the interactive effects of dynamic environmental variability and community change on aggregate community contribution to ecosystem properties, as studies have rarely integrated directional community changes and dynamic environmental conditions simultaneously (but see e.g. Rodil et al. 2011, Pratt et al. 2014).

Here I experimentally explore the interactive effects of dynamic environmental conditions (tidal regimes) and rearrangements of dominance patterns within communities on ecosystem process (particle reworking and bioirrigation = bioturbation) and functioning (nutrient cycling). I investigate the impacts of different tidal regimes with varying lengths of tidal (aerial) exposure to represent present day (6 h) and a possible future scenario of inundation (9 h) in line with current sea-level rise projections (Rahmstorf 2007). Coastal systems are highly vulnerable to impacts of climate change (Doney et al. 2012) and future levels of projected sea-level rise are expected to cause extensive areas of intertidal habitats to be lost due to a reduction of the intertidal zone (coastal squeeze), as expansion of coastal habitats inland of the high water mark is often impeded due to human coastal defence constructions (Pontee 2013). I hypothesise (H1) that increased emersion periods within the tidal cycles will lead to reduced aggregate community effects on sediment particle reworking activity, burrow ventilation behaviour and the associated generation of nutrients, as intertidal organisms are know to reduce their general activity

during low tide (Palmer 2000, de Backer et al. 2010). Furthermore (H2), as the study species *Hediste diversicolor, Corophium volutator* and *Hydrobia ulvae* occupy different layers of the sediment and have different strategies of coping with dry conditions during emersion (Barns 2006, Last et al. 2009, de Backer et al. 2010), I expect the relative impact of tidal regime to varying with changes in relative community compositions. If the expectations are met, this would support the call to integrate more realism, specifically environmental dynamics, in biodiversity and ecosystem functioning research (Hillebrand and Matthiessen 2009), as the real world ecosystem consequences of altered biodiversity might differ from those observed in overly simplified mesocosm studies (Stachowicz et al. 2008b, Clare et al. 2016).

4.3 Methods

4.3.1 Experimental design and setup

Surficial sediment (less than 3 cm depth) and individuals of the mud snail *Hydorbia ulvae* were collected from the Hamble Estuary (mean particle size ± s.d.: 3.87 ± 0.08 µm, TOC mean ± s.d.: 9.67 ± 0.95 %), United Kingdom (50°52'22.7"N 1°18'49.4"W). Individuals of the mud shrimp *Corophium volutator* and the polychaete *Hediste diversicolor* were collected from Langston Harbour, United Kingdom, (50°49'57.4"N 0°58'37.4"W and 50°50'45.9"N 1°00'05.1"W). *Hydrobia ulvae* and *Corophium volutator* were sieved size selectively (>500 µm) from the surface sediment and *Hediste diversicolor* individuals of similar body size were collected by hand. The sediment was sieved (500 µm mesh) to remove macrofauna, allowed to settle for 48 h (to retain the fine fraction, <63 µm) and homogenised to equalize the distribution between mesocosms. Treatments were evenly split in two successive experimental runs because of limited space in the experimental system and organisms and sediment were collected separately in June and July 2015 for each experimental run respectively.

Aquaria consisted of transparent square acrylic cores (12x12 cm, 35 cm high), filled to 10 cm with sediment and 2.8 l of overlying seawater, were maintained in temperature controlled room at 18 °C and continually aerated. Before the experimental phase organisms were allowed to acclimate to the laboratory conditions for 7 days, during which they were fed every three days (day 1, day 4, day 7). The natural tidal times during collection of the organisms and the tidal times in the aquaria were synchronized to minimize offset of internal rhythmics (Last et al. 2009, de Backer et al. 2010, Vieira et al. 2010). After the acclimation phase the water was changed to remove excess nutrients associated with assembly.

Replicate (n = 4) macrofaunal communities with alternate dominance compositions were assembled by altering species biomass distributions. Specifically, communities with evenly distributed biomass ($J^{1.00}$, Pielou's evenness index, Pielou 1966) and with each species being dominant in biomass, while keeping the two remaining species constant ($J^{0.64}$, Pielou's

evenness index, Pielou 1966, Appendix 3, table A3.1), were established. As nutrient cycling is primarily a microbial process, control aquaria containing no macrofauna (n = 4) were included to distinguish the extent of macrofaunal mediation of nutrient cycling. To test effects of varying tidal regimes, each community was maintained across three simulated tidal regimes (1 - no tides with constant immersion, 2 - 6:6 hour circle with 6 hours and 12 min immersion and emersion, 3 - 9:3 hour circle with 9 hours and 18 min of immersion and 3 hours and 6 min of emersion) leading to a total of 60 experimental aquaria (4 communities × 3 tidal regimes × 4 replicates + 12 controls without macrofauna). The tidal regimes included a daily phase shift of approximately 48 minutes simulating the natural shift of the tidal phases in relation to day and night times. Light conditions were kept constant with a 12:12 hour light/dark cycle. As organism activity can be modified by tidal and light regimes (Lindqvist et al. 2013), the experiment was run for 15 days to achieve a full phase shift of the tidal regimes in relation to the light conditions (figure 4.1 & 4.2).

To create the tidal regimes in the aquaria custom made peristaltic pump units (Williamson Manufacturing Company Ltd, West Sussex, United Kingdom) were used. Each unit consisted of 10 peristaltic pumps (200-SMB series, Williamson Manufacturing Company Ltd, UK) with adjustable pump speed and direction. To simulate the tides sine-wave functions were calculated (Appendix 3 table A3.2) representing the respective tidal regimes. The rate of inflow and outflow was constant (6:6, 15.05 ml min^{-1}; 9:3, 10.03 ml min^{-1}) and immersion periods were separated by a period of emersion with no flow (6:6, 6 hours 12 min; 9:3, 3 hours 6 min, figure 4.1 & 4.2). One corner of each aquarium was separated by a perspex inset which included a mesh (315 µm) to allow the exchange of water without sediment disturbance (Figure 4.3). The water was pumped out below the level of the sediment surface and pumped back and forth into independent empty aerated storage aquaria for each experimental unit.

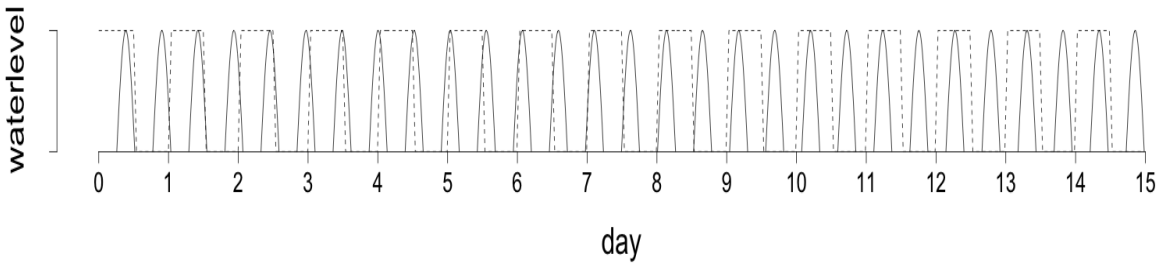

Figure 4.1: Tidal wave function for the 6:6 tidal regime (6 hours 12 minutes immersion followed by 6 hours 12 min emersion). The solid line shows the water level above the sediment surface and the dotted line shows the 12h:12h light/dark circle. Flow rates were continuous throughout the tidal simulations and only changed in direction.

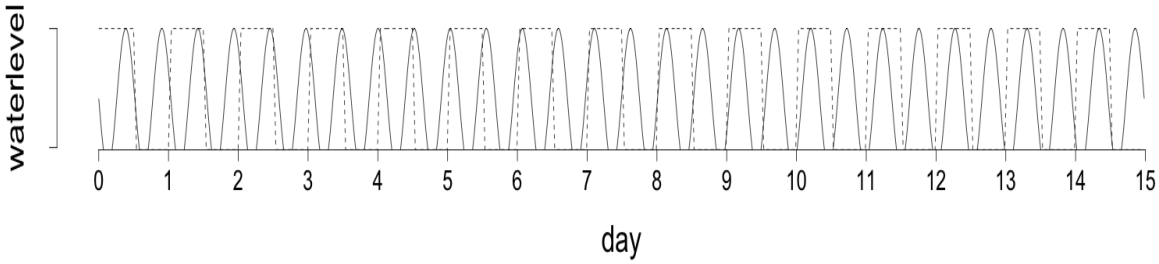

Figure 4.2: Tidal wave function for the 9:3 tidal regime (9 hours 18 minutes immersion followed by 3 hours 6 min emersion). The solid line shows the water level above the sediment surface and the dotted line shows the 12h:12h light/dark circle. Flow rates were continuous throughout the tidal simulations and only changed in direction.

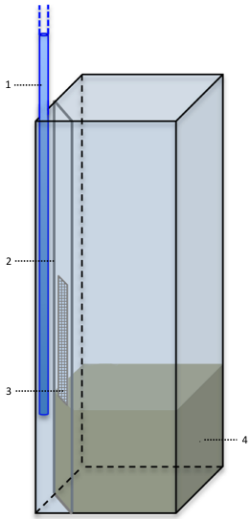

Figure 4.3: Schematic of experimental aquaria. (1) silicon tubing leading to pump units, (2) perspex inset separating one corner with (3) 315 μm mesh to allow water exchange without sediment disruption, (4) sediment

4.3.2 Quantification of ecosystem process and functioning

Faunal mediated sediment particle reworking was estimated non-invasively using a sediment profile imaging camera (Canon EOS set to 15 s exposure, aperture f5.6 and ISO 400; 3888 x 2592 pixels, effective resolution at aquarium side = 193 x 193 µm per pixel), optically modified to allow preferential imaging of fluorescently labelled particulate tracers (luminophores, red colour, size class less than 125 µm; Brianclegg Ltd., UK) under UV light (f-SPI, Solan et al. 2004), that were introduced on the first day of the experiment (60g aquarium^{-1}). Vertical luminophore particle re-distribution was determined from stitched composite images (RGB colour, JPEG compression, GNU Image Manipulation Program, Version 2.8.4, http://www.gimp.org/, Kimball, S., Mattis, P., GIMP (1995), Date of access 01/08/2015) of all four sides of each aquarium obtained in a UV illuminated dark room, using a custom-made semi-automated macro that runs within ImageJ (Version 1.47), a java-based public domain program developed at the US National Institutes of Health (http://rsb.info.nih.gov/ij/index.html, Rasband, W., ImageJ., (1997), Date of access 01/08/2015). From these data, following Hale et al. (2014), the mean ($^{f\text{-}SPI}L_{mean}$, time dependent indication of mixing), median ($^{f\text{-}SPI}L_{median}$, typical short-term depth of mixing) and maximum ($^{f\text{-}SPI}L_{max}$, maximum extent of mixing over the long-term) mixed depth of particle redistribution were calculated. To provide an indication of surficial activity, the vertical deviation of the sediment-water interface was measured (upper – lower limit; surface boundary roughness, SBR).

After imaging of the cores the tidal cycle was stopped at high tide. Nutrient concentrations ([NH_4-N], [NO_x-N], [PO_4-P]) were quantified from pre-filtered (Fisherbrand, nylon 0.45 µm, ⌀ 25mm) water samples (10 ml, taken centrally 5 cm above the sediment-water interface) using a flow injection auto-analyser (FIAstar 5010 series, Foss-Tecator) with an artificial seawater carrier solution

To estimate bioirrigation the redistribution of the inert tracer sodium bromide was measured. To achieve a concentration of ~10 mM 2.88 g of sodium bromide were added to each core. Water samples of 5 ml volume were taken from the middle of the core approximately 5 cm over the sediment surface directly after bromide addition and after a period of 4 hours. During this time the aeration was stopped to prevent additional water movement that is not

caused by bioirrigation activity. The samples were filtered (Fisherbrand, QL100) and bromide concentrations were determined using a flow injection auto-analyser (FIAstar 5000 with a Tecator 5027 auto sampler, Foss). The change in concentration over a 4-hour period ($\Delta[Br^-]$) was calculated (negative values indicate bioirrigation activity, Forster et al. 1999).

Statistical analyses

Linear models for each of the measured response variables (SBR, $^{f\text{-}SPI}L_{mean,}$ $^{f\text{-}SPI}L_{median}$, $^{f\text{-}SPI}L_{max}$, $\Delta[Br^-]$, $[NH_4\text{-}N]$, $[NO_X\text{-}N]$, $[PO_4\text{-}P]$) with community composition and tidal regime as explanatory variables were developed. To account for variance between the two runs, experimental run was included as a random factor in the initial statistical model and Akaike Information Criteria (AIC) and residual plots between the initial model and a reduced model without "run" as a random effect were compared, following restricted maximum likelihood (REML) estimation (Pinheiro and Bates 2000). Following this procedure, the linear models were assessed for normality (Q-Q-plot), heterogeneity of variance (plotted residual vs. fitted values) and influential data points (cook's distance). When the graphical analysis indicated variance heterogeneity, the residual spread with individual explanatory variables was incorporated into the statistical model using generalized least squares (GLS) estimation. To find the optimal variance-covariate term the respective GLS model was compared to the initial regression model using the Akaike Information Criteria (AIC) and graphical assessment of the model residuals plotted versus the fitted values following restricted maximum likelihood (REML) estimation (Pinheiro and Bates 2000). To find the optimal fixed structure a manual backward selection using the likelihood ratio test obtained by maximum likelihood (ML) estimation was applied (Pinheiro and Bates 2000). For all statistical analyses the control treatments that did not include any macrofauna were excluded, as the interest was in differences between communities rather than the effect of the presence of macrofauna. All statistical analyses were performed using the 'R' statistical and programming environment (R Core Team 2014) and the 'nlme' package (Pinheiro et al. 2014). All data used in the statistical analyses are provided in Appendix 3 (table A3.3).

4.4 Results

The simulation of tides within the mesocosms reduced surface boundary roughness, median mixing depth, bioirrigation activity and NH_4-N concentrations. However, the results only partly support hypothesis one, as not all response variables were affected by tidal regime and there was no difference when emersion period was further increased from ~6 hours to ~9 hours. The analyses did not show any interactive effects between tidal regime and community composition, refuting hypothesis two. However, there were independent effects of community composition on most measures of ecosystem processes and functioning, except surface boundary roughness and PO_4-P concentrations.

4.4.1 Effects of community dominance pattern and tidal regime on ecosystem process

Community composition had a significant effect on mean, median and maximum particle mixing depth and bioirrigation activity (table 4.1). Thereby, for mean and median mixing depth, communities dominated by *H. diversicolor* or *H. ulvae* showed increased particle mixing depths compared to communities dominated by *C. volutator* or the even mixture, while there was no difference between communities dominated by *H. diversicolor* and communities dominated by *H. ulvae* (figure 4.4, Appendix 3 Model S1 & S2). For maximum particle depth communities dominated by *H. diversicolor* showed larger depth than communities dominated by *C. volutator*, while there was no difference between any other community composition (figure 4.4, Appendix 3 Model S3). Bioirrigation activity was increased in communities dominated by *H. diversicolor* and *H. ulvae* compared to treatments dominated by *C. volutator* and the even mixture of species (figure 4.4, Appendix 3 Model S5, negative values indicate increased bioirrigation activity).

Tidal regime had a significant effect on surface boundary roughness, median particle mixing depth and bioirrigation activity (table 4.1). All three processes were increased if no tides were simulated in the cores while there was no difference between tidal regimes (figure 4.4, Appendix 3 Model S4 and S5).

Table 4-1: Summary of statistical analyses for the effects of community dominance pattern (CD) and tidal regime (TR). The test statistic indicates F value or L-ratio depending on the statistical model (see statistical model summary Appendix 3, model S1-S8)

response variable	explanatory variable	d.f.	test statistic	p
${}^{f\text{-}SPI}L_{mean}$	CD	3	22.12	**0.0001**
${}^{f\text{-}SPI}L_{median}$	CD	3	33.11	**0.0001**
${}^{f\text{-}SPI}L_{median}$	TR	2	30.38	**<0.001**
${}^{f\text{-}SPI}L_{max}$	CD	3	10.78	**0.04**
SBR	TR	2	22.21	**<0.0001**
$\Delta[Br^-]$	CD	3	19.48	**<0.001**
$\Delta[Br^-]$	TR	2	13.87	**<0.001**
$[NH_4\text{-}N]$	CD	3	7.75	**<0.001**
$[NH_4\text{-}N]$	TR	2	14.72	**<0.0001**
$[NO_x\text{-}N]$	CD	3	33.25	**<0.0001**

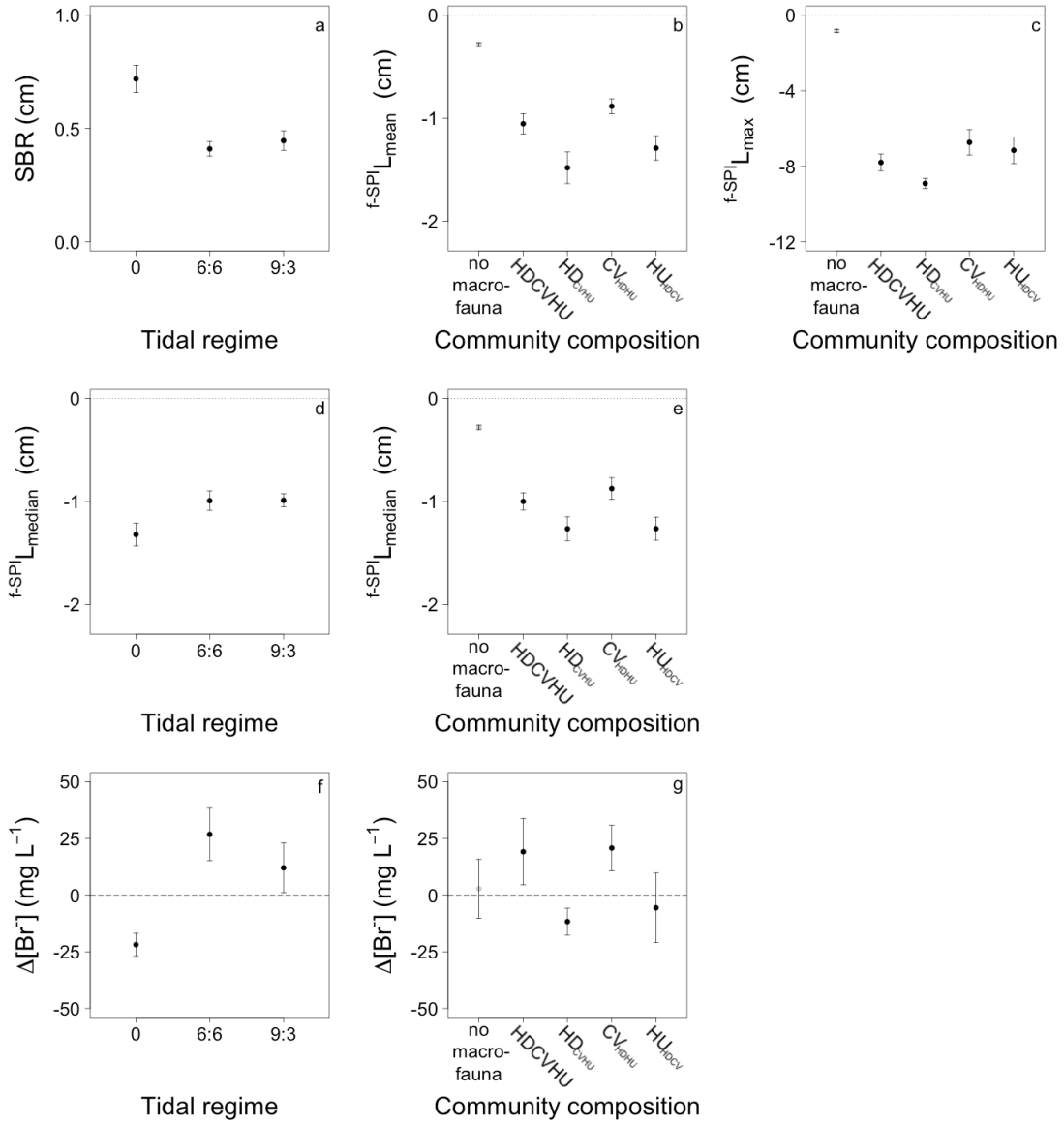

Figure 4.4: Effects of community composition and tidal regime on ecosystem processes. (a) Surface boundary roughness (mean ± s.e.) (b) mean particle mixing depth (mean ± s.e.) (c) maximum particle mixing depth (mean ± s.e.) (d, e) median particle mixing depth (mean ± s.e.) (f, g) bioirrigation activity (mean ± s.e., negative values below the dashed line, that represents no net activity, indicate increased bioirrigation activity). The dotted line indicates the sediment surface. For tidal regime 0 indicates constant immersion, 6:6, 6 hours 12 min immersion and emersion and 9:3, 9 hours 18 min immersion followed by 3 hours 6 min emersion. For community composition the size of the species abbreviations indicate relative biomass (Appendix 3 table A3.1). HD = *Hediste diversicolor*, CV = *Corophium volutator*, HU = *Hydrobia ulvae*. Controls without macrofauna (grey) were excluded form the statistical analyses and are presented for information only.

4.4.2 Effects of community dominance pattern and tidal regime on ecosystem functioning

[NH_4-N] and [NO_X-N] differed between community composition (table 4.1). Treatments dominated by *C. volutator* and the even mixture of species showed increased concentrations compared to treatments dominated by *H. diversicolor* and *H. ulvae* (figure 4.5, Appendix 3 Model S6 and S7).

[NH_4-N] were additionally affected by tidal regime (table 4.1) and concentrations were higher under continuous immersion, while there was no difference between both tidal simulation regimes (figure 4.5, Appendix 3 Model S6). There was no effect of either community composition or tidal regime on [PO4-P] (Appendix 3 Model S8).

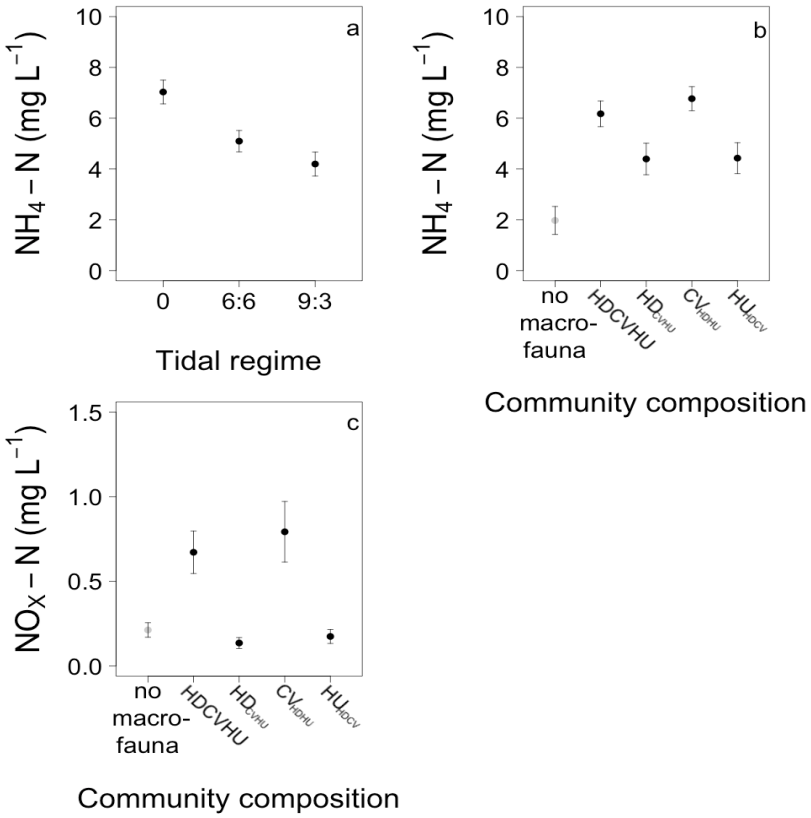

Figure 4.5: Effects of community composition and tidal regime on nutrient concentrations. (a, b) NH_4-N concentrations (mean ± s.e.) (c) NO_X-N concentrations (mean ± s.e.). For tidal regime 0 indicates constant immersion, 6:6, 6 hours 12 min immersion and emersion and 9:3, 9 hours 18 min immersion followed by 3 hours 6 min emersion. For community composition the size of the species abbreviations indicate relative biomass (Appendix 3 table A3.1). HD = *Hediste diversicolor*, CV = *Corophium volutator*, HU = *Hydrobia ulvae*. Controls without macrofauna (grey) were excluded form the statistical analyses and are presented for information only.

4.5 Discussion

While the results reaffirm previous work demonstrating the importance of species identity effects alongside changes in the relative abundance/biomass and dominance orders of species within communities for aggregate community contribution to ecosystem properties (Orwin et al. 2014, Winfree et al. 2015, Clare et al. 2016, Wohlgemuth et al. 2016), I demonstrate that regular environmental dynamics can affect the magnitude of the faunal mediation of ecosystem process and functions. Importantly, however, there was no interactive effect between varying community arrangements and tidal regimes, indicating that the relation between community change and community mediation of ecosystem properties does not change in the face of regular environmental dynamics. This may be caused by the strong control of biological activity by tidal rhythms in intertidal systems (Palmer 2000). As infaunal species tend to respond similarly to tidal rhythms by largely reducing most activities during emersion (Barnes 2006, Last et al. 2009, de Backer et al. 2010, Vieira et al. 2010), the negative impacts of tidal regimes on aggregate community contribution to ecosystem processes are independent of species distributions within communities. However, the relation between diversity and/or community arrangements and ecosystem functioning may change if regular environmental fluctuations are disrupted by stochastic environmental events (e.g. heat waves, droughts or floods, storms; Meehl et al. 2007) that cause stressful environmental conditions beyond the regular fluctuations that species are adapted or acclimated to. In this case there is evidence that environmental stress alters species interactions (Mulder et al. 2001, Fugère et al. 2012) and diversity effects on ecosystem functioning (Wittebolle et al. 2009, Steudel et al. 2012), if species differ in their response towards stressors (Zhang and Zhang 2006, Wittebolle et al. 2009).

It is important to consider these findings in the context of sea level rise and the consequential squeeze of many intertidal areas between rising water levels and coastal defences (Pontee 2013). The results demonstrate that changes in immersion/emersion periods do not necessarily change the functional impact of communities in intertidal systems. Importantly, however, there is evidence that alterations of other physical and biotic properties of intertidal habitats that co-occur with changes in immersion/emersion in response to sea level rise

(e.g. sediment characteristics, morphodynamics, see Pethick 1993, Fujii & Raffaelli 2008) may affect aggregate community processes and contributions to ecosystem properties (Yamanaka et al. 2013). Nevertheless, the results indicate that directional changes in the magnitude of environmental drivers do not necessarily always affect faunal mediation of ecosystem processes and functioning. This is, however, likely only the case if changes in environmental conditions do not exceed certain thresholds that might trigger organism responses (Brun et al. 2008), or exceed the limit of species to adjust to the environmental conditions, which may otherwise change local species distributions (Petes et al. 2007), restrict species distribution ranges (Tomanek 2002, Cheung et al. 2009) or even contribute to regime shifts (Mollmann et al. 2015), with knock-on effects on ecosystem functioning (Rodil et al. 2011, Pratt et al. 2014, Wohlgemuth et al. 2016). Hence, gradual directional environmental changes may have stronger impacts in systems where organisms live close to their physiological limits than in communities that experience large environmental fluctuations across diurnal, seasonal or other cycles. Furthermore, the results indicate, that while adjustments in cyclic natural variations that are already present in a system (here varying tidal regimes) may not alter faunal mediation of ecosystem properties, the introduction of new dynamics or conditions (here tidal dynamics vs. constant immersion) may change the magnitude of community performance. Hence, the functional consequences of future global change, that is likely going to lead to novel climatic conditions that species and communities do not experience presently (Williams and Jackson 2007), may have strong impacts on the faunal mediation of ecosystem properties.

In conclusion, the results demonstrate that cyclic natural variations and directional changes in such, do not necessarily alter the relation between community arrangements and ecosystem process or functioning, although the present study cannot account for long term processes that may alter community response to environmental variability (Stachowicz et al. 2008b, Godbold and Solan 2013, Clare et al. 2016). As only the magnitude of ecosystem properties was affected by environmental dynamics, the relation between altered communities and ecosystem functioning identified in mesocosm experiments that lack such dynamic may still be relevant in natural systems. However, in the context of global change that is going to lead to

increased frequencies of extreme events (Meehl et al. 2007) and novel climatic conditions (Williams and Jackson 2007) community responses and buffering effects of diversity (Yachi and Loreau 1999, Wittebolle et al. 2009) towards such disruptions, rather than towards gradual directional changes in cyclic environmental fluctuations, may additionally alter community performances. Furthermore, the present findings alongside others (Rodil et al. 2011, Godbold et al. 2011, Pratt et al. 2014, Wohlgemuth et al. 2016) also suggest that changes in community structures, which occur alongside directional environmental changes (Hewitt et al. 2008, Kraan et al. 2015, Morley et al. 2016), have the potential to additionally modify community contribution to ecosystem properties.

4.6 Acknowledgements

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Chapter 5: Species contributions to ecosystem functioning can be population dependent and modified by biotic and abiotic factors

Contents of this chapter have been submitted to Proceedings of the Royal Society B

5.1 Abstract

There is unequivocal evidence that altered biodiversity, through changes in the expression and distribution of functional traits, can have large impacts on ecosystem properties. However, trait-based summaries of how organisms affect ecosystem properties often assume that traits are constant within and among populations, and that species contributions to ecosystem functioning are not overly affected by the presence of other species or variations in abiotic conditions. Here, the validity of these assumptions is evaluated using an experiment in which three geographically distinct populations of intertidal sediment-dwelling invertebrates are reciprocally substituted. The results show that the mediation of macronutrient generation by these species can vary between different populations and show that interspecific interactions and/or changes in abiotic conditions can further modify functionally important aspects of the behaviour of individuals within a population. The results demonstrate the importance of knowing how, when and why traits are expressed, and suggest that these dimensions of species functionality are not sufficiently well-constrained in order to accurately project the functional consequences of change. Information about the ecological role of key species and assumptions about the form of species-environment interactions needs urgent refinement.

5.2 Introduction

A wealth of empirical studies over the past two decades have provided unequivocal evidence that altering biodiversity leads to concomitant changes in ecosystem functioning that, ultimately, can affect the benefits that humans derive from ecological systems (Cardinale et al. 2012). Indeed, recent consensus emphasizes the functional importance of individual species, rather than species diversity, in mediating ecosystem processes that are important in maintaining efficient and productive ecosystems (Díaz et al. 2006, Mokany et al. 2008, Gagic et al. 2015). This has revitalised interest in applying trait-based indices of functional diversity, in both terrestrial (Lavorel et al. 2007, Díaz et al. 2007, Mace et al. 2014) and marine ecosystems (Gibson et al. 2001, Petchey and Gaston 2006, Mace et al. 2014), in order to provide a mechanistic understanding of the biotic control of ecosystem functioning and/or service delivery. Whilst most of these approaches use non-phylogenetic biological attributes (i.e. physiological, morphological or phenological characteristics, Violle et al. 2007) to focus on how species mediate ecosystem functioning, they typically disregard variation in trait values (exceptions exist, Cianciaruso et al. 2009, Griffiths et al. 2016) and, instead, focus on mean performance. In doing so, the contributory roles of species are assumed to be well-defined and, therefore, sufficient to adequately characterise the functional importance of species (Violle et al. 2012), yet these perceptions are seldom explored empirically or objectively validated (Hale et al. 2014, Murray et al. 2014). Nonetheless, these functional summaries are increasingly being adopted within predictive tools that incorporate community dynamics to project ecosystem responses to environmental change for the purposes of ecosystem management and planning (Suding et al. 2008, Laughlin 2014, Mace et al. 2014).

As the allocation of species to a functional group and/or assignment of functionally important traits is frequently based on single mean trait values per species (Villéger et al. 2008, De Bello et al. 2011), assessments of species contributions to functioning often underestimate the importance of intraspecific trait variation (but see Laughlin et al. 2012) and assume that an organism's functional effects and responses will be the same within and between populations over time (Violle et al. 2012, McCain et al. 2016). However, the expression of functional traits within species is unlikely to be

homogenously distributed, as individuals behave differently depending on the biotic and/or environmental conditions they experience (Albert et al. 2010a, Clark et al. 2011, Godbold et al. 2011, Langenheder et al. 2012, Godbold and Solan 2013). Such context-dependent changes in behaviour, including responses to temperature (Ouellette et al. 2004), hydrodynamic regimes (Törnroos et al. 2015), resource availability and quality (Hodge 2004, Hawlena et al. 2011), or biotic interactions (e.g. predation, (Maire et al. 2010); competition, (Ashton et al. 2010)), can mean that the functional role of an individual may fundamentally change and be transient over time and in space, with corresponding effects on ecosystem properties (Levinton and Kelaher 2004, Needham et al. 2010, Godbold et al. 2011).

Theory, as well as observations in plant communities (Siefert et al. 2015), suggest that the relative importance of intraspecific variation in trait expression will decline with increasing scale as more variation is considered (Albert et al. 2011). The present study tests this supposition in a marine system by exploring variability in sediment particle reworking activity, burrow ventilation behaviour, and the associated generation of nutrients for three distinct populations of sediment-dwelling invertebrate species that are common in mid-latitude eastern Atlantic and Mediterranean intertidal mudflats. I hypothesize that undefined differences in location-specific environmental settings (H1) lead to inter-population variation (H2) in behaviour (bioturbation and bioirrigation) with consequences for sediment nutrient release that reflect differences in the extent and nature of organism-sediment coupling. A prominence of these sources of variation would emphasise the importance of the individual and/or population, rather than the species *per se*, and would highlight the need to incorporate sources of performance variability within biodiversity-ecosystem functioning models and ecosystem management strategies.

5.3 Methods

5.3.1 Experimental design and setup

Surficial sediment (less than 3 cm depth) and fauna were collected in August 2014 from three sites in the U.K; a northern (Ythan Estuary, 57˚20'09.1"N 2˚00'20.6"W), central (Humber Estuary, 53˚38'31.2"N 0˚04'08.0"E) and southern (Hamble Estuary, 50˚52'23.1"N 1˚18'49.3"W) estuary. Individuals of the gastropod *Hydrobia ulvae* and the mud shrimp *Corophium volutator* were collected by sieving (>500 μm), and individuals of the polychaete *Hediste diversicolor* by hand. Sediment from each location was independently sieved (500 μm mesh) in a seawater bath to remove macrofauna, allowed to settle for 48 h (to retain the fine fraction, <63 μm) and thoroughly mixed. Sediment grain size parameters were measured using laser diffraction (Malvern Mastersizer 2000) and calculated using standard logarithmic graphical measures (Blott and Pye 2001). Total organic carbon (TOC) was determined by loss on ignition (see Appendix 4, figure A4.1 and table A4.1).

Aquaria consisted of transparent square acrylic cores (internal dimensions, LWH, 12 × 12 × 35 cm), filled to ~10 cm with sediment with ~20 cm of overlying seawater (UV sterilised, 10 μm filtered, salinity 33) and maintained in a water bath. After 24 hours the overlying water was exchanged to remove excess nutrients associated with assembly. Replicate aquaria (n = 3) of each species in monoculture, and in a three species mixture, for each population (hereafter, Ythan, Humber or Hamble) were assembled. In order to distinguish the effects of species interactions in the species mixture from the effects of density, biomass was fixed at 2 g wet biomass aquaria^{-1}. To account for the effects of site-specific differences in sediment conditions (environmental setting), each species-population combination was maintained in each sediment source (i.e. 4 species x 3 populations x 3 environmental settings, in triplicate = 108 aquaria, figure 5.1). In addition, aquaria (n = 27) without macro-invertebrates were included to distinguish the contribution of macrofauna from that of the meiofauna and microbial processes. All aquaria were continually aerated and maintained at 14 ± 1 ˚C (within the annual temperature range of all study site locations) under a 12h light:dark regime for 12 days.

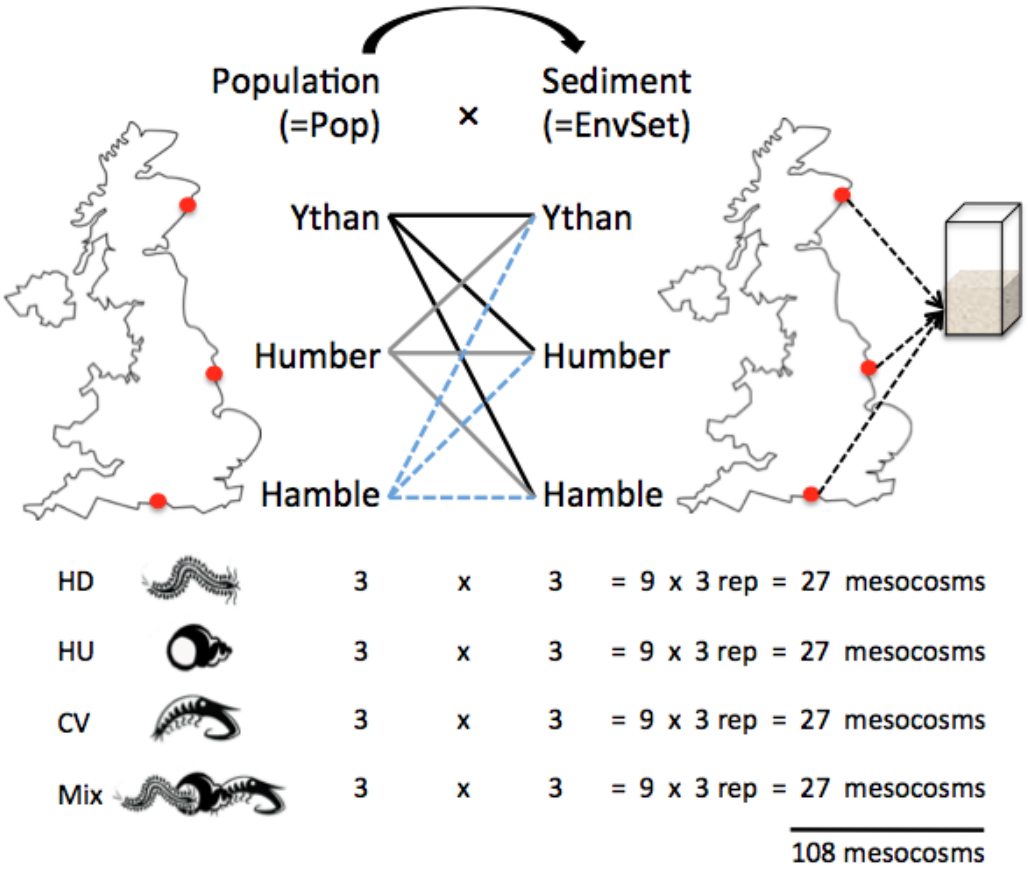

Figure 5.1: Schematic of experimental design. Sediment and Organisms were collected from three sites (Ythan Estuary, Humber Estuary and Hamble Estuary) and, for each species identity (HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, CV = *Corophium volutator*, Mix = species mixture), each population (Pop) was planted into sediment from each location (EnvSet; Ythan, Humber and Hamble Estuary) in laboratory mesocosms in Southampton.

5.3.2 Quantification of ecosystem process and functioning

Faunal mediated sediment particle reworking was estimated non-invasively using a sediment profile imaging camera (Canon 400D, set to 10 s exposure, aperture f5 and speed equivalent to ISO 400; 3888 × 2592 pixels, effective resolution = 63.1 μm $pixel^{-1}$), modified to enable the preferential imaging of the fluorescent labelled particulate tracers (luminophores, pink colour, size class less than 125 μm; Brianclegg Ltd., UK) under UV light (f-SPI, (Solan et al. 2004a)). Stitched composite images (RGB colour, JPEG compression, GMU Image Manipulation Program, Version 2.8.4, www.gimp.org/, Kimball, S., Mattis, P., GIMP (1995), Date of access 01/10/2014), compiled from images of all four sides of each aquarium in a UV illuminated imaging box (Schiffers et al. 2011) after 12 days were analysed, using a custom-made semi-automated macro that runs within ImageJ (Version 1.47), a java-based public domain program developed at the US National Institutes of Health (http://rsb.info.nih.gov/ij/index.html, Rasband, W., ImageJ., (1997), Date of access 01/10/2014). From these data, following (Hale et al. 2014), the mean ($^{f\text{-}SPI}L_{mean,}$) and maximum ($^{f\text{-}SPI}L_{max}$) depth of particle reworking was calculated. In addition, surficial activity was estimated using the maximum vertical deviation of the sediment-water interface (upper – lower limit; surface boundary roughness, SBR).

Burrow ventilation was estimated from absolute changes in the concentration of the inert tracer sodium bromide ($\Delta[Br^-]$, mg L^{-1}; negative values indicate increased activity) over a 4 h period during the daytime on day 12. Bromide concentrations were determined from pre-filtered (Fisherbrand, QL100, ⌀ 70 mm) water samples (5 ml, taken centrally, 5 cm above the sediment-water interface) using a flow injection auto-analyser and standard protocols (FIAstar 5010 series, Foss-Tecator).

Nutrient concentrations (NH_4-N, NO_x-N, PO_4-P) were quantified from pre-filtered (Fisherbrand, nylon 0.45 μm, ⌀ 25mm) water samples (10 ml, taken centrally, 5 cm above the sediment-water interface) using a flow injection auto-analyser (FIAstar 5010 series, Foss-Tecator) with an artificial seawater carrier solution on day 12.

5.3.3 Statistical analysis

For each species (*Hediste* diversicolor, *Hydrobia ulvae*, *Corophium volutator*, and in mixture), separate statistical models for each of the response variables (ecosystem processes: $^{f\text{-}SPI}L_{mean}$, $^{f\text{-}SPI}L_{max}$, SBR, $\Delta[Br^-]$; ecosystem functioning: $[NH_4\text{-}N]$, $[NO_x\text{-}N]$, $[PO_4\text{-}P]$) with environmental setting and population as explanatory variables were developed. As each species is functionally different (Hale et al. 2014) and species effects in mixture are likely not additive as species interact with each other which modifies their behaviour compared to single species treatments (Emmerson et al. 2001), the species mixture could be treated as a unique 'species'. In this study system species interactions are likely to be negative caused by overlapping habitat use and disruption of borrow systems, which may lead to behavioural adjustments of the species affecting particle mixing and bioirrigation activities (Mermillod-Blondin et al. 2005, Godbold et al. 2011). The inclusion of species in mixture allows determination of whether any observed variability that relates to environmental setting and/or population is conserved when biotic context is altered. As the main focus was to compare species contributions to functioning, and not to detect presence versus absence effects, aquaria that contained no invertebrates were not included in these statistical analyses but are presented for comparative purposes.

Initial linear models were assessed for normality (Q-Q-plot), heterogeneity of variance (plotted residual vs. fitted values) and influential data points (cook's distance) (Pinheiro and Bates 2000). When data exploration indicated variance heterogeneity, generalized least squares (GLS) estimations were applied, that specifically incorporate variance in the residual spread with the explanatory variables, using appropriate variance functions (here *varIdent* for nominal explanatory variables) (Pinheiro and Bates 2000). The optimal fixed structure was obtained by manual backward selection using the likelihood ratio test under maximum likelihood (ML) estimation (Pinheiro and Bates 2000). Coefficient tables are presented (see Appendix 4, models S1-S23) without correction for the alpha-error, as Bonferroni correction increases the beta error and tends to obscure multiple significant results if p-values are moderate and the statistical power is low (Moran 2003). All statistical analyses were performed using the R statistical and programming environment (R Core Team

2014) and the *nlme* package (Pinheiro et al. 2014). All data are provided in Appendix 4 (table A4.2).

5.4 Results

The analyses reveal population specific variation as well as effects of environmental setting for most measures of particle mixing and sediment nutrient generation for all study species (*Hydorbia ulvae*, *Hediste diversicolor*, *Corophium volutator*, and the species mixture), supporting hypothesis one and two.

Analysis of sediment properties confirm that particle size distributions and total organic carbon content are largely congruent between locations (Appendix 4, figure A4.1), although some differences do arise when comparisons are based on bulk sediment descriptors (Appendix 4, table A4.1), providing endorsement that differences between populations and additional undefined sediment conditions (environmental setting), rather than solely sediment particle size distribution, affect the way in which species moderate nutrient generation.

5.4.1 Effects of environmental setting and population on ecosystem process

Surface boundary roughness (SBR) and the vertical redistribution of sediment particles ($^{f\text{-}SPI}L_{mean}$ and $^{f\text{-}SPI}L_{max}$) were clearly influenced by a combination of interactive and additive effects of environmental setting and population that were dependent on species identity (table 5.1). The faunal mediation of SBR was influenced by an independent effect of environmental setting for *Hydrobia ulvae* (figure 5.2a) and by the independent effects of environmental setting (figure 5.2b) and population (figure 5.3) for *Corophium volutator* (table 5.1). In contrast, there was no evidence that environmental setting or population affect the mediation of SBR when *Hediste diversicolor* is present in monoculture or when species are in mixture (both intercept only models; $F = 1.44$, d.f. = 2, $p = 0.26$ and $F = 2.2$, d.f. = 2, $P = 0.13$, respectively).

Table 5-1: Summary of statistical analyses for the effects of environemtal setting (EnvSet) and population (Pop) for each species. The test statistic indicates F value or L-ratio depending on the statistical model (see statistical model summary Appendix 3, model S1-S23). HU = *Hydorbia ulvae*, HD = *Hediste diversicolor*, CV = *Corophium volutator*, Mix = species mixture.

species	response variable	explanatory variable	d.f.	test statistic	p
HU	$^{f\text{-}SPI}L_{mean}$	EnvSet	2	22.46	**<0.0001**
HU	$^{f\text{-}SPI}L_{mean}$	Pop	2	9.14	**0.001**
HU	$^{f\text{-}SPI}L_{max}$	EnvSet	2	31.74	**<0.0001**
HU	$^{f\text{-}SPI}L_{max}$	Pop	2	8.35	**0.02**
HU	SBR	EnvSet	2	14.33	**<0.001**
HU	$[NH_4\text{-}N]$	EnvSet*Pop	4	9.55	**0.049**
HU	$[NO_x\text{-}N]$	EnvSet	2	80.41	**<0.0001**
HU	$[PO_4\text{-}P]$	EnvSet	2	54.01	**<0.0001**
HD	$^{f\text{-}SPI}L_{mean}$	EnvSet	2	27.77	**<0.0001**
HD	$^{f\text{-}SPI}L_{mean}$	Pop	2	20.31	**<0.0001**
HD	$^{f\text{-}SPI}L_{max}$	EnvSet	2	11.89	**0.003**
HD	$[\Delta Br^-]$	Pop	2	3.43	0.05
HD	$[NH_4\text{-}N]$	EnvSet	2	31.38	**<0.0001**
HD	$[NH_4\text{-}N]$	Pop	2	4.16	**0.03**
HD	$[NO_x\text{-}N]$	EnvSet	2	7.79	**0.002**
HD	$[PO_4\text{-}P]$	EnvSet	2	21.65	**0.0002**
CV	$^{f\text{-}SPI}L_{mean}$	EnvSet*Pop	4	4.72	**0.009**
CV	SBR	EnvSet	2	14.18	**<0.001**
CV	SBR	Pop	2	6.26	**0.04**
CV	$[\Delta Br^-]$	Pop	2	3.41	0.05
CV	$[NH_4\text{-}N]$	EnvSet	2	37.25	**<0.0001**
CV	$[NH_4\text{-}N]$	Pop	2	16.84	**<0.001**

CV	[NO_x-N]	EnvSet	2	25.04	**<0.0001**
CV	[PO_4-P]	EnvSet*Pop	4	14.83	**0.005**
Mix	$^{f\text{-}SPI}L_{mean}$	EnvSet*Pop	4	13.06	**0.01**
Mix	$^{f\text{-}SPI}L_{max}$	EnvSet*Pop	4	9.99	**0.04**
Mix	[NH_4-N]	EnvSet	2	26.62	**<0.0001**
Mix	[NH_4-N]	Pop	2	9.6	**0.008**
Mix	[NO_x-N]	EnvSet	2	52.94	**<0.0001**
Mix	[PO_4-P]	EnvSet*Pop	4	10.78	**0.03**

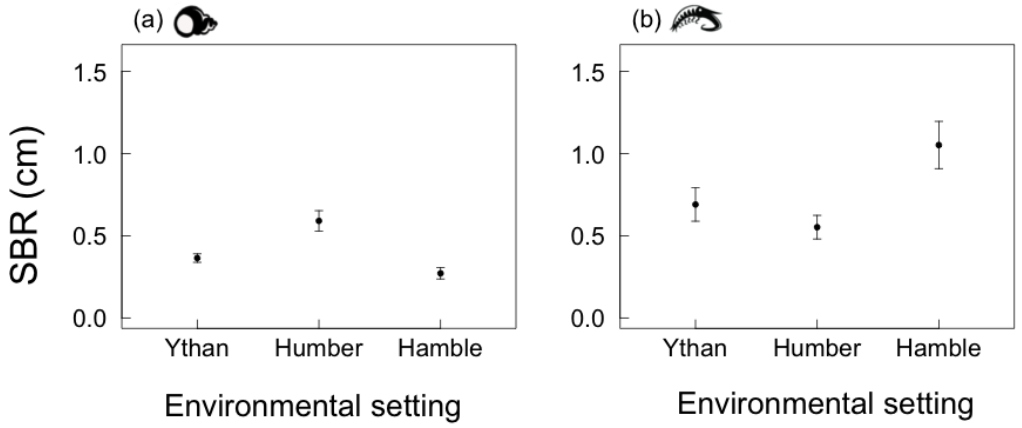

Figure 5.2: The effects of environmental setting on the surface boundary roughness (SBR, mean ± s.e., n = 3) for (a) *Hydrobia ulvae* and (b) *Corophium volutator*.

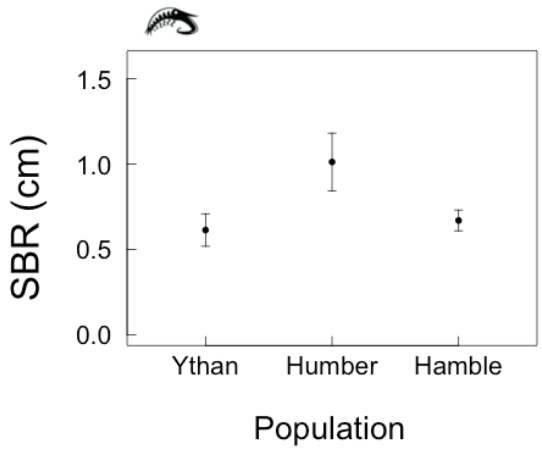

Figure 5.3: The effects of population on the surface boundary roughness (SBR, mean ± s.e., n = 3) for *Corophium volutator*.

The mediation of $^{f\text{-}SPI}L_{mean}$ (figure 5.4) was influenced by either independent effects of environmental setting and population or by their interaction (table 5.1). In general, the mean depth of particle mixing tended to be greatest for populations from the Humber followed by the Ythan and Hamble, and/or in sediments from the Ythan, followed by the Hamble and the Humber, although these patterns were not universal across all species treatments (figure 5.4). For $^{f\text{-}SPI}L_{max}$ (figure 5.5), there was an effect of environmental setting for *H. diversicolor*, and independent effects of environmental setting and population for *H. ulvae* (table 5.1). There was also evidence for an interactive effect between environmental setting and population for the species mixture (table 5.1). The highest values of $^{f\text{-}SPI}L_{max}$ were for the environmental setting of the Ythan and/or when the population originated from the Ythan (figure 5.5). In contrast, when *Corophium volutator* was present in monoculture there was no evidence that environmental setting or population are influential in determining $^{f\text{-}SPI}L_{max}$ (intercept only model; $F = 1.14$, d.f. = 2, $P = 0.34$).

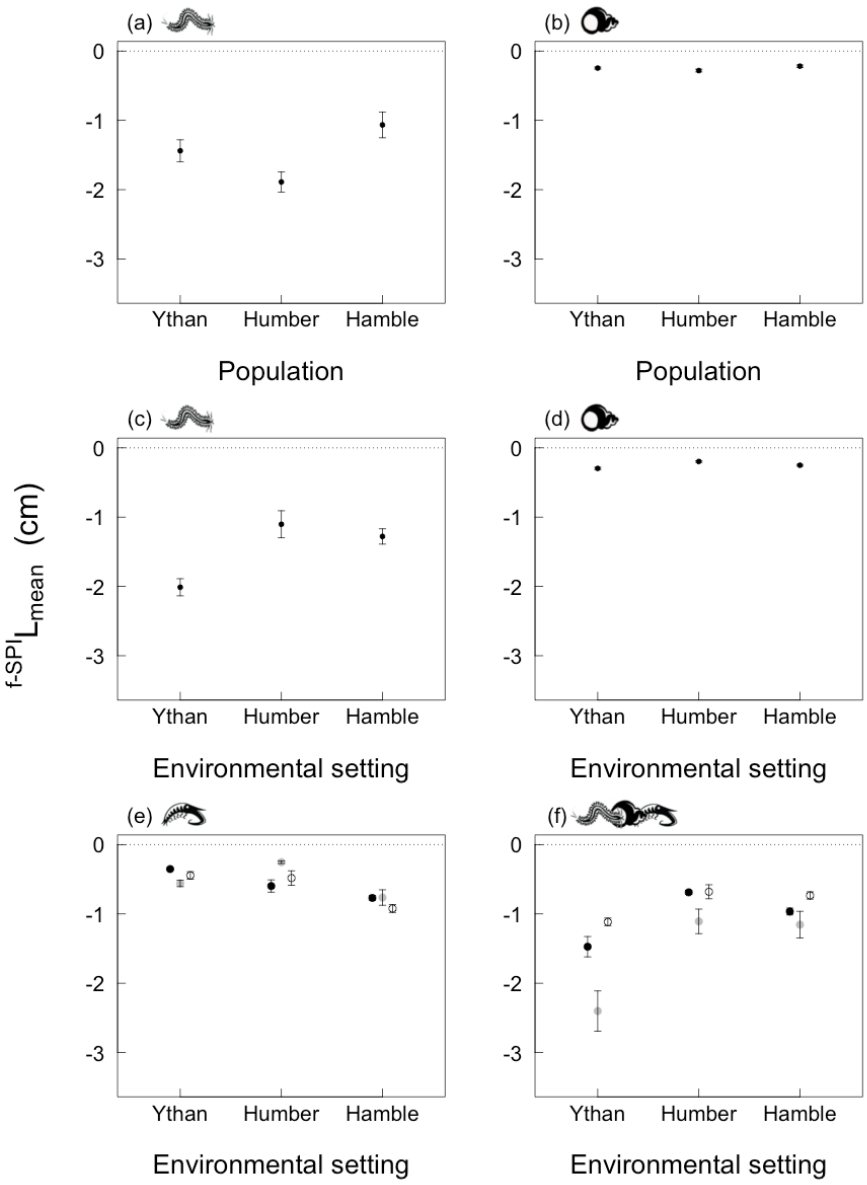

Figure 5.4: Independent effects of population and environmental setting on the mean depth of sediment particle reworking ($^{f\text{-}SPI}L_{mean}$, cm, mean ± s.e., n = 3) for (a, c) *Hediste diversicolor*, (b, d) *Hydrobia ulvae* and the interactive effect of environmental setting and population for (e) *Corophium volutator* and (f) the species mixture. In panel (e) and (f) symbols indicate different populations: Black circles = population from Ythan Estuary, grey circles = population from Humber Estuary, white circles = population from Hamble Estuary. The dotted line indicates the sediment surface and negative values indicate increased particle mixing.

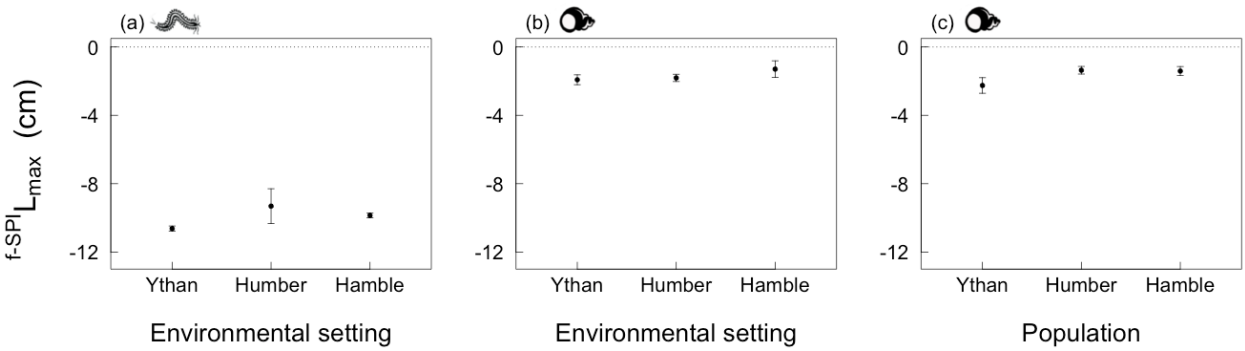

Figure 5.5: Effects of environmental setting and population on the maximum depth of sediment particle reworking ($^{f\text{-}SPI}L_{max}$, cm, mean ± s.e., n = 3) for (a) *Hediste diversicolor* and (b, c) *Hydrobia ulvae*. The dotted line indicates the sediment surface and negative values indicate increased particle mixing.

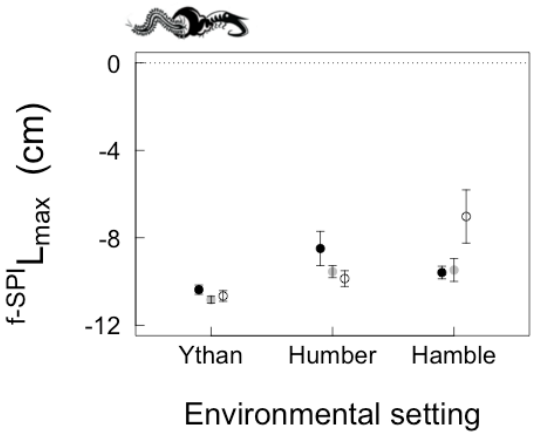

Figure 5.6: The interactive effect of environmental setting and population on the maximum depth of sediment particle reworking ($^{f\text{-}SPI}L_{max}$, cm, mean ± s.e., n = 3) for the species mixture. The symbols indicate different populations: Black circles = populations from Ythan Estuary, grey circles = populations from Humber Estuary, white circles = populations from Hamble Estuary. The dotted line indicates the sediment surface and negative values indicate increased mixing depth.

There were marginal effects of population on burrow ventilation ([ΔBr$^-$]) for *H. diversicolor* and *C. volutator* (table 5.1), indicating greatest activity in populations from the Ythan, followed by populations originating from the Humber and Hamble (figure 5.7). There was no effect of environmental setting or population when *H. ulvae* is present in monoculture (intercept only model; F = 2.34, d.f. = 2, P = 0.12) or when species are in mixture (intercept only model; F = 1.94, d.f. = 2, P = 0.17).

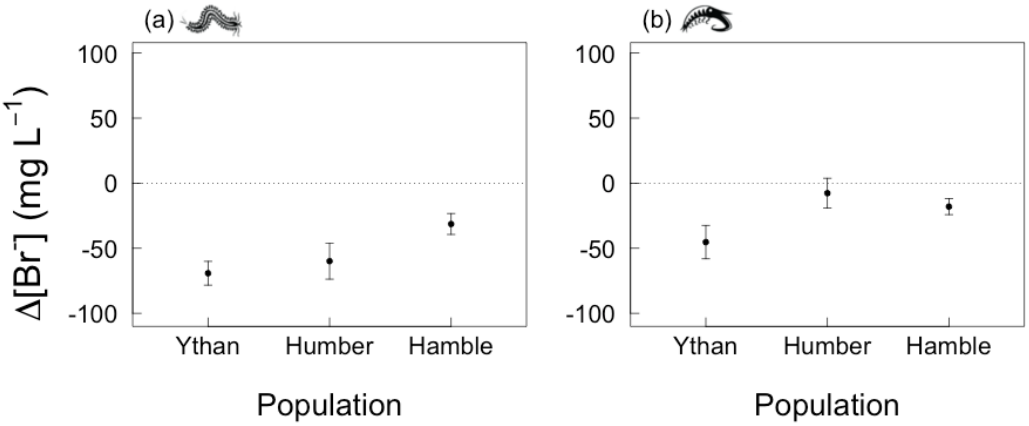

Figure 5.7: The effect of population on burrow ventilation activity (Δ[BR$^-$], mg L^{-1}, mean ± s.e., n = 3) for (a) *Hediste diversicolor* and (b) *Corophium volutator*. Negative values indicate increased activity.

5.4.2 Effects of environmental setting and population on ecosystem functioning

There were consistent effects of environmental setting across all species treatments for all nutrients, but the influence of population varies with nutrient identity ([NH_4-N]: predominantly additive, figure 5.8; [NO_x-N]: no effect, figure 5.10; [PO_4-P]: all interactive, figure 5.11, table 5.1). For [NH_4-N] there are independent effects of both, environmental setting and population, for *H. diversicolor*, *C. volutator* and the species mixture. For *H. ulvae*, there was some weak evidence that these effects may be fully interactive (table 5.1, figure 5.9). In general, [NH_4-N] were higher in treatments with sediment from the Humber relative to those from the Hamble or the Ythan (figure 5.8). The role of population was less pronounced, but populations of *H. diversicolor* and *C. volutator* from the Ythan returned higher [NH_4-N] relative to populations from the Hamble and Humber. For the species mixture, populations from the Humber returned higher [NH_4-N] than the Hamble and Ythan (figure 5.8).

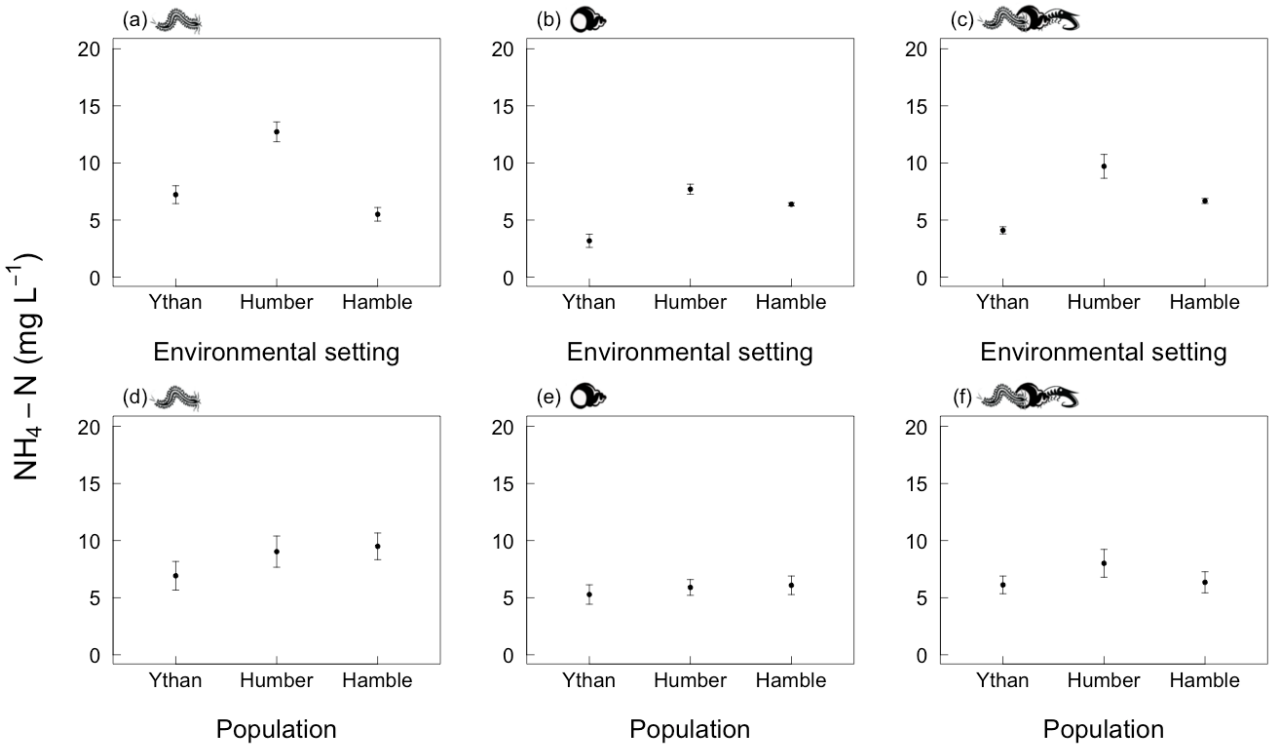

Figure 5.8: The effects of environmental setting and population on [NH_4-N] (mg L^{-1}, mean ± s.e., n = 3) for (a, d) *Hediste diversicolor*, (b, e) *Corophium volutator* and (c, f) the species mixture.

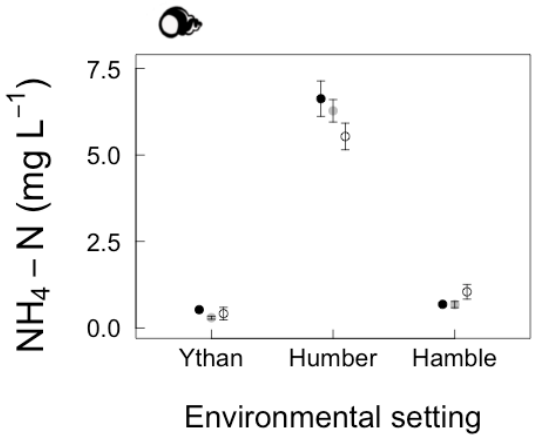

Figure 5.9: The interactive effect of environmental setting and population on [NH_4-N] (mg L^{-1}, mean ± s.e., n = 3) for *Hydrobia ulvae.* The symbols indicate different population origins: Black circles = populations from Ythan Estuary,

grey circles = populations from Humber Estuary, white circles = populations from Hamble Estuary.

There was a consistent effect of environmental setting, but not population, on [NO_x-N] across all species treatments (table 5.1). For *H. diversicolor* and *H. ulvae* [NO_x-N] were greater in sediments from the Hamble or the Ythan (figure 5.10) relative to those of the Humber. In contrast, for *C. volutator* and the species mixture, the highest [NO_x-N] were in sediments from the Ythan, followed by the Humber and Hamble (figure 5.10).

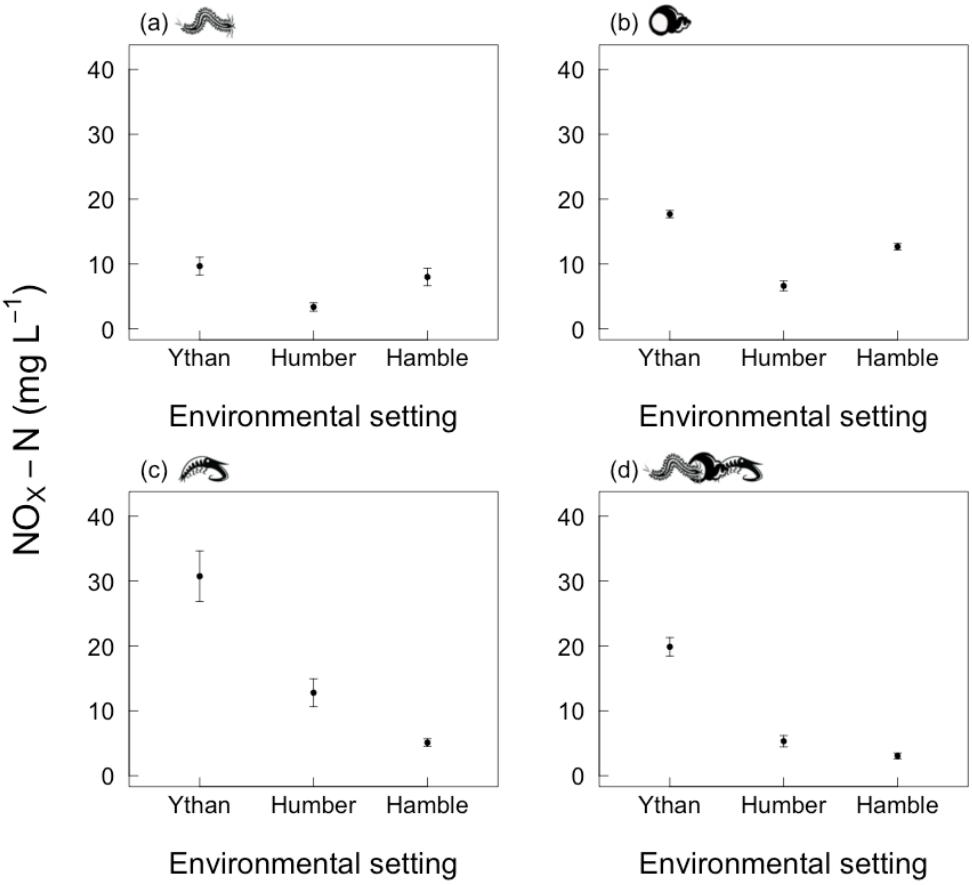

Figure 5.10: The effects of environmental setting on [NO_x-N] (mg L^{-1}, mean ± s.e., n = 3) for (a) *Hediste diversicolor*, (b) *Hydrobia ulvae*, (c) *Corophium volutator* and (d) the species mixture.

There was a single independent effect of environmental setting on [PO_4-P] for *H. diversicolor* and *H. ulvae* and an interactive effect of environmental setting and population origin for *C. volutator* and the species mixture (table 5.1). [PO_4-P] were higher in treatments with sediment from the Ythan, followed by the Humber and Hamble (figure 5.11). This trend was also reflected in the *C. volutator* and species mixture treatments, where the interaction was largely driven by population specific differences within environmental settings (figure 5.11).

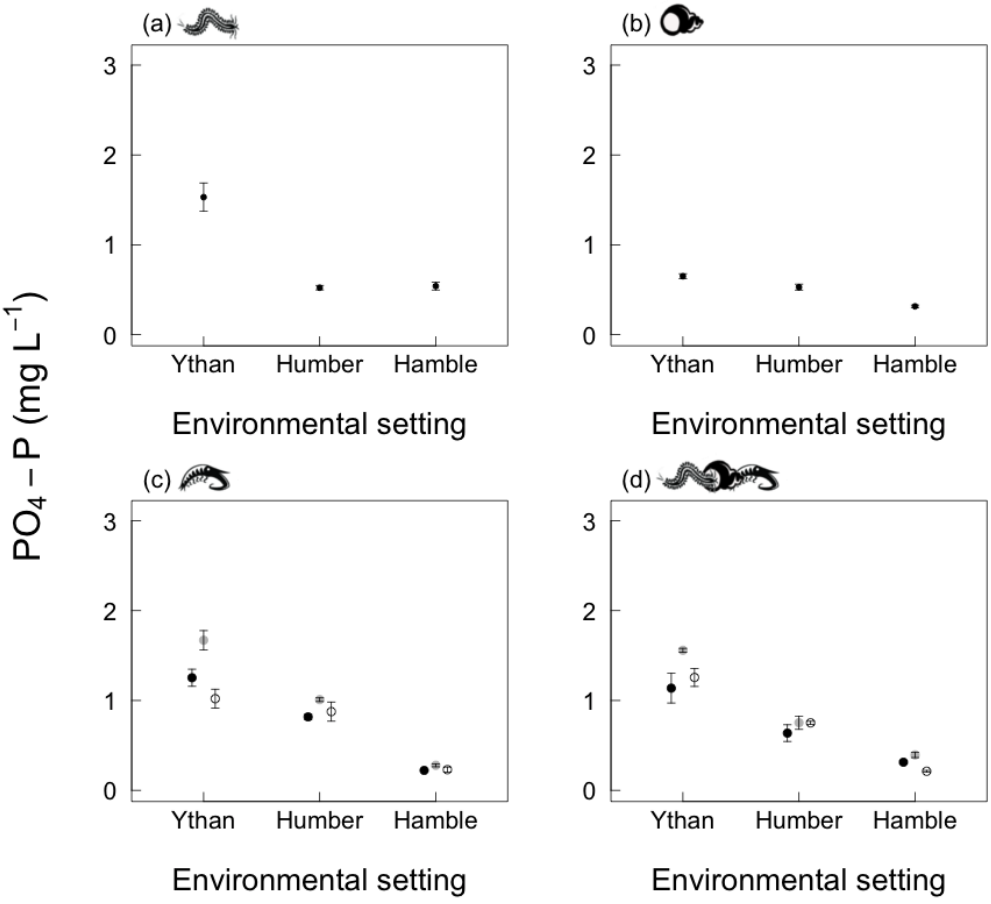

Figure 5.11: The effects of environmental setting on [PO_4-P] (mg L^{-1}, mean ± s.e., n = 3) for (a) *Hediste diversicolor* and (b) *Hydrobia ulvae* and the interactive effect of environmental setting and population for (c) *Corophium volutator* and (d) the species mixture. In panel (c) and (d) symbols indicate different populations: Black circles = population from Ythan Estuary, grey circles = population from Humber Estuary, white circles = population from Hamble Estuary.

5.5 Discussion

The use of functional traits to inform ecosystem management and policy relies on relating species functional effect traits, or functional diversity metrics, to ecosystem processes. However, concerns have been expressed about how important intraspecific variation is in defining functional trait structure (Albert et al. 2012, Poisot et al. 2015, Vilà-Cabrera et al. 2015) and how transferable functional designations may be across regions and with changing context, particularly in human dominated landscapes (Abelleira Martínez et al. 2016, Fontana et al. 2016). Here, the experiments with intertidal sediment communities reveal that the presence of specific traits does not necessarily predetermine either the degree of species-environment interaction, or the way in which species mediate biogeochemical cycling; these can vary between populations and can be further moderated by dynamic shifts in abiotic and/or biotic circumstance (Miner et al. 2005). Indeed, the findings indicate that the combined effects of abiotic/biotic conditions and historical precedent that are encapsulated in a specific location have the potential to determine the basal level of species-environmental interaction (Godbold and Solan 2009, Zettler et al. 2013, Perring et al. 2016). Individuals within a population may further regulate their own functional performance through additional morphological, physiological or behavioural responses to transient changes in circumstance (Levinton and Kelaher 2004, Hawlena et al. 2011, Godbold et al. 2011, Reimchen and Cox 2016). Hence, the net functional contributions of species to ecosystem properties will reflect the relative importance and interdependency of both short- and long-term processes that have altered, are altering, or are yet to fully alter the nature of species-environment coupling (Godbold and Solan 2013).

It is important to consider the findings in light of current practices that adopt single mean trait values to characterise how species mediate ecosystem properties (Pearson 2001). Inherent in most functional metrics is the assumption that intraspecific trait variability is likely to be negligible relative to interspecific differences in species performance. Yet, with few exceptions (Kazakou et al. 2014), it is unlikely that functional effects will be synonymous with species taxonomy or be capable of being applied generically (Murray et al. 2014, Malerba et al. 2016) because functional equivalence tends not to occur across local and regional scales, as well as beyond annual cycles (Pey et al.

2014); a problem that will be compounded when multiple and/or more comprehensive trait descriptors are considered (Hale et al. 2014, Woodin et al. 2016). Although trait variation can be identified at local scales (Torres Dowdall et al. 2012), scaling up will need to accommodate the long-term adjustment of species to local conditions and the history of environmental variation (Hereford 2009, Rudman et al. 2015). For example, one of the study species (*Hediste diversicolor*) is known to adapt its feeding strategy to local resource supply leading to morphological and behavioural differentiation (Maltagliati et al. 2006) that, in turn, is likely to affect bioturbation activities of locally adapted populations. These adaptations can involve adjustments of morphological (Maltagliati et al. 2006, Palkovacs and Post 2009, Charmantier et al. 2016), behavioural (Palkovacs and Post 2009, Urban 2013, Charmantier et al. 2016) or physiological (Nithart 2000, Chiba et al. 2016) traits in response to certain biotic and abiotic conditions. Whilst the specific abiotic and/or biotic factors that lead to variation in trait expression are not easy to predict (Hultine and Marshall 2000, Albert et al. 2010a), the relationship between functional diversity and ecosystem properties has a strong theoretical base (e.g. Micheli and Halpern 2005) and species responses to specific circumstances are well known. For example, the effects of timing (Post and Forchhammer 2008, Bellard et al. 2012) and environmental context (Miner et al. 2005) can moderate species-environment interactions and the expression of functionally relevant traits (Hodge 2004, Hawlena et al. 2011) and/or behaviours (Needham et al. 2010, Godbold et al. 2011, Canal et al. 2015). Importantly, when the response of individuals to changing circumstances link to the effect traits that determine the functional contribution of an organism, the summed response of the assemblage can be sufficient to affect ecological patterns and processes at larger scales (Suding et al. 2008, Gogina et al. 2017). Conversely, when species-environment interactions decouple (Hupfer and Lewandowski 2008, Teal et al. 2013, Wohlgemuth et al. 2016) or do not balance (abiotic > biotic control, (Boyero et al. 2016)), the underlying reciprocal relationship between species and the environment is minimised and the relative importance of biotic control may be diminished or masked (Godbold and Solan 2009).

Whilst the intrinsic variability within species and the importance of local population adaptation has been recognised and is informing evolutionary

thinking (Pfennig et al. 2010, Torres Dowdall et al. 2012), equivalent information is yet to be fully incorporated into predictive models that explore the functional contribution of populations to ecosystem properties (Poisot et al. 2015). The findings lend support to the growing consensus that community-level dynamics and intraspecific variability (McGill et al. 2006, Albert et al. 2011, Violle et al. 2012) need to be incorporated when predicting the ecosystem consequences of altered biodiversity over large scales or extended time periods (Suding et al. 2008, Laughlin 2014, Mace et al. 2014), especially when the risk of altered trait expression covaries with environmental forcing (Solan et al. 2004b). Hence, a focus for ecosystem management strategies that are tasked with conserving the functional integrity of ecosystems under global change will be to account for the circumstances under which response and effect traits are linked (Suding et al. 2008), and when and where intraspecific versus interspecific trait variability are most influential in determining ecosystem functioning and services (Volf et al. 2016).

5.6 Acknowledgements

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Chapter 6: General Discussion

There is increasing awareness (Hillebrand et al. 2008, Naeem 2009) and empirical evidence (Chapter 1, Wilsey and Potvin 2000, Mulder et al. 2004, Maestre et al. 2012) in biodiversity and ecosystem functioning (BEF) research, that changes in community structure, such as evenness, compositional changes and alterations of dominance rank orders, are important for the mediation of ecosystem properties in response to anthropogenic and natural forcing. While high levels of evenness can reduce the variability of ecosystem properties in response to community change (Chapter 1, Daly et al. 2015) or environmental forcing (Wittebolle et al. 2009), evenness *per se* does not necessarily affect the magnitude of ecosystem process and functions (but see e.g. Ward et al. 2010, Chapter 1 - median particle mixing depth); a consistent finding across a variety of environmental contexts (Chapter 2-3). Ecosystem properties are rather mediated by co-occurring changes in species composition (Avolio et al. 2014) and rearrangements in the rank order of species dominance (Chapter 1, Mokany et al. 2008, Tolkkinen et al. 2013). It has been shown that the identity of the dominating species can alter the magnitude and direction of evenness effects and, particularly for lower levels of evenness, exert a disproportionate influence on net community contribution to ecosystem properties (Chapter 1, Bílá et al. 2014, Winfree et al. 2015). This is particularly important, given that natural communities are usually characterised by low evenness and dominance of only few species (McGill et al. 2007). While long term processes that could not be accounted for here, may increase the importance of species interactions and diversity effects (Stachowicz et al. 2008a, Clare et al. 2016), strong species identity effects have been reported repeatedly in the BEF literature (Cardinale et al. 2012) and also been demonstrated in long-term studies under natural conditions (O'Connor and Crowe 2005, Winfree et al. 2015, Massaccesi et al. 2015), supporting the generality of species identity effects for ecosystem functioning.

While the general importance of the identity of dominant species for community mediation of ecosystem properties was a consistent feature throughout the experimental contexts investigated in this thesis (Chapter 1-3), the explicit functional impact of individual species varied between the different

contexts. Organism-environment interactions occur at the level of individuals and depend on the expression of their functional traits (physiological, morphological or phenological characteristics of an individual, Violle et al. 2007). However, individual organisms are inherently different from each other, which affects trait variability across several organizational levels: from genotype to phenotype and their ecological strategies (Violle et al. 2012) causing significant trait-variation within populations. Furthermore, individuals continually respond and adapt to the environmental conditions they experience (Agrawal 2001, Miner et al. 2005, Hereford 2009), which can structure trait variation between populations experiencing varying environmental contexts (Albert et al. 2010a, Torres Dowdall et al. 2012). As a result, there is a large context dependent intra-and interspecific variability in trait expression and consequently organism-environment interactions (e.g. Ouellette et al. 2004, de Backer et al. 2010, Maire et al. 2010, Törnroos et al. 2015), which, as empirically demonstrated (Chapter 1-4, Needham et al. 2011, Godbold and Solan 2013, Solan et al. 2016), affects species functional roles and impacts on aggregate community contributions to ecosystem process and functioning. In particular, local habitat conditions (Chapter 2-4, Godbold et al. 2011), environmental dynamics (Chapter 3, Godbold and Solan 2013) and directional (O'Connor 2009, Bulling et al. 2010, Canal et al. 2015) or stochastic (Cardinale and Palmer 2002, Rodil et al. 2011, Villnäs et al. 2012) forcing can fundamentally alter the functional effects of species and communities. Collectively, these findings demonstrate that variation between individuals, populations and species in response to multiple aspects of environmental change matters for the faunal mediation of ecosystem process and function.

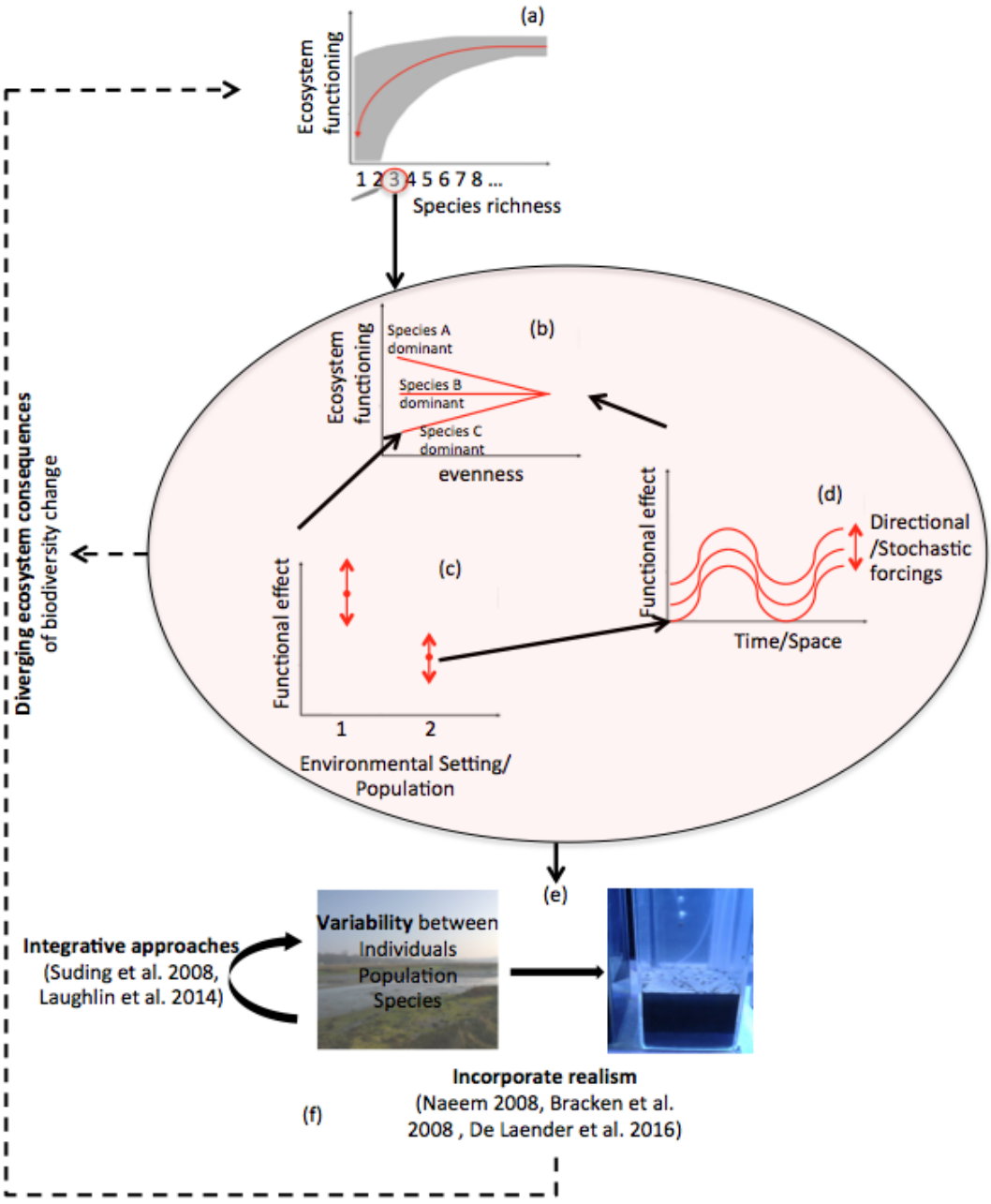

Figure 6.1: Conceptual summary of main findings (a) Current knowledge of biodiversity –ecosystem functioning relations is largely based on species richness (Cardinale et al. 2012), but there is a large variability of faunal mediation of ecosystem functioning within each level of species richness: (b) Changes in evenness can affect ecosystem functioning (Chapter 1, Wittebolle et al. 2008, Hillebrand et al. 2008) depending on the dominant species identity (Chapter 1, Massaccesi et al. 2015), which can have disproportionate effects on ecosystem properties at realistic low evenness levels (Chapter 1, Winfree et al. 2015). (c) The explicit functional impact of organisms however, varies between individuals (Chapter 1-4, Violle et al. 2012), populations (Chapter 4, Albert et al. 2010) and species (Chapter 1-4, Cardinale et al. 2012) depending on multiple aspects of environmental context (Chapter 2 & 3, Needham et al. 2010, Godbold et al. 2011). (d) Environmental dynamics and superimposed

directional environmental changes can further modify the faunal mediation of ecosystem functioning by leading to spatio-temporal variation in species abundances (Kraan et al. 2015, Morley et al. 2016) and performances (Last et al. 2009, De Backer et al. 2010, Godbold et al. 2013) and affect aggregate community contributions to ecosystem properties (Chapter 3). (e) In consequence, there is a large context dependent variability within each level of species richness that is not captured by species based approaches. Therefore, the biodiversity ecosystem functioning relation under more realistic biodiversity change will differ from current expectation. (f) To overcome this limitation BEF research should use integrative approaches based on dynamic trait expression in relation to the environment (Suding et al. 2008, Laughlin et al. 2014) and introduce directional realistic biodiversity changes (Bracken et al. 2008, Naeem 2008, De Laender et al. 2016,)

Hence, exploring ecosystem consequences of changing biodiversity using a species based approach that assigns static trait values to an organism, as often used in current ecological research (Violle et al. 2012), lacks the explicit incorporation of a large part of functionally important trait variability, which may contribute to the uncertainty around the biodiversity- ecosystem functioning relation (Balvanera et al. 2006, Cardinale et al. 2012). Therefore, trait-based approaches may be a better tool to study biodiversity effects on ecosystem functioning (Mouillot et al. 2011, Gagic et al. 2015) and have the potential to capture intraspecific and context dependent variability in trait expression (Laughlin et al. 2012, Lavorel et al. 2013, Fontana et al. 2016). However, while context dependent variation in the expression of species traits can be important for community mediation of ecosystem properties (Chapter 2-4), this is not necessarily the case for all ecosystem processes and functions considered (Chapter 2-4, De Smet et al. 2016) and the functional effect of certain combinations of traits can differ even between closely related ecosystem processes (Murray et al. 2014). Furthermore, the relative importance of intraspecific trait variability compared to interspecific is still debated (Albert et al. 2010b, De Bello et al. 2011, Albert 2015) and may not always be of relevance (Griffiths et al. 2016). These discrepancies highlight the importance of trait selection (Violle et al. 2007, Luck et al. 2012) and linking of species response and effect traits (Suding et al. 2008) to ecosystem functions, when using trait based approaches for model predictions (Laughlin et al. 2012, Mace et al. 2014) or management strategies aimed at maintaining ecosystem functionality (Laughlin 2014). However, currently there often is a lack of the necessary trait information to adequately characterise species functional

effects and trait information is seldom objectively validated or explored empirically (Hale et al. 2014, Murray et al. 2014). Hence, there is a need to gain a better understanding of species traits relevant to organism environment interactions and particular ecosystem functions to accurately predict organism response and effects in relation to changing environmental conditions. Furthermore, as future environmental conditions will differ from current conditions (Williams and Jackson 2007), it may also be necessary to integrate evolutionary dynamics and ecological processes (Hendry et al. 2010), as species can adapt in ecologically relevant timescales (e.g. Yoshida et al. 2003). This is likely going to change the expression of species traits and functional roles of organisms in the future (O'Connor 2009, Godbold and Solan 2013).

The incorporation of more realistic community changes alongside multiple aspects of environmental change has demonstrated that the ecosystem consequences of altered biodiversity are likely to diverge from current expectations, as there is a large variability of ecosystem functioning within each level of species richness, which is not captured by many experimental designs to date based on random alterations of species richness (Cardinale et al. 2012). Furthermore, in natural systems diversity change does not occur randomly (Zavaleta and Hulvey 2004), and the ecosystem consequences of directional change in biodiversity differ from random alterations (Solan et al. 2004b, Zavaleta and Hulvey 2004, Bracken et al. 2008). This might be particularly important in natural communities with low evenness levels, where a change of species dominance may lead to a disproportionate change in ecosystem functioning (Chapter 1), indicating that various aspects of biodiversity and community change, such as species richness, evenness and identity of the dominant species are interlinked and together mediate ecosystem functioning (Chapter 1, Maestre et al. 2012, Zhang et al. 2012, Soininen et al. 2012, Orwin et al. 2014). Furthermore, the ecosystem consequences associated with diversity and community change will depend on how the underlying forcing affects the trait expression and performance of the community (De Laender et al. 2016, Chapter 2-4) as well as how multiple drivers of change interact (Crain et al. 2008, Mrowicki and O'Connor 2015, O'Connor et al. 2015, Chapter 2). Hence there is a need for BEF research to move towards more integrative approaches that capture effects of realistic

change in communities (Naeem 2008) alongside environmental forcing (De Laender et al. 2016) as both are inextricably linked (Hughes et al. 2007).

Appendices

Appendix 1

Table A1.1: Realised mean (± s.d.) biomass (g) for each permutation of dominance arrangement within each evenness level. HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, CV = *Corophium volutator*. Realised evenness levels (mean ± s.d.) were: J = 1.00, 0.99 ± 0.0002 (n = 5); J = 0.92, 0.92 ± 0.01 (n = 30); J = 0.64, 0.64 ± 0.01 (n = 30); J = 0.42, 0.42 ± 0.01 (n = 15).

J	HD	± sd	HU	± sd	CV	± sd	total
1.00	0.629	0.029	0.667	0.004	0.653	0.016	1.95
0.92	1.035	0.048	0.666	0.002	0.334	0.005	2.04
0.92	0.994	0.046	0.335	0.003	0.671	0.010	2.00
0.92	0.657	0.040	1.003	0.005	0.336	0.004	2.00
0.92	0.311	0.038	1.003	0.003	0.665	0.003	1.98
0.92	0.320	0.022	0.665	0.002	1.006	0.013	1.99
0.92	0.628	0.020	0.335	0.002	1.019	0.037	1.98
0.64	1.501	0.032	0.334	0.002	0.155	0.003	1.99
0.64	1.525	0.059	0.156	0.002	0.332	0.005	2.01
0.64	0.329	0.011	1.514	0.003	0.157	0.004	2.00
0.64	0.155	0.003	1.512	0.002	0.331	0.008	2.00
0.64	0.317	0.027	0.157	0.001	1.518	0.010	1.99
0.64	0.155	0.005	0.335	0.003	1.515	0.012	2.00
0.42	1.755	0.038	0.125	0.002	0.125	0.004	2.01
0.42	0.118	0.010	1.753	0.002	0.125	0.003	2.00
0.42	0.122	0.005	0.125	0.001	1.749	0.013	2.00

Table A1.2: Summary of data used for statistical analysis. Data in the absence of macrofauna is shown for comparison but was not included in the analyses. SpD = specific arrangements of species dominance, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, CV = *Corophium volutator*

SpD	Replicate	$^{f\text{-}SPI}L_{mean}$ (cm)	$^{f\text{-}SPI}L_{median}$ (cm)	$^{f\text{-}SPI}L_{max}$ (cm)	SBR (cm)	$\Delta[Br^-]$ (mg L^{-1})	$[NH_4\text{-}N]$ (mg L^{-1})	$[NO_X\text{-}N]$ (mg L^{-1})	$[PO_4\text{-}P]$ (mg L^{-1})
$J^{0.42}$ CV>HU=HD	1	2.086	1.718	11.601	1.917	-71.812	3.458	1.048	0.053
$J^{0.42}$ CV>HU=HD	2	3.624	3.405	11.933	1.332	-114.194	0.494	1.220	0.149
$J^{0.42}$ CV>HU=HD	3	2.361	2.366	11.118	0.975	197.692	1.759	0.850	0.013
$J^{0.42}$ CV>HU=HD	4	3.135	3.361	10.999	0.516	-38.074	0.244	0.934	0.060
$J^{0.42}$ CV>HU=HD	5	1.792	1.878	9.531	1.087	32.636	2.009	1.044	0.035
$J^{0.42}$ HD>CV=HU	1	1.919	0.356	10.866	0.701	-7.026	2.895	0.578	0.065
$J^{0.42}$ HD>CV=HU	2	3.073	0.587	11.262	1.024	-13.750	3.044	0.301	0.101
$J^{0.42}$ HD>CV=HU	3	2.061	0.442	10.978	0.885	-32.608	2.424	0.721	0.062
$J^{0.42}$ HD>CV=HU	4	3.207	1.613	11.312	0.570	46.785	3.534	0.489	0.063
$J^{0.42}$ HD>CV=HU	5	1.375	0.412	10.999	0.881	30.107	3.207	0.453	0.071
$J^{0.42}$ HU>CV=HD	1	1.235	0.378	10.951	0.694	52.142	1.942	0.865	0.052
$J^{0.42}$ HU>CV=HD	2	1.288	0.529	10.987	0.609	64.318	1.355	0.740	0.107
$J^{0.42}$ HU>CV=HD	3	1.122	0.578	10.709	0.561	41.718	1.820	0.733	0.074
$J^{0.42}$ HU>CV=HD	4	1.087	0.514	9.949	0.771	-19.256	2.176	0.893	0.040
$J^{0.42}$ HU>CV=HD	5	1.003	0.374	10.759	0.782	-20.893	na	na	na
$J^{0.64}$ CV>HD>HU	1	2.794	2.761	11.337	0.680	56.236	1.832	1.093	0.034
$J^{0.64}$ CV>HD>HU	2	3.316	3.586	11.147	0.961	-4.644	0.681	1.097	0.055
$J^{0.64}$ CV>HD>HU	3	3.246	3.039	10.662	0.876	198.649	0.807	0.926	0.098
$J^{0.64}$ CV>HD>HU	4	3.374	3.482	9.817	0.883	11.597	0.209	0.991	0.051
$J^{0.64}$ CV>HD>HU	5	3.492	3.383	10.908	1.346	-1.422	0.581	1.283	0.044
$J^{0.64}$ CV>HU>HD	1	3.153	3.497	12.000	1.578	-79.117	0.648	1.168	0.024
$J^{0.64}$ CV>HU>HD	2	3.122	3.010	10.576	1.707	-45.670	1.214	1.035	0.052
$J^{0.64}$ CV>HU>HD	3	3.709	3.225	11.721	1.098	-46.438	na	na	na
$J^{0.64}$ CV>HU>HD	4	3.213	3.458	10.079	0.934	-79.149	0.500	0.970	0.069
$J^{0.64}$ CV>HU>HD	5	2.288	2.255	11.265	0.953	-40.154	1.516	1.074	0.057
$J^{0.64}$ HD>CV>HU	1	3.096	2.131	11.640	0.906	-30.025	3.016	0.596	0.052
$J^{0.64}$ HD>CV>HU	2	3.070	1.617	10.701	0.687	-33.481	2.918	0.509	0.065

$J^{0.64}$ HD>CV>HU	3	2.043	0.791	11.146	0.871	402.515	2.880	0.280	0.115
$J^{0.64}$ HD>CV>HU	4	1.980	0.948	11.069	0.851	4.642	1.901	0.329	0.123
$J^{0.64}$ HD>CV>HU	5	2.456	1.582	11.291	0.937	-19.543	2.845	0.722	0.032
$J^{0.64}$ HD>HU>CV	1	2.486	0.886	11.526	0.749	-46.087	2.745	0.454	0.101
$J^{0.64}$ HD>HU>CV	2	1.862	0.551	11.037	0.710	53.278	2.777	0.583	0.069
$J^{0.64}$ HD>HU>CV	3	2.634	0.570	11.044	1.066	450.477	2.695	0.659	0.059
$J^{0.64}$ HD>HU>CV	4	2.860	1.095	10.908	0.607	62.172	3.189	0.723	0.027
$J^{0.64}$ HD>HU>CV	5	0.082	0.000	7.966	0.942	-35.894	na	na	na
$J^{0.64}$ HU>CV>HD	1	2.019	1.558	10.787	0.891	-56.915	2.165	0.523	0.056
$J^{0.64}$ HU>CV>HD	2	1.786	0.720	11.880	1.089	-74.428	1.802	0.805	0.070
$J^{0.64}$ HU>CV>HD	3	2.047	1.372	10.890	0.632	407.152	1.624	0.388	0.111
$J^{0.64}$ HU>CV>HD	4	1.833	0.917	10.755	0.480	3.987	1.923	0.716	0.037
$J^{0.64}$ HU>CV>HD	5	1.894	1.079	11.689	0.767	24.200	1.634	0.754	0.083
$J^{0.64}$ HU>HD>CV	1	1.813	0.708	11.002	0.799	-67.550	2.144	0.758	0.064
$J^{0.64}$ HU>HD>CV	2	2.026	0.880	11.059	0.693	5.874	2.233	0.575	0.096
$J^{0.64}$ HU>HD>CV	3	2.175	0.519	11.163	0.780	77.335	1.740	0.894	0.078
$J^{0.64}$ HU>HD>CV	4	1.578	0.473	11.129	0.564	4.358	2.111	0.652	0.099
$J^{0.64}$ HU>HD>CV	5	1.305	0.556	10.546	0.692	97.362	2.074	0.961	0.035
$J^{0.92}$ CV>HD>HU	1	2.303	2.138	10.728	0.900	483.384	1.979	0.553	0.126
$J^{0.92}$ CV>HD>HU	2	3.490	3.043	11.435	0.658	-2.068	1.312	0.957	0.056
$J^{0.92}$ CV>HD>HU	3	2.741	2.807	11.318	1.360	-0.458	1.465	0.491	0.135
$J^{0.92}$ CV>HD>HU	4	2.559	2.226	11.009	1.113	-38.862	0.671	1.164	0.058
$J^{0.92}$ CV>HD>HU	5	2.853	2.372	11.573	0.869	191.682	na	na	na
$J^{0.92}$ CV>HU>HD	1	2.818	2.622	10.210	0.819	-57.455	1.492	0.630	0.073
$J^{0.92}$ CV>HU>HD	2	2.421	2.328	11.003	1.121	-172.552	1.898	0.617	0.082
$J^{0.92}$ CV>HU>HD	3	2.242	2.071	10.790	1.404	-332.760	2.115	0.761	0.070
$J^{0.92}$ CV>HU>HD	4	2.473	2.377	10.682	0.998	189.481	2.238	0.734	0.043
$J^{0.92}$ CV>HU>HD	5	2.410	2.441	10.704	1.317	37.796	na	na	na
$J^{0.92}$ HD>CV>HU	1	3.436	2.862	11.391	0.922	-49.534	1.949	0.520	0.082
$J^{0.92}$ HD>CV>HU	2	2.551	1.867	10.476	0.674	-121.498	2.228	0.549	0.093
$J^{0.92}$ HD>CV>HU	3	2.513	2.189	11.167	0.449	-29.659	1.595	0.478	0.127
$J^{0.92}$ HD>CV>HU	4	1.677	1.422	11.172	0.771	209.782	2.948	0.416	0.073

$J^{0.92}$ HD>CV>HU	5	2.860	2.199	11.297	0.676	-34.748	2.046	0.635	0.075
$J^{0.92}$ HD>HU>CV	1	2.663	1.831	11.916	0.995	-65.144	1.822	0.723	0.127
$J^{0.92}$ HD>HU>CV	2	2.301	0.945	11.210	0.910	19.606	2.122	0.612	0.096
$J^{0.92}$ HD>HU>CV	3	1.525	0.456	11.414	0.855	-52.193	2.692	0.530	0.080
$J^{0.92}$ HD>HU>CV	4	2.066	0.814	11.307	0.688	35.870	2.721	0.817	0.010
$J^{0.92}$ HD>HU>CV	5	1.909	1.178	11.442	0.780	-72.350	2.845	0.513	0.078
$J^{0.92}$ HU>CV>HD	1	2.453	2.371	10.777	0.684	-12.230	1.386	0.731	0.093
$J^{0.92}$ HU>CV>HD	2	2.104	2.028	11.477	0.666	313.601	1.359	0.547	0.149
$J^{0.92}$ HU>CV>HD	3	2.894	2.927	10.390	1.261	42.820	0.975	0.775	0.050
$J^{0.92}$ HU>CV>HD	4	2.925	3.038	10.068	1.464	-198.486	1.063	0.674	0.046
$J^{0.92}$ HU>CV>HD	5	0.102	0.040	7.677	0.660	2.745	na	na	na
$J^{0.92}$ HU>HD>CV	1	2.073	1.237	10.933	0.840	-41.563	2.433	0.570	0.086
$J^{0.92}$ HU>HD>CV	2	2.023	1.160	11.373	0.602	-27.928	2.034	0.728	0.065
$J^{0.92}$ HU>HD>CV	3	2.378	0.973	11.062	0.398	1.985	2.374	0.636	0.065
$J^{0.92}$ HU>HD>CV	4	2.551	1.790	11.201	0.741	459.424	2.623	0.590	0.030
$J^{0.92}$ HU>HD>CV	5	2.508	1.357	11.241	0.634	162.190	2.213	0.651	0.084
$J^{1.00}$	1	1.884	1.633	10.791	0.573	82.075	2.289	0.593	0.059
$J^{1.00}$	2	2.410	2.038	11.301	0.542	-8.305	2.576	0.438	0.088
$J^{1.00}$	3	2.493	2.206	10.802	1.389	-36.312	2.156	0.612	0.061
$J^{1.00}$	4	3.499	2.545	11.443	1.083	246.772	2.360	0.623	0.059
$J^{1.00}$	5	2.882	2.336	11.083	1.049	45.685	1.103	0.512	0.159
no macrofauna	1	0.110	0.051	3.443	0.623	-23.936	0.285	1.131	0.128
no macrofauna	2	0.070	0.017	0.740	0.510	-14.977	0.238	0.944	0.168
no macrofauna	3	0.088	0.034	5.298	0.547	51.632	0.259	1.342	0.074
no macrofauna	4	0.143	0.000	9.609	0.535	190.181	0.074	1.235	0.062
no macrofauna	5	0.133	0.040	7.714	0.374	-87.699	-0.041	1.038	0.099

Statistical model summary

Summary of the statistical models (Model S1 to S24). For Model S1 to S8 evenness is treated as a continuous independent variable and for Model S9 to S16 as a categorical independent variable. For each model, the initial linear regression model and the minimal adequate model is listed. Where it was necessary to account for a violation of homogeneity of variance, a linear regression with GLS estimation was used and a summary of the coefficient table is provided. The coefficients indicate the relative performance of each treatment level relative to the relevelled baseline (as indicated). Coefficients ± SE, t-values and respective significance values are presented. Levels of significance for $p<0.05$, $p<0.01$ and $p<0.001$ are highlighted in grey shading (darker shading with increasing significance). Abbreviations: HD, *Hediste diversicolor*; HU, *Hydrobia ulvae*; CV, *Corophium volutator*.

Statistical models for the effects of evenness

(i) Evenness treated as a continuous variable

Model S1: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{mean}$~ J)

No minimal adequate model, intercept only (J, F = 2.23, d.f. = 1, p = 0.140)

Model S2: Maximum mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{max}$~ J)

No minimal adequate model, intercept only (J, F = 0.04, d.f. = 1, p = 0.84)

Model S3: Surface boundary roughness (SBR, cm)

Initial linear regression model:

Lm(SBR~ J)

No minimal adequate model, intercept only (J, F = 0.003, d.f. = 1, p = 0.956)

Model S4: Bioirrigation ($\Delta[Br^-]$, mg L^{-1})

Initial linear regression model:

Lm($\Delta[Br^-]$ ~ J)

No minimal adequate model, intercept only (J, F = 0.17, d.f. = 1, p = 0.68)

Model S5: Median mixed depth of particle reworking ($^{f\text{-}SPI}L_{median}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{median}$~ J)

Minimal adequate model:

gls($^{f\text{-}SPI}L_{median}$~ J, weights = varExp (form = ~ J), method = 'ML')

(J, L-ratio = 4.37, d.f. = 1, p = 0.037)

Coefficient table (method = 'REML'):

	Coefficient	± SE	t-value	p
Intercept	0.848	0.467	1.817	0.073
Slope (J)	1.195	0.567	2.105	0.039

Model S6: NH_4-N concentration ([NH_4-N], mg L^{-1})

Initial linear regression model:

Lm([NH_4-N] ~ J)

No minimal adequate model, intercept only (J, F = 0.17, d.f. = 1, p = 0.68)

Model S7: PO_4-P concentration ([PO_4-P], mg L^{-1})

Initial linear regression model:

Lm([PO_4-P] ~ J)

No minimal adequate model, intercept only (J, F = 2.90, d.f. = 1, p = 0.093)

Model S8: NO_x-N concentration ([NO_x-N], mg L^{-1})

Initial linear regression model:

Lm([NO_x-N] ~ J)

Minimal adequate model:

gls([NO_x-N] ~ J, weights = varExp(form = ~ J), method = 'ML')

(J, L-ratio = 8.25, d.f. = 1, p = 0.004)

Coefficient table (method = 'REML'):

	Coefficient	± SE	t-value	p
Intercept	0.995	0.111	8.982	<0.0001
Slope (J)	-0.384	0.131	-2.919	0.005

(ii) Evenness treated as nominal variable

Model S9: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{mean}$~ J)

No minimal adequate model, intercept only (J, F = 1.36, d.f. = 3, p = 0.262)

Model S10: Max mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{max}$~ J)

No minimal adequate model, intercept only (J, F = 0.064, d.f. = 3, p = 0.979)

Model S11: Surface boundary roughness (SBR, cm)

Initial linear regression model:

Lm(SBR~ J)

No minimal adequate model, intercept only (J, F = 0.05, d.f. = 3, p = 0.985)

Model S12: Bioirrigation ($\Delta[Br^-]$, mg L^{-1})

Initial linear regression model:

$Lm(\Delta[Br^-] \sim J)$

No minimal adequate model, intercept only (J, L-ratio = 1.84, d.f. = 3, p = 0.864)

Model S13: Median mixed depth of particle reworking ($^{f\text{-}SPI}L_{median}$, cm)

Initial linear regression model:

$Lm(^{f\text{-}SPI}L_{median} \sim J)$

Minimal adequate model:

$gls(^{f\text{-}SPI}L_{median} \sim J$, weights = varIdent(form = ~1|J), method = 'ML')

(J, L-ratio = 8.49, d.f. = 3, p = 0.037)

Coefficient table (method = 'REML'): Intercept ± SE (For baseline J = 1): 2.151 ± 0.154, t = 13.988, p = <0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold.

	$J^{1.00}$		
$J^{0.92}$	-0.248 ± 0.211 -1.177 **0.243**	$J^{0.92}$	
$J^{0.64}$	-0.463 ± 0.262 -1.767 **0.081**	-0.215 ± 0.256 -0.839 **0.404**	$J^{0.64}$
$J^{0.42}$	-0.917 ± 0.321 -2.855 **0.006**	-0.669 ± 0.317 -2.114 **0.038**	-0.454 ± 0.353 -1.286 **0.202**

Model S14: NH_4-N concentration ([NH_4-N], mg L^{-1})

Initial linear regression model:

Lm([NH_4-N] ~ J)

No minimal adequate model, intercept only (J, F = 0.49, d.f. = 3, p = 0.691)

Model S15: PO_4 concentration ([PO_4-P], mg L^{-1})

Initial linear regression model:

Lm([PO_4-P] ~ J)

No minimal adequate model, intercept only (J, F = 1.2, d.f. = 3, p = 0.317)

Model S16: NO_x-N concentration ([NO_x-N], mg L^{-1})

Initial linear regression model:

Lm([NO_x-N] ~ J)

Minimal adequate model:

gls([NO_x-N] ~ J, weights = varIdent(form = ~1|J), method = 'ML')

(J, L-ratio = 12.92, d.f. = 3, p = 0.005)

Coefficient table (method 'REML'): Intercept ± SE (For baseline J = 1): 0.556 ± 0.035, t = 15.761, p = <0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold.

	$J^{1.00}$		
$J^{0.92}$	0.096 ± 0.046 2.073 **0.042**	$J^{0.92}$	
$J^{0.64}$	0.213 ± 0.061 3.469 **0.001**	0.117 ± 0.059 1.987 **0.051**	$J^{0.64}$
$J^{0.42}$	0.221 ± 0.077 2.867 **0.006**	0.124 ± 0.075 1.663 **0.101**	0.008 ± 0.085 0.093 **0.927**	$J^{0.42}$

Models for the effects of specific arrangements of species dominance (SpD)

Model S17: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{mean}$~ SpD)

Minimal adequate model:

gls($^{f\text{-}SPI}L_{mean}$~ SpD, weights = varIdent (form = ~ 1|SpD), method = 'ML')

(SpD, L-ratio = 78.76, d.f. = 15, p = <0.0001)

Coefficient table model S17 (method = 'REML'): Intercept ± SE (For baseline J = 1): 2.633 ± 0.269, t = 9.807, p = <0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold. CV = *Corophium volutator*, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*

	$J^{1.00}$												
$J^{0.64}$ **CV>HD>HU**	0.611 ± 0.294 2.078 **0.042**	$J^{0.64}$ **CV>HD>HU**											
$J^{0.92}$ **CV>HD>HU**	0.156 ± 0.334 0.466 **0.643**	-0.455 ± 0.232 -1.966 **0.054**	$J^{0.92}$ **CV>HD>HU**										
$J^{0.64}$ **CV>HU>HD**	0.463 ± 0.353 1.314 **0.194**	-0.147 ± 0.258 -0.571 **0.570**	0.308 ± 0.303 1.017 **0.313**	$J^{0.64}$ **CV>HU>HD**									
$J^{0.92}$ **CV>HU>HD**	-0.161 ± 0.285 -0.564 **0.575**	-0.772 ± 0.152 -5.061 **<0.0001**	-0.316 ± 0.220 -1.440 **0.155**	-0.624 ± 0.248 -2.521 **0.014**	$J^{0.92}$ **CV>HU>HD**								
$J^{0.42}$ **CV>HU=HD**	-0.034 ± 0.433 -0.077929 **0.9381**	-0.645 ± 0.360 -1.790069 **0.078**	-0.189 ± 0.393 -0.482 **0.632**	-0.497 ± 0.410 -1.214 **0.229**	0.127 ± 0.353 0.360 **0.720**	$J^{0.42}$ **CV>HU=HD**							
$J^{0.64}$ **HD>HU>CV**	-0.649 ± 0.571 -1.136 **0.260**	-1.260 ± 0.518 -2.433 **0.018**	-0.804 ± 0.541 -1.486 **0.142**	-1.112 ± 0.553 -2.010 **0.049**	-0.488 ± 0.513 -0.952 **0.345**	-0.615 ± 0.608 -1.012 **0.315**	$J^{0.64}$ **HD>HU>CV**						
$J^{0.92}$ **HD>HU>CV**	-0.541 ± 0.329 -1.643 **0.105**	-1.152 ± 0.225 -5.122 **<0.0001**	-0.696 ± 0.275 -2.533 **0.014**	-1.004 ± 0.298 -3.374 **0.001**	-0.380 ± 0.213 -1.787 **0.079**	-0.507 ± 0.389 -1.302 **0.198**	0.108 ± 0.539 0.200 **0.842**	$J^{0.92}$ **HD>HU>CV**					
$J^{0.64}$ **HD>CV>HU**	-0.104 ± 0.360 -0.289 **0.773**	-0.715 ± 0.269 -2.663 **0.010**	-0.260 ± 0.312 -0.834 **0.407**	-0.568 ± 0.332 -1.711 **0.092**	0.056 ± 0.258 0.2181 **0.828**	-0.071 ± 0.416 -0.170 **0.866**	0.544 ± 0.558 0.975 **0.333**	0.436 ± 0.307 1.423 **0.160**	$J^{0.64}$ **HD>CV>HU**				
$J^{0.92}$ **HD>CV>HU**	-0.026 ± 0.392 -0.067 **0.947**	-0.637 ± 0.309 -2.060 **0.044**	-0.182 ± 0.347 -0.524 **0.602**	-0.490 ± 0.366 -1.339 **0.185**	0.134 ± 0.301 0.447 **0.656**	0.007 ± 0.444 0.017 **0.987**	0.622 ± 0.579 1.075 **0.286**	0.514 ± 0.343 1.500 **0.139**	0.078 ± 0.373 0.209 **0.835**	$J^{0.92}$ **HD>CV>HU**			
$J^{0.42}$ **HD>CV=HU**	-0.306 ± 0.443 -0.693 **0.491**	-0.917 ± 0.371 -2.469 **0.016**	-0.462 ± 0.404 -1.145 **0.257**	-0.770 ± 0.420 -1.835 **0.071**	-0.146 ± 0.364 -0.400 **0.690**	-0.273 ± 0.489 -0.558 **0.579**	0.342 ± 0.614 0.557 **0.580**	0.234 ± 0.400 0.586 **0.560**	-0.202 ± 0.426 -0.474 **0.637**	-0.280 ± 0.453 -0.619 **0.538**	$J^{0.42}$ **HD>CV=HU**		
$J^{0.64}$ **HU>CV>HD**	-0.718 ± 0.273 -2.626 **0.011**	-1.329 ± 0.130 -10.222 **<0.0001**	-0.873 ± 0.205 -4.265 **0.0001**	-1.181 ± 0.234 -5.040 **<0.0001**	-0.557 ± 0.107 -5.181 **<0.0001**	-0.684 ± 0.344 -1.991 **0.051**	-0.069 ± 0.506 -0.136 **0.892**	-0.177 ± 0.197 -0.897 **0.373**	-0.613 ± 0.246 -2.495 **0.015**	-0.691 ± 0.290 -2.386 **0.020**	-0.411 ± 0.355 -1.157 **0.252**	$J^{0.64}$ **HU>CV>HD**	
$J^{0.92}$ **HU>CV>HD**	-0.538 ± 0.586 -0.918 **0.362**	-1.149 ± 0.534 -2.150 **0.035**	-0.694 ± 0.557 -1.245 **0.218**	-1.001 ± 0.569 -1.760 **0.083**	-0.377 ± 0.529 -0.713 **0.479**	-0.504 ± 0.622 -0.811 **0.421**	0.111 ± 0.725 0.153 **0.879**	0.003 ± 0.555 0.005 **0.996**	-0.434 ± 0.574 -0.756 **0.453**	-0.512 ± 0.594 -0.862 **0.392**	-0.231 ± 0.629 -0.368 **0.714**	0.180 ± 0.523 0.343 **0.733**	$J^{0.92}$ **HU>CV>HD**
$J^{0.64}$ **HU>HD>CV**	-0.854 ± 0.310 -2.752 **0.008**	-1.465 ± 0.196 -7.468 **<0.0001**	-1.010 ± 0.252 -4.006 **0.0002**	-1.317 ± 0.277 -4.763 **<0.0001**	-0.693 ± 0.182 -3.809 **0.0003**	-0.820 ± 0.374 -2.195 **0.032**	-0.205 ± 0.527 -0.390 **0.698**	-0.313 ± 0.246 -1.274 **0.207**	-0.750 ± 0.286 -2.618 **0.011**	-0.828 ± 0.325 -2.548 **0.013**	-0.548 ± 0.385 -1.424 **0.159**	-0.136 ± 0.164 -0.833 **0.408**	-0.316 ± 0.544 -0.581 **0.563**	$J^{0.64}$ **HU>HD>CV**
$J^{0.92}$ **HU>HD>CV**	-0.327 ± 0.290 -1.127 **0.264**	-0.938 ± 0.162 -5.780 **<0.0001**	-0.483 ± 0.227 -2.129 **0.037**	-0.790 ± 0.254 -3.115 **0.003**	-0.166 ± 0.145 -1.147 **0.256**	-0.293 ± 0.357 -0.821 **0.415**	0.322 ± 0.516 0.624 **0.535**	0.214 ± 0.220 0.973 **0.334**	-0.223 ± 0.264 -0.842 **0.403**	-0.301 ± 0.306 -0.983 **0.329**	-0.020 ± 0.368 -0.055 **0.956**	0.391 ± 0.121 3.230 **0.002**	0.211 ± 0.532 0.397 **0.693**	0.527 ± 0.190 2.770 **0.007**	$J^{0.92}$ **HU>HD>CV**
$J^{0.42}$ **HU>HD=CV**	-1.486 ± 0.273 -5.438 **<0.0001**	-2.097 ± 0.130 -16.127 **<0.0001**	-1.642 ± 0.205 -8.017 **<0.0001**	-1.950 ± 0.234 -8.319 **<0.0001**	-1.326 ± 0.108 -12.323 **<0.0001**	-1.453± 0.344 -4.228 **0.0001**	-0.839 ± 0.506 -1.655 **0.103**	-0.946 ± 0.197 -4.796 **<0.0001**	-1.382 ± 0.246 -5.621 **<0.0001**	-1.460 ± 0.290 -5.038 **<0.0001**	-1.180 ± 0.355 -3.320 **0.002**	-0.769 ± 0.072 -10.633 **<0.0001**	-0.948 ± 0.523 -1.812 **0.075**	-0.632 ± 0.164 -3.863 **0.0003**	-1.160 ± 0.121 -9.579 **<0.0001**	$J^{0.42}$ **HU>HD=CV**

Model S18: Median mixed depth of particle reworking ($^{f\text{-}SPI}L_{median}$, cm)

Initial linear regression model:

$Lm(^{f\text{-}SPI}L_{median} \sim SpD)$

Minimal adequate model:

$Lm(^{f\text{-}SPI}L_{median} \sim SpD)$

(SpD, F = 4.17, d.f. = 15, p = <0.0001)

Coefficient table model S18 (method = 'REML'): 2.151 ± 0.233, t = 9.251, p = <0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold. CV = *Corophium volutator*, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*

	J1.00													
J0.64 CV>HD>HU	1.099 ± 0.329 3.341 **0.001**	J0.64 CV>HD>HU												
J0.92 CV>HD>HU	0.366 ± 0.329 1.112 **0.270**	-0.733 ± 0.329 -2.229 **0.029**	J0.92 CV>HD>HU											
J0.64 CV>HU>HD	0.937 ± 0.329 2.850 **0.006**	-0.161 ± 0.329 -0.490 **0.625**	0.572 ± 0.329 1.739 **0.087**	J0.64 CV>HU>HD										
J0.92 CV>HU>HD	0.216 ± 0.329 0.658 **0.513**	-0.882 ± 0.329 -2.683 **0.009**	-0.149 ± 0.329 -0.454 **0.652**	-0.721 ± 0.329 -2.192 **0.032**	J0.92 CV>HU>HD									
J0.42 CV>HU=HD	0.394 ± 0.329 1.198 **0.236**	-0.705 ± 0.329 -2.143 **0.036**	0.028 ± 0.329 0.086 **0.932**	-0.544 ± 0.329 -1.653 **0.103**	0.178 ± 0.329 0.540 **0.591**	J0.42 CV>HU=HD								
J0.64 HD>HU>CV	-1.531 ± 0.329 -4.655 **<0.0001**	-2.630 ± 0.329 -7.996 **<0.0001**	-1.897 ± 0.329 -5.767 **<0.0001**	-2.469 ± 0.329 -7.505 **<0.0001**	-1.747 ± 0.329 -5.313 **<0.0001**	-1.925 ± 0.329 -5.853 **<0.0001**	J0.64 HD>HU>CV							
J0.92 HD>HU>CV	-1.107 ± 0.329 -3.365 **0.001**	-2.205 ± 0.329 -6.706 **<0.0001**	-1.472 ± 0.329 -4.476 **<0.0001**	-2.044 ± 0.329 -6.215 **<0.0001**	-1.323 ± 0.329 -4.023 **<0.0001**	-1.501 ± 0.329 -4.562 **<0.0001**	0.424 ± 0.329 1.290 **0.202**	J0.92 HD>HU>CV						
J0.64 HD>CV>HU	-0.738 ± 0.329 -2.243 **0.028**	-1.837 ± 0.329 -5.584 **<0.0001**	-1.103 ± 0.329 -3.355 **0.001**	-1.675 ± 0.329 -5.094 **<0.0001**	-0.954 ± 0.329 -2.901 **0.005**	-1.132 ± 0.329 -3.441 **0.001**	0.793 ± 0.329 2.412 **0.019**	0.369 ± 0.329 1.122 **0.266**	J0.64 HD>CV>HU					
J0.92 HD>CV>HU	-0.044 ± 0.329 -0.133 **0.895**	-1.143 ± 0.329 -3.474 **0.001**	-0.409 ± 0.329 -1.244 **0.218**	-0.981 ± 0.329 -2.983 **0.004**	-0.260 ± 0.329 -0.791 **0.432**	-0.438 ± 0.329 -1.330 **0.188**	1.487 ± 0.329 4.522 **<0.0001**	1.063 ± 0.329 3.232 **0.002**	0.694 ± 0.329 2.110 **0.039**	J0.92 HD>CV>HU				
J0.42 HD>CV=HU	-1.469 ± 0.329 -4.467 **<0.0001**	-2.568 ± 0.329 -7.808 **<0.0001**	-1.835 ± 0.329 -5.579 **<0.0001**	-2.407 ± 0.329 -7.317 **<0.0001**	-1.686 ± 0.329 -5.125 **<0.0001**	-1.863 ± 0.329 -5.665 **<0.0001**	0.062 ± 0.329 0.188 **0.851**	-0.363 ± 0.329 -1.102 **0.274**	-0.731 ± 0.329 -2.224 **0.030**	-1.426 ± 0.329 -4.334 **<0.0001**	J0.42 HD>CV=HU			
J0.64 HU>CV>HD	-1.022 ± 0.329 -3.108 **0.003**	-2.121 ± 0.329 -6.448 **<0.0001**	-1.388 ± 0.329 -4.219 **<0.0001**	-1.960 ± 0.329 -5.958 **<0.0001**	-1.238 ± 0.329 -3.765 **<0.0001**	-1.416 ± 0.329 -4.305 **<0.0001**	0.509 ± 0.329 1.548 **0.127**	0.085 ± 0.329 0.257 **0.798**	-0.284 ± 0.329 -0.864 **0.391**	-0.978 ± 0.329 -2.975 **0.004**	0.447 ± 0.329 1.360 **0.179**	J0.64 HU>CV>HD		
J0.92 HU>CV>HD	-0.071 ± 0.329 -0.215 **0.830**	-1.170 ± 0.329 -3.556 **0.001**	-0.436 ± 0.329 -1.327 **0.189**	-1.008 ± 0.329 -3.065 **0.003**	-0.287 ± 0.329 -0.873 **0.386**	-0.465 ± 0.329 -1.413 **0.163**	1.460 ± 0.329 4.440 **<0.0001**	1.036 ± 0.329 3.150 **0.002**	0.667 ± 0.329 2.028 **0.047**	-0.027 ± 0.329 -0.082 **0.935**	1.398 ± 0.329 4.252 **<0.0001**	0.951 ± 0.329 2.892 **0.005**	J0.92 HU>CV>HD	
J0.64 HU>HD>CV	-1.524 ± 0.329 -4.634 **<0.0001**	-2.623 ± 0.329 -7.975 **<0.0001**	-1.890 ± 0.329 -5.746 **<0.0001**	-2.462 ± 0.329 -7.484 **<0.0001**	-1.741 ± 0.329 -5.292 **<0.0001**	-1.918 ± 0.329 -5.832 **<0.0001**	0.007 ± 0.329 0.021 **0.983**	-0.418 ± 0.329 -1.269 **0.209**	-0.786 ± 0.329 -2.391 **0.020**	-1.480 ± 0.329 -4.501 **<0.0001**	-0.055 ± 0.329 -0.167 **0.868**	-0.502 ± 0.329 -1.527 **0.132**	-1.453 ± 0.329 -4.419 **<0.0001**	J0.64 HU>HD>CV
J0.92 HU>HD>CV	-0.848 ± 0.329 -2.579 **0.012**	-1.947 ± 0.329 -5.920 **<0.0001**	-1.214 ± 0.329 -3.691 **<0.0001**	-1.786 ± 0.329 -5.429 **<0.0001**	-1.065 ± 0.329 -3.237 **0.002**	-1.242 ± 0.329 -3.777 **<0.0001**	0.683 ± 0.329 2.076 **0.042**	0.258 ± 0.329 0.786 **0.435**	-0.110 ± 0.329 -0.336 **0.738**	-0.805 ± 0.329 -2.446 **0.017**	0.621 ± 0.329 1.888 **0.064**	0.174 ± 0.329 0.529 **0.599**	-0.777 ± 0.329 -2.364 **0.021**	0.676 ± 0.329 2.055 **0.044**	J0.92 HU>HD>CV
J0.42 HU>HD=CV	-1.677 ± 0.329 -5.098 **<0.0001**	-2.776 ± 0.329 -8.439 **<0.0001**	-2.042 ± 0.329 -6.210 **<0.0001**	-2.614 ± 0.329 -7.948 **<0.0001**	-1.893 ± 0.329 -5.756 **<0.0001**	-2.071 ± 0.329 -6.296 **<0.0001**	-0.146 ± 0.329 -0.443 **0.659**	-0.570 ± 0.329 -1.733 **0.088**	-0.939 ± 0.329 -2.855 **0.006**	-1.633 ± 0.329 -4.965 **<0.0001**	-0.208 ± 0.329 -0.631 **0.530**	-0.655 ± 0.329 -1.990 **0.051**	-1.606 ± 0.329 -4.883 **<0.0001**	-0.153 ± 0.329 -0.464 **0.644**	-0.829 ± 0.329 -2.519 **0.014**	J0.42 HU>HD=CV

Model S19: Surface boundary roughness (SBR, cm)

Initial linear regression model:

Lm(SBR~ SpD)

Minimal adequate model:

gls(SBR~ SpD, weights = varIdent (form = ~ 1|SpD), method = 'ML')

(SBR, L-ratio = 36.98, d.f. = 15, p = 0.001)

Coefficient table model S19 (method = 'REML'): Intercept ± SE (For baseline J = 1): 0.927 ± 0.162, t = 5.717, p = <0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold. CV = *Corophium volutator*, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*

	J1.00																
J0.64 CV>HD>HU	0.022 ± 0.196 0.114 **0.910**	J0.64 CV>HD>HU															
J0.92 CV>HD>HU	0.0528 ± 0.201 0.262 **0.794**	0.0305 ± 0.162 0.188 **0.851**	J0.92 CV>HD>HU														
J0.64 CV>HU>HD	0.327 ± 0.230 1.423 **0.160**	0.304 ± 0.196 1.554 **0.125**	0.282 ± 0.142 1.983 **0.052**	J0.64 CV>HU>HD													
J0.92 CV>HU>HD	0.205 ± 0.194 1.057 **0.294**	0.183 ± 0.152 1.198 **0.235**	0.555 ± 0.180 3.091 **0.003**	-0.274 ± 0.202 -1.358 **0.179**	J0.92 CV>HU>HD												
J0.42 CV>HU=HD	0.238 ± 0.2814 0.847 **0.400**	0.216 ± 0.255 0.848 **0.400**	0.434 ± 0.131 3.314 **0.002**	-0.122 ± 0.194 -0.628 **0.532**	-0.152 ± 0.160 -0.952 **0.344**	J0.42 CV>HU=HD											
J0.64 HD>HU>CV	-0.112 ± 0.182 -0.616 **0.540**	-0.135 ± 0.137 -0.979 **0.331**	0.467 ± 0.242 1.927 **0.058**	-0.088 ± 0.281 -0.314 **0.755**	0.034 ± 0.253 0.133 **0.895**	-0.351 ± 0.244 -1.434 **0.156**	J0.64 HD>HU>CV										
J0.92 HD>HU>CV	-0.082 ± 0.171 -0.478 **0.634**	-0.104 ± 0.122 -0.853 **0.397**	0.117 ± 0.113 1.031 **0.307**	-0.439 ± 0.182 -2.406 **0.019**	-0.317 ± 0.134 -2.357 **0.022**	-0.320 ± 0.236 -1.356 **0.180**	0.031 ± 0.098 0.312 **0.756**	J0.92 HD>HU>CV									
J0.64 HD>CV>HU	-0.077 ± 0.168 -0.458 **0.648**	-0.099 ± 0.118 -0.841 **0.403**	0.147 ± 0.093 1.578 **0.120**	-0.408 ± 0.171 -2.389 **0.020**	-0.286 ± 0.118 -2.419 **0.018**	-0.315 ± 0.234 -1.347 **0.183**	0.035 ± 0.094 0.377 **0.707**	0.005 ± 0.069 0.068 **0.946**	J0.64 HD>CV>HU								
J0.92 HD>CV>HU	-0.229 ± 0.179 -1.275 **0.207**	-0.251 ± 0.134 -1.876 **0.065**	0.152 ± 0.088 1.719 **0.090**	-0.403 ± 0.168 -2.400 **0.019**	-0.282 ± 0.114 -2.461 **0.017**	-0.467 ± 0.242 -1.927 **0.058**	-0.117 ± 0.113 -1.031 **0.307**	-0.147 ± 0.093 -1.578 **0.120**	-0.152 ± 0.088 -1.719 **0.090**	J0.92 HD>CV>HU							
J0.42 HD>CV=HU	-0.115 ± 0.181 -0.637 **0.526**	-0.137 ± 0.135 -1.015 **0.314**	0.114 ± 0.110 1.031 **0.307**	-0.442 ± 0.181 -2.443 **0.017**	-0.320 ± 0.132 -2.418 **0.019**	-0.353 ± 0.243 -1.454 **0.151**	-0.003 ± 0.115 -0.024 **0.981**	-0.033 ± 0.095 -0.351 **0.727**	-0.038 ± 0.090 -0.421 **0.675**	0.114 ± 0.110 1.031 **0.307**	J0.42 HD>CV=HU						
J0.64 HU>CV>HD	-0.155 ± 0.193 -0.805 **0.424**	-0.178 ± 0.152 -1.172 **0.246**	0.073 ± 0.130 0.565 **0.574**	-0.482 ± 0.193 -2.493 **0.015**	-0.360 ± 0.149 -2.418 **0.019**	-0.394 ± 0.253 -1.558 **0.124**	-0.043 ± 0.134 -0.322 **0.748**	-0.074 ± 0.117 -0.629 **0.532**	-0.078 ± 0.113 -0.691 **0.492**	0.073 ± 0.130 0.565 **0.574**	-0.040 ± 0.131 -0.307 **0.760**	J0.64 HU>CV>HD					
J0.92 HU>CV>HD	0.020 ± 0.237 0.084534 **0.933**	-0.002 ± 0.204 -0.011 **0.991**	0.249 ± 0.189 1.317 **0.193**	-0.307 ± 0.237 -1.293 **0.201**	-0.185 ± 0.203 -0.912 **0.365**	-0.218 ± 0.288 -0.759 **0.451**	0.132 ± 0.192 0.691 **0.492**	0.102 ± 0.181 0.562 **0.576**	0.097 ± 0.178 0.544 **0.588**	0.249 ± 0.189 1.317 **0.193**	0.135 ± 0.190 0.711 **0.480**	0.175 ± 0.202 0.868 **0.389**	J0.92 HU>CV>HD				
J0.64 HU>HD>CV	-0.222 ± 0.167 -1.324 **0.190**	-0.244 ± 0.117 -2.082 **0.041**	0.007 ± 0.087 0.083 **0.934**	-0.548 ± 0.168 -3.270 **0.002**	-0.426 ± 0.114 -3.750 **<0.001**	-0.460 ± 0.234 -1.968 **0.053**	-0.109 ± 0.093 -1.178 **0.243**	-0.140 ± 0.067 -2.082 **0.041**	-0.145 ± 0.060 -2.405 **0.019**	0.007 ± 0.087 0.083 **0.934**	-0.107 ± 0.089 -1.191 **0.238**	-0.066 ± 0.113 -0.587 **0.559**	-0.242 ± 0.178 -1.360 **0.179**	J0.64 HU>HD>CV			
J0.92 HU>HD>CV	-0.284 ± 0.178 -1.593 **0.116**	-0.306 ± 0.132 -2.315 **0.024**	-0.055 ± 0.107 -0.516 **0.607**	-0.611 ± 0.179 -3.420 **0.001**	-0.489 ± 0.129 -3.782 **<0.001**	-0.522 ± 0.242 -2.162 **0.034**	-0.172 ± 0.111 -1.544 **0.128**	-0.202 ± 0.091 -2.222 **0.030**	-0.207 ± 0.086 -2.409 **0.019**	-0.055 ± 0.107 -0.516 **0.607**	-0.169 ± 0.109 -1.557 **0.124**	-0.129 ± 0.128 -1.002 **0.320**	-0.304 ± 0.188 -1.618 **0.111**	-0.062 ± 0.085 -0.735 **0.465**	J0.92 HU>HD>CV		
J0.42 HU>HD=CV	-0.244 ± 0.168 -1.452 **0.152**	-0.266 ± 0.118 -2.257 **0.027**	-0.015 ± 0.088 -0.169 **0.866**	-0.570 ± 0.168 -3.392 **0.001**	-0.449 ± 0.114 -3.918 **<0.001**	-0.482 ± 0.234 -2.060 **0.044**	-0.132 ± 0.094 -1.404 **0.165**	-0.162 ± 0.069 -2.366 **0.021**	-0.167 ± 0.062 -2.709 **0.009**	-0.015 ± 0.088 -0.169 **0.866**	-0.129 ± 0.090 -1.424 **0.159**	-0.088 ± 0.114 -0.779 **0.439**	-0.264 ± 0.178 -1.481 **0.143**	-0.022 ± 0.060 -0.369 **0.713**	0.040 ± 0.086 0.468 **0.642**	J0.42 HU>HD=CV

Model S20: Max mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{max}$~ SpD)

No minimal adequate model, intercept only (SpD, F = 1.29, d.f. = 15, p = 0.237)

Model S21: Bioirrigation ($\Delta[Br^-]$, mg L^{-1})

Initial linear regression model:

Lm($\Delta[Br^-]$ ~ SpD)

Minimal adequate model:

gls($\Delta[Br^-]$ ~ SpD, weights = varIdent (form = ~ 1|SpD), method = 'ML')

(SpD, L-ratio = 26.06, d.f. = 15, p = 0.037)

Coefficient table model S21 (method = 'REML'): Intercept ± SE (For baseline J = 1): -65.983 ± 49.668, t = -1.328, p = 0.189. Coefficients ± SE and t-values are presented. Significance values are in bold. CV = *Corophium volutator*, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*

	$J^{1.00}$																			
$J^{0.64}$ **CV>HD>HU**	13.900 ± 62.673 0.222 **0.825**	$J^{0.64}$ **CV>HD>HU**																		
$J^{0.92}$ **CV>HD>HU**	-60.752 ± 109.759 -0.554 **0.582**	-74.653 ± 105.077 -0.710 **0.480**	$J^{0.92}$ **CV>HD>HU**																	
$J^{0.64}$ **CV>HU>HD**	124.089 ± 50.416 2.461 **0.017**	110.189 ± 39.189 2.812 **0.007**	184.841 ± 98.260 1.881 **0.065**	$J^{0.64}$ **CV>HU>HD**																
$J^{0.92}$ **CV>HU>HD**	133.081 ± 101.972 1.305 **0.197**	119.181 ± 96.913 1.230 **0.223**	193.833 ± 132.331 1.465 **0.148**	8.992 ± 89.477 0.100 **0.920**	$J^{0.92}$ **CV>HU>HD**															
$J^{0.42}$ **CV>HU≡HD**	64.734 ± 73.867 0.876 **0.384**	50.833 ± 66.711 0.762 **0.449**	125.486 ± 112.114 1.119 **0.267**	-59.355 ± 55.356 -1.072 **0.288**	-68.348 ± 104.502 -0.654 **0.515**	$J^{0.42}$ **CV>HU≡HD**														
$J^{0.64}$ **HD>HU>CV**	-30.806 ± 103.813 -0.297 **0.768**	-44.706 ± 98.849 -0.452 **0.653**	29.947 ± 133.755 0.224 **0.824**	-154.895 ± 91.570 -1.692 **0.096**	-163.887 ± 127.442 -1.286 **0.203**	-95.539 ± 106.299 -0.899 **0.372**	$J^{0.64}$ **HD>HU>CV**													
$J^{0.92}$ **HD>HU>CV**	92.826 ± 54.593 1.700 **0.094**	78.925 ± 44.435 1.776 **0.081**	153.578 ± 100.468 1.529 **0.131**	-31.263 ± 24.257 -1.289 **0.202**	-40.256 ± 91.896 -0.438 **0.663**	28.092 ± 59.185 0.475 **0.637**	123.631 ± 93.934 1.316 **0.193**	$J^{0.92}$ **HD>HU>CV**												
$J^{0.64}$ **HD>CV>HU**	1.162 ± 98.178 0.012 **0.991**	-12.739 ± 92.914 -0.137 **0.891**	61.914 ± 129.431 0.478 **0.634**	-122.927 ± 85.129 -1.444 **0.154**	-131.919 ± 122.896 -1.073 **0.287**	-63.572 ± 100.804 -0.631 **0.531**	31.967 ± 124.428 0.257 **0.798**	-91.664 ± 87.667 -1.046 **0.300**	$J^{0.64}$ **HD>CV>HU**											
$J^{0.92}$ **HD>CV>HU**	71.115 ± 75.006 0.948 **0.347**	57.215 ± 67.970 0.842 **0.403**	131.867 ± 112.868 1.168 **0.247**	-52.974 ± 56.867 -0.932 **0.355**	-61.966 ± 105.310 -0.588 **0.558**	6.382 ± 78.411 0.081 **0.935**	101.921 ± 107.094 0.952 **0.345**	-21.710 ± 60.601 -0.358 **0.721**	69.953 ± 101.642 0.688 **0.494**	$J^{0.92}$ **HD>CV>HU**										
$J^{0.42}$ **HD>CV≡HU**	61.282 ± 51.781 1.183 **0.241**	47.381 ± 40.930 1.158 **0.251**	122.034 ± 98.967 1.233 **0.222**	-62.807 ± 17.006 -3.693 **0.001**	-71.800 ± 90.253 -0.796 **0.429**	-3.452 ± 56.601 -0.061 **0.952**	92.087 ± 92.328 0.997 **0.322**	-31.544 ± 26.979 -1.169 **0.247**	60.120 ± 85.944 0.700 **0.487**	-9.834 ± 58.080 -0.169 **0.866**	$J^{0.42}$ **HD>CV≡HU**									
$J^{0.64}$ **HU>CV>HD**	5.185 ± 101.491 0.051 **0.959**	-8.716 ± 96.408 -0.090 **0.928**	65.937 ± 131.961 0.500 **0.619**	-118.904 ± 88.929 -1.337 **0.186**	-127.897 ± 125.558 -1.019 **0.312**	-59.549 ± 104.033 -0.572 **0.569**	35.990 ± 127.058 0.283 **0.778**	-87.641 ± 91.362 -0.959 **0.341**	4.023 ± 122.497 0.033 **0.974**	-65.931 ± 104.845 -0.629 **0.532**	-56.097 ± 89.710 -0.625 **0.534**	$J^{0.64}$ **HU>CV>HD**								
$J^{0.92}$ **HU>CV>HD**	36.293 ± 96.090 0.378 **0.707**	22.393 ± 90.704 0.247 **0.806**	97.045 ± 127.854 0.759 **0.451**	-87.796 ± 82.711 -1.061 **0.293**	-96.788 ± 121.234 -0.798 **0.428**	-28.440 ± 98.771 -0.288 **0.774**	67.099 ± 122.786 0.546 **0.587**	-56.532 ± 85.322 -0.663 **0.510**	35.131 ± 118.061 0.298 **0.767**	-34.822 ± 99.626 -0.350 **0.728**	-24.988 ± 83.550 -0.299 **0.766**	31.109 ± 120.830 0.257 **0.798**	$J^{0.92}$ **HU>CV>HD**							
$J^{0.64}$ **HU>HD>CV**	42.508 ± 57.731 0.736 **0.464**	28.607 ± 48.238 0.593 **0.555**	103.260 ± 102.207 1.010 **0.316**	-81.581 ± 30.674 -2.660 **0.010**	-90.573 ± 93.794 -0.966 **0.338**	-22.226 ± 62.092 -0.358 **0.722**	73.313 ± 95.792 0.765 **0.447**	-50.318 ± 37.142 -1.355 **0.180**	41.346 ± 89.655 0.461 **0.646**	-28.607 ± 63.443 -0.451 **0.654**	-18.774 ± 32.868 -0.571 **0.570**	37.323 ± 93.271 0.400 **0.690**	6.215 ± 87.363 0.071 **0.944**	$J^{0.64}$ **HU>HD>CV**						
$J^{0.92}$ **HU>HD>CV**	-44.838 ± 106.727 -0.420 **0.676**	-58.739 ± 101.905 -0.576 **0.566**	15.914 ± 136.029 0.117 **0.907**	-168.927 ± 94.861 -1.781 **0.080**	-177.919 ± 129.827 -1.370 **0.175**	-109.572 ± 109.147 -1.004 **0.319**	-14.033 ± 131.278 -0.107 **0.915**	-137.664 ± 97.146 -1.417 **0.161**	-46.000 ± 126.869 -0.363 **0.718**	-115.953 ± 109.922 -1.055 **0.295**	-106.120 ± 95.593 -1.110 **0.271**	-50.023 ± 129.450 -0.386 **0.701**	-81.131 ± 125.260 -0.648 **0.520**	-87.346 ± 98.943 -0.883 **0.381**	$J^{0.92}$ **HU>HD>CV**				
$J^{0.42}$ **HU>HD≡CV**	42.377 ± 52.894 0.801 **0.426**	28.477 ± 42.330 0.673 **0.504**	103.130 ± 99.554 1.036 **0.304**	-81.712 ± 20.143 -4.057 **<0.0001**	-90.704 ± 90.896 -0.998 **0.322**	-22.356 ± 57.621 -0.388 **0.699**	73.183 ± 92.957 0.787 **0.434**	-50.448 ± 29.058 -1.736 **0.087**	41.216 ± 86.619 0.476 **0.636**	-28.738 ± 59.075 -0.486 **0.628**	-18.904 ± 23.349 -0.810 **0.421**	37.193 ± 90.357 0.412 **0.682**	6.084 ± 84.245 0.072 **0.943**	-0.130 ± 34.596 -0.004 **0.997**	87.216 ± 96.201 0.907 **0.368**	$J^{0.42}$ **HU>HD≡CV**			

Model S22: NH_4-N concentration ([NH_4-N], mg L^{-1})

Initial linear regression model:

Lm([NH_4-N] ~ SpD)

Minimal adequate model:

gls([NH_4-N] ~ SpD, weights = varIdent (form = ~ 1|SpD), method = 'ML')

(SpD, L-ratio = 79.21, d.f. = 15, p = <0.0001)

Coefficient table model S22: Intercept ± SE (For baseline J = 1): 0.556 ± 0.064, t = 8.696, p = <0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold. CV = *Corophium volutator*, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*

	$J^{1.00}$												
$J^{0.64}$ CV>HD>HU	0.522 ± 0.090 5.782 **<0.0001**	$J^{0.64}$ CV>HD>HU											
$J^{0.92}$ CV>HD>HU	0.237 ± 0.096 2.459 **0.017**	-0.287 ± 0.096 -2.992 **0.004**	$J^{0.92}$ CV>HD>HU										
$J^{0.64}$ CV>HU>HD	0.506 ± 0.096 5.282 **<0.0001**	-0.016 ± 0.096 -0.170 **0.866**	0.271 ± 0.101 2.678 **0.010**	$J^{0.64}$ CV>HU>HD									
$J^{0.92}$ CV>HU>HD	0.130 ± 0.096 1.355 **0.181**	-0.393 ± 0.096 -4.096 **0.0001**	-0.106 ± 0.101 -1.047 **0.300**	-0.376 ± 0.101 -3.725 **<0.001**	$J^{0.92}$ CV>HU>HD								
$J^{0.42}$ CV>HU=HD	0.464 ± 0.090 5.131 **<0.0001**	-0.059 ± 0.090 -0.651 **0.518**	0.228 ± 0.096 2.379 **0.021**	-0.043 ± 0.096 -0.444 **0.659**	0.334 ± 0.096 3.482 **0.001**	$J^{0.42}$ CV>HU=HD							
$J^{0.64}$ HD>HU>CV	0.049 ± 0.096 0.513 **0.610**	-0.473 ± 0.096 -4.938 **<0.0001**	-0.187 ± 0.101 -1.846 **0.070**	-0.457 ± 0.101 -4.524 **<0.0001**	-0.081 ± 0.101 -0.799 **0.427**	-0.414 ± 0.096 -4.325 **0.0001**	$J^{0.64}$ HD>HU>CV						
$J^{0.92}$ HD>HU>CV	0.083 ± 0.090 0.923 **0.360**	-0.439 ± 0.090 -4.859 **<0.0001**	-0.152 ± 0.096 -1.589 **0.118**	-0.423 ± 0.096 -4.411 **<0.0001**	-0.047 ± 0.096 -0.485 **0.629**	-0.380 ± 0.090 -4.208 **0.0001**	0.034 ± 0.096 0.357 **0.722**	$J^{0.92}$ HD>HU>CV					
$J^{0.64}$ HD>CV>HU	-0.068 ± 0.090 -0.757 **0.452**	-0.591 ± 0.090 -6.539 **<0.0001**	-0.304 ± 0.096 -3.173 **0.002**	-0.575 ± 0.096 -5.995 **<0.0001**	-0.198 ± 0.096 -2.069 **0.043**	-0.532 ± 0.090 -5.888 **<0.0001**	-0.118 ± 0.096 -1.227 **0.225**	-0.152 ± 0.090 -1.680 **0.098**	$J^{0.64}$ HD>CV>HU				
$J^{0.92}$ HD>CV>HU	-0.036 ± 0.090 -0.398 **0.692**	-0.558 ± 0.090 -6.180 **<0.0001**	-0.272 ± 0.096 -2.835 **0.006**	-0.542 ± 0.096 -5.657 **<0.0001**	-0.166 ± 0.096 -1.731 **0.089**	-0.500 ± 0.090 -5.529 **<0.0001**	-0.085 ± 0.096 -0.889 **0.378**	-0.119 ± 0.090 -1.321 **0.192**	0.032 ± 0.090 0.359 **0.721**	$J^{0.92}$ HD>CV>HU			
$J^{0.42}$ HD>CV=HU	-0.047 ± 0.090 -0.522 **0.603**	-0.570 ± 0.090 -6.304 **<0.0001**	-0.283 ± 0.096 -2.951 **0.005**	-0.553 ± 0.096 -5.774 **<0.0001**	-0.177 ± 0.096 -1.848 **0.070**	-0.511 ± 0.090 -5.653 **<0.0001**	-0.096 ± 0.096 -1.005 **0.310**	-0.130 ± 0.090 -1.445 **0.154**	0.021 ± 0.090 0.235 **0.815**	-0.011 ± 0.090 -0.124 **0.902**	$J^{0.42}$ HD>CV=HU		
$J^{0.64}$ HU>CV>HD	0.082 ± 0.090 0.903 **0.370**	-0.441 ± 0.090 -4.879 **<0.0001**	-0.154 ± 0.096 -1.607 **0.113**	-0.425 ± 0.096 -4.430 **<0.0001**	-0.048 ± 0.096 -0.504 **0.616**	-0.382 ± 0.090 -4.228 **0.0001**	0.032 ± 0.096 0.339 **0.736**	-0.002 ± 0.090 -0.020 **0.984**	0.150 ± 0.090 1.66 **0.102**	0.118 ± 0.090 1.302 **0.198**	0.129 ± 0.090 1.426 **0.159**	$J^{0.64}$ HU>CV>HD	
$J^{0.92}$ HU>CV>HD	0.126 ± 0.096 1.316 **0.193**	-0.396 ± 0.096 -4.135 **0.0001**	-0.110 ± 0.101 -1.084 **0.283**	-0.380 ± 0.101 -3.762 **<0.001**	-0.004 ± 0.101 -0.037 **0.971**	-0.337 ± 0.096 -3.521 **0.001**	0.077 ± 0.101 0.762 **0.449**	0.043 ± 0.096 0.446 **0.657**	0.195 ± 0.096 2.030 **0.047**	0.162 ± 0.096 1.692 **0.096**	0.173 ± 0.096 1.809 **0.076**	0.0446 ± 0.096 0.465 **0.644**	$J^{0.92}$ HU>CV>HD
$J^{0.64}$ HU>HD>CV	0.212 ± 0.090 2.351 **0.022**	-0.310 ± 0.090 -3.431 **0.001**	-0.023 ± 0.096 -0.243 **0.809**	-0.294 ± 0.096 -3.065 **0.003**	0.083 ± 0.096 0.861 **0.393**	-0.251 ± 0.090 -2.780 **0.007**	0.163 ± 0.096 1.703 **0.094**	0.129 ± 0.090 1.428 **0.159**	0.281 ± 0.090 3.108 **0.003**	0.248 ± 0.090 2.749 **0.008**	0.260 ± 0.090 2.873 **0.006**	0.131 ± 0.090 1.448 **0.153**	0.086 ± 0.09583 0.900 **0.372**	$J^{0.64}$ HU>HD>CV
$J^{0.92}$ HU>HD>CV	0.079 ± 0.090 0.879 **0.383**	-0.443 ± 0.090 -4.903 **<0.0001**	-0.156 ± 0.096 -1.630 **0.108**	-0.427 ± 0.096 -4.453 **<0.0001**	-0.051 ± 0.096 -0.527 **0.600**	-0.384 ± 0.090 -4.252 **0.0001**	0.030 ± 0.096 0.316 **0.753**	-0.004 ± 0.090 -0.044 **0.965**	0.148 ± 0.090 1.636 **0.107**	0.115 ± 0.090 1.277 **0.207**	0.127 ± 0.090 1.401 **0.166**	-0.002 ± 0.090 -0.024 **0.981**	-0.047 ± 0.096 -0.488 **0.628**	-0.133 ± 0.090 -1.472 **0.146**	$J^{0.92}$ HU>HD>CV
$J^{0.42}$ HU>HD=CV	0.252 ± 0.096 2.631 **0.011**	-0.270 ± 0.096 -2.820 **0.007**	0.017 ± 0.101 0.163 **0.871**	-0.254 ± 0.101 -2.514 **0.015**	0.122 ± 0.101 1.210 **0.231**	-0.211 ± 0.096 -2.206 **0.031**	0.203 ± 0.101 2.010 **0.049**	0.169 ± 0.096 1.761 **0.084**	0.321 ± 0.096 3.345 **0.001**	0.288 ± 0.096 3.007 **0.004**	0.299 ± 0.096 3.124 **0.003**	0.171 ± 0.096 1.780 **0.080**	0.126 ± 0.101 1.247 **0.217**	0.040 ± 0.096 0.415 **0.680**	0.173 ± 0.096 1.803 **0.077**	$J^{0.42}$ HU>HD=CV

Model S23: NO_x-N concentration ([NO_x-N], mg L^{-1})

Initial linear regression model:

Lm([NO_x-N] ~ SpD)

Minimal adequate model:

gls([NO_x-N] ~ SpD, weights = varIdent (form = ~ 1|SpD), method = 'ML')

(SpD, L-ratio = 8.53, d.f. = 15, p = <0.0001)

Coefficient table model S23 (method = 'REML'): Intercept ± SE (For baseline J = 1): 2.097 ± 0.258, t = 8.140, p < 0.0001. Coefficients ± SE and t-values are presented. Significance values are in bold. CV = *Corophium volutator*, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*

	J1.00														
J0.64 CV>HD>HU	-1.275 ± 0.374 -3.406 **0.001**	J0.64 CV>HD>HU													
J0.92 CV>HD>HU	-0.740 ± 0.373 -1.985 **0.052**	0.535 ± 0.382 1.398 **0.167**	J0.92 CV>HD>HU												
J0.64 CV>HU>HD	-1.127 ± 0.351 -3.212 **0.002**	0.148 ± 0.361 0.408 **0.685**	-0.387 ± 0.360 -1.076 **0.286**	J0.64 CV>HU>HD											
J0.92 CV>HU>HD	-0.161 ± 0.305 -0.528 **0.600**	1.114 ± 0.317 3.513 **0.001**	0.579 ± 0.315 1.836 **0.071**	0.966 ± 0.289 3.340 **0.002**	J0.92 CV>HU>HD										
J0.42 CV>HU=HD	-0.504 ± 0.634 -0.795 **0.430**	0.771 ± 0.640 1.205 **0.233**	0.236 ± 0.639 0.370 **0.713**	0.623 ± 0.626 0.995 **0.324**	-0.343 ± 0.602 -0.570 **0.571**	J0.42 CV>HU=HD									
J0.64 HD>HU>CV	0.755 ± 0.282 2.680 **0.010**	2.030 ± 0.294 6.895 **<0.0001**	1.495 ± 0.292 5.111 **<0.0001**	1.882 ± 0.264 7.124 **<0.0001**	0.916 ± 0.199 4.593 **<0.0001**	1.259 ± 0.590 2.133 **0.037**	J0.64 HD>HU>CV								
J0.92 HD>HU>CV	0.344 ± 0.325 1.056 **0.295**	1.618 ± 0.336 4.811 **<0.0001**	1.084 ± 0.335 3.237 **0.002**	1.471 ± 0.310 4.739 **<0.0001**	0.505 ± 0.257 1.960 **0.055**	0.848 ± 0.612 1.384 **0.172**	-0.411 ± 0.229 -1.796 **0.078**	J0.92 HD>HU>CV							
J0.64 HD>CV>HU	0.615 ± 0.329 1.870 **0.067**	1.890 ± 0.340 5.558 **<0.0001**	1.355 ± 0.338 4.005 **<0.0001**	1.743 ± 0.314 5.544 **<0.0001**	0.776 ± 0.262 2.961 **0.004**	1.119 ± 0.614 1.822 **0.074**	-0.140 ± 0.234 -0.596 **0.554**	0.272 ± 0.285 0.952 **0.345**	J0.64 HD>CV>HU						
J0.92 HD>CV>HU	0.056 ± 0.341 0.165 **0.869**	1.331 ± 0.352 3.783 **<0.0001**	0.796 ± 0.350 2.274 **0.027**	1.184 ± 0.327 3.619 **0.001**	0.217 ± 0.277 0.784 **0.436**	0.560 ± 0.621 0.903 **0.370**	-0.698 ± 0.251 -2.781 **0.007**	-0.287 ± 0.299 -0.960 **0.341**	-0.559 ± 0.303 -1.842 **0.071**	J0.92 HD>CV>HU					
J0.42 HD>CV=HU	0.924 ± 0.316 2.924 **0.005**	2.199 ± 0.327 6.715 **<0.0001**	1.664 ± 0.326 5.108 **<0.0001**	2.051 ± 0.301 6.823 **<0.0001**	1.085 ± 0.246 4.417 **<0.0001**	1.428 ± 0.607 2.351 **0.022**	0.169 ± 0.216 0.785 **0.435**	0.580 ± 0.270 2.148 **0.036**	0.309 ± 0.275 1.124 **0.266**	0.868 ± 0.289 3.000 **0.004**	J0.42 HD>CV=HU				
J0.64 HU>CV>HD	-0.267 ± 0.277 -0.966 **0.338**	1.008 ± 0.290 3.480 **0.001**	0.473 ± 0.288 1.644 **0.106**	0.860 ± 0.259 3.323 **0.002**	-0.106 ± 0.192 -0.552 **0.583**	0.237 ± 0.588 0.403 **0.689**	-1.022 ± 0.152 -6.728 **<0.0001**	-0.611 ± 0.223 -2.743 **0.008**	-0.882 ± 0.228 -3.868 **<0.0001**	-0.324 ± 0.245 -1.319 **0.193**	-1.191 ± 0.209 -5.701 **<0.0001**	J0.64 HU>CV>HD			
J0.92 HU>CV>HD	-0.901 ± 0.278 -3.245 **0.002**	0.374 ± 0.291 1.286 **0.204**	-0.161 ± 0.289 -0.558 **0.579**	0.226 ± 0.260 0.870 **0.388**	-0.740 ± 0.194 -3.817 **<0.0001**	-0.397 ± 0.588 -0.675 **0.502**	-1.656 ± 0.154 -10.754 **<0.0001**	-1.245 ± 0.224 -5.553 **<0.0001**	-1.516 ± 0.230 -6.605 **<0.0001**	-0.957 ± 0.247 -3.881 **<0.0001**	-1.825 ± 0.210 -8.672 **<0.0001**	-0.634 ± 0.145 -4.385 **<0.0001**	J0.92 HU>CV>HD		
J0.64 HU>HD>CV	-0.036 ± 0.271 -0.134 **0.894**	1.238 ± 0.284 4.356 **<0.0001**	0.704 ± 0.282 2.492 **0.016**	1.091 ± 0.253 4.313 **<0.0001**	0.125 ± 0.184 0.677 **0.501**	0.468 ± 0.585 0.799 **0.428**	-0.791 ± 0.142 -5.587 **<0.0001**	-0.380 ± 0.216 -1.761 **0.084**	-0.652 ± 0.221 -2.943 **0.005**	-0.093 ± 0.239 -0.388 **0.700**	-0.960 ± 0.202 -4.764 **<0.0001**	0.231 ± 0.131 1.758 **0.084**	0.865 ± 0.134 6.467 **<0.0001**	J0.64 HU>HD>CV	
J0.92 HU>HD>CV	0.239 ± 0.276 0.864 **0.391**	1.513 ± 0.289 5.232 **<0.0001**	0.979 ± 0.287 3.406 **0.001**	1.366 ± 0.259 5.284 **<0.0001**	0.400 ± 0.192 2.083 **0.042**	0.743 ± 0.588 1.264 **0.211**	-0.516 ± 0.151 -3.409 **0.001**	-0.105 ± 0.222 -0.472 **0.639**	-0.377 ± 0.228 -1.653 **0.104**	0.182 ± 0.245 0.743 **0.460**	-0.685 ± 0.209 -3.286 **0.002**	0.506 ± 0.142 3.567 **0.001**	1.140 ± 0.144 7.913 **<0.0001**	0.275 ± 0.131 2.104 **0.040**	J0.92 HU>HD>CV
J0.42 HU>HD=CV	-0.274 ± 0.310 -0.882 **0.381**	1.001 ± 0.322 3.112 **0.003**	0.467 ± 0.320 1.458 **0.150**	0.854 ± 0.294 2.900 **0.005**	-0.113 ± 0.238 -0.473 **0.638**	0.230 ± 0.604 0.381 **0.704**	-1.028 ± 0.207 -4.973 **<0.0001**	-0.617 ± 0.263 -2.344 **0.023**	-0.889 ± 0.268 -3.318 **0.002**	-0.330 ± 0.283 -1.167 **0.248**	-1.198 ± 0.252 -4.758 **<0.0001**	-0.006 ± 0.200 -0.032 **0.975**	0.628 ± 0.201 3.115 **0.003**	-0.237 ± 0.192 -1.234 **0.222**	-0.512 ± 0.199 -2.567 **0.013**	J0.42 HU>HD=CV

Model S24: PO_4-P concentration ([PO_4-P], mg L^{-1})

Initial linear regression model:

Lm([PO_4-P] ~ SpD)

No minimal adequate model, intercept only (SpD, F= 0.57, d.f. = 15, p = 0.889)

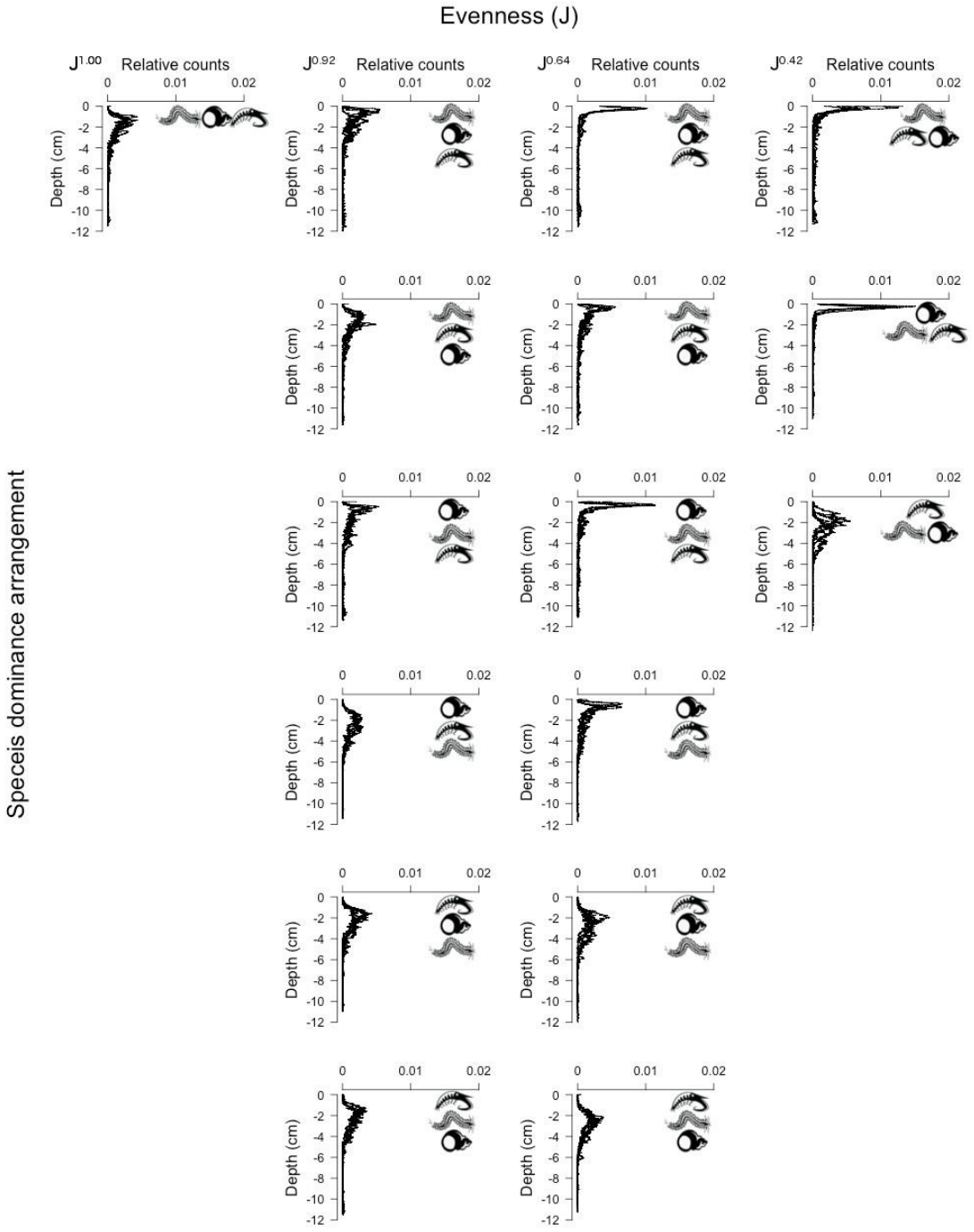

Figure A1.1: Sediment particle reworking profiles (n = 5) for all arrangements of species dominance across 4 evenness levels ($J^{1.00}$, $J^{0.92}$, $J^{0.64}$, $J^{0.42}$). Relative counts are standardised (count/total count) to allow comparison between replicates and treatments. The arrangement of species dominance (vertically, from most to least biomass; equal dominance is represented by horizontal positioning and indicates species that share the same amount of biomass) is

indicated graphically in the inset of each panel:  = *Corophium volutator*,  = *Hydrobia ulvae*,  = *Hediste diversicolor.*

Appendix 2

Table A2.1: Mean biomass (g) and standard deviation for the experimental design for each dominant species identity (ID). HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, MB = *Macoma balthica*

ID	*H. diversicolor*	± s.d.	*H. ulvae*	± s.d.	*M. balthica*	± s.d.	Total	± s.d.
HD_{HUMB}	1.55	0.034	0.225	0.002	0.223	0.004	1.998	0.035
HU_{HDMB}	0.223	0.047	1.55	0.009	0.223	0.004	1.996	0.049
MB_{HDHU}	0.229	0.028	0.225	0.002	1.55	0.009	1.999	0.028

Statistical model summary

Summary of the statistical models (Model S1 to S7). For each model, I list the initial linear regression model and the minimal adequate model. GLS estimation was applied to the linear models were it was necessary to account for a violation of variance homogeneity. The model coefficients are presented in summary tables. The coefficients indicate the relative performance of each treatment level relative to the relevelled baseline (as indicated). Coefficients ± SE, t-values and respective significance values are presented. Abbreviations: ID, Dominant species identity; HD, *Hediste diversicolor*; HU, *Hydrobia ulvae*; MB, *Macoma balthica*.

Model S1: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{mean}$~ ID×Predator×Enrichment)

Minimal adequate model:

Gls($^{f\text{-}SPI}L_{mean}$~ ID+Predator+Enrichment, weights = varIdent (form = ~1|Enrichment), method = 'REML')

Coefficient tables: Intercept ± SE (For baseline ID = HD_{HUMB}, no predator present and not enriched with algae): 0.744 ± 0.061 t-value = 12.103 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

	HD_{HUMB}	**HU_{HDMB}**	**MB_{HDHU}**
HD_{HUMB}	**/**	-0.129 ± 0.031 -4.148 **0.0001**	-0.047 ± 0.031 -1.508 0.135
HU_{HDMB}	0.129 ± 0.031 4.148 **0.0001**	**/**	0.082 ± 0.031 2.639 **0.01**
MB_{HDHU}	0.047 ± 0.031 1.508 0.135	-0.082 ± 0.031 -2.639 **0.01**	**/**

	No *Crangon*	***Crangon***
No *Crangon*	**/**	-0.173 ± 0.025 -6.788 **<0.0001**
Crangon	0.173 ± 0.025 6.788 **<0.0001**	**/**

	No algae	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	**/**	-0.232 ± 0.06 -3.877 **<0.001**	-0.155 ± 0.064 -2.403 **0.018**	-0.231 ± 0.064 -3.598 **<0.001**
Ulva	0.232 ± 0.06 3.877 **<0.001**	**/**	0.078 ± 0.034 2.309 **0.023**	0.001 ± 0.033 0.022 0.983
Fucus	0.155 ± 0.064 2.403 **0.018**	-0.078 ± 0.034 -2.309 **0.023**	**/**	-0.077 ± 0.041 -1.875 0.064
Ulva + Fucus	0.231 ± 0.064 3.598 **<0.001**	-0.001 ± 0.033 -0.022 0.983	-0.077 ± 0.041 -1.875 0.064	/

Model S2: Maximum mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{max}$~ ID×Predator×Enrichment)

Minimal adequate model

Gls($^{f\text{-}SPI}L_{max}$~ ID, weights = varIdent (form = ~1|ID), method = 'REML')

Coefficient table: Intercept ± SE (For baseline ID = HD_{HUMB}): 8.302 ± 0.127 t-value = 65.371 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

	HD_{HUMB}	**HU_{HDMB}**	**MB_{HDHU}**
HD_{HUMB}	**/**	1.51 ± 0.452 3.342 **0.001**	1.033 ± 0.324 3.183 **0.002**
HU_{HDMB}	-1.51 ± 0.452 -3.342 **0.001**	**/**	-0.478 ± 0.526 -0.908 0.366
MB_{HDHU}	-1.033 ± 0.324 -3.183 **0.002**	0.478 ± 0.526 0.908 0.366	**/**

Model S3: Surface boundary roughness (SBR, cm)

Initial linear regression model:

Lm(SBR~ ID×Predator×Enrichment)

Minimal adequate model:

Lm(SBR~ Predator)

Coefficient table: Intercept ± SE (For baseline no predator present): 0.857 ± 0.048 t-value = 17.732 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

	No *Crangon*	***Crangon***
No *Crangon*	**/**	-0.249 ± 0.068 -3.639 **<0.001**
Crangon	0.249 ± 0.068 3.639	**/**

<0.001	

Model S4: Bioirrigation ($\Delta[Br^-]$, mg l^{-1})

Initial linear regression model:

Lm($\Delta[Br^-]$ ~ ID×Predator×Enrichment)

Minimal adequate model:

Gls($\Delta[Br^-]$ ~ Predator+Enrichment+Predator:Enrichment, weights = varIdent (form = ~1|ID×Predator), method = 'REML')

Coefficient table: Intercept ± SE (For baseline no predator present and enriched with *Ulva lactuca*): -28.497 ± 9.938, t-value = -2.868 p-value = 0.005. Order in table from top to bottom: Intercept ± SE, t-value, p-value. Negative values indicate increased activity.

	No *Crangon*	***Crangon***
No *Crangon*	**/**	-26.484 ± 11.800 -2.244 **0.027**
Crangon	26.484 ± 11.800 2.244 **0.027**	**/**

Model S5: NH_4-N concentration ([NH_4-N], mg l^{-1})

Initial linear regression model:

Lm([NH_4-N] ~ ID×Predator×Enrichment)

Minimal adequate model:

Lm([NH_4-N] ~ ID)

Coefficient table: Intercept ± SE (For baseline ID = HD_{HUMB}): 11.75 ± 0.753 t-value = 15.6 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

	HD_{HUMB}	**HU_{HDMB}**	**MB_{HDHU}**
HD_{HUMB}	**/**	2.637 ± 1.065 2.476 **0.015**	1.994 ± 1.065 1.872 0.064
HU_{HDMB}	-2.637 ± 1.065 -2.476 **0.015**	**/**	-0.643 ± 1.065 -0.604 0.548
MB_{HDHU}	-1.994 ± 1.065 -1.872 0.064	0.643 ± 1.065 0.604 0.548	**/**

Model S6: NO_x-N concentration ([NO_x-N], mg l^{-1})

Initial linear regression model:

Lm([NO_x-N] ~ ID×Predator×Enrichment)

Minimal adequate model:

Gls([NO_x-N] ~ ID+Predator+Enrichment+ID:Enrichment, weights = varIdent(form = ~1|ID×Enrichment), method = 'REML')

Coefficient table: Intercept ± SE (For baseline ID = HD_{HUMB}, no predator present and not enriched with algae): 0.352 ± 0.061 t-value = 5.806 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

	No *Crangon*	***Crangon***
No *Crangon*	**/**	0.04 ± 0.01 3.946 **<0.001**
Crangon	-0.04 ± 0.01 -3.946 **<0.001**	**/**

Coefficient table: Intercept ± SE (For baseline ID = HD_{HUMB} and not enriched with algae): 0.352 ± 0.061 t-value = 5.806 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

HD	**No algae**	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	/	0.258 ± 0.064 4.060 **0.0001**	0.215 ± 0.065 3.314 **0.001**	0.240 ± 0.063 3.815 **0.0003**
Ulva	-0.258 ± 0.064 -4.060 **0.0001**	/	-0.043 ± 0.031 -1.369 0.175	-0.018 ± 0.026 -0.677 0.500
Fucus	-0.215 ± 0.065 -3.314 **0.001**	0.043 ± 0.031 1.369 0.175	/	0.025 ± 0.030 0.827 0.411
Ulva + Fucus	-0.240 ± 0.063 -3.815 **0.0003**	0.018 ± 0.026 0.677 0.500	-0.025 ± 0.030 -0.827 0.411	/

Coefficient table: Intercept ± SE (For baseline ID = HU_{HDMB} and not enriched with algae): 0.843 ± 0.143 t-value = 5.878, p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

HU	**No algae**	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	/	0.701 ± 0.146 4.802 **<0.0001**	0.680 ± 0.147 4.638 **<0.0001**	0.594 ± 0.151 3.934 **0.0002**
Ulva	-0.701 ± 0.146 -4.802 **<0.0001**	/	-0.022 ± 0.041 -0.529 0.598	-0.108 ± 0.055 -1.975 0.052
Fucus	-0.680 ± 0.147 -4.638 **<0.0001**	0.022 ± 0.041 0.529 0.598	/	-0.086 ± 0.056 -1.541 0.127
Ulva + Fucus	-0.594 ± 0.151 -3.934	0.108 ± 0.055 1.975	0.086 ± 0.056 1.541	/

0.0002	0.052	0.127	

Coefficient table: Intercept ± SE (For baseline ID = MB_{HDHU} and not enriched with algae): 0.212 ± 0.044 t-value = 4.854 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

MB	**No algae**	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	/	0.155 ± 0.044 3.532 **0.0007**	0.148 ± 0.045 3.249 **0.002**	0.096 ± 0.055 1.755 0.083
Ulva	-0.155 ± 0.044 -3.532 **0.0007**	/	-0.008 ± 0.015 -0.497 0.621	-0.059 ± 0.034 -1.754 0.083
Fucus	-0.148 ± 0.045 -3.249 **0.002**	0.008 ± 0.015 0.497 0.621	/	-0.052 ± 0.036 -1.449 0.151
Ulva + Fucus	-0.096 ± 0.055 -1.755 0.083	0.059 ± 0.034 1.754 0.083	0.052 ± 0.036 1.449 0.151	/

Model S7: PO_4-P concentration ([PO_4-P], mg l^{-1})

Initial linear regression model:

Lm([PO_4-P] ~ ID×Predator×Enrichment)

Minimal adequate model:

Gls([PO_4-P] ~ ID+Enrichment+ID:Enrichment, weights = varIdent(form = ~1|Predator×Enrichment), method = 'REML')

Coefficient table: Intercept ± SE (For baseline ID = HD_{HUMB} and not enriched with algae): 0.077 ± 0.008 t-value = 9.558 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

HD	**No algae**	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	**/**	-0.361 ± 0.037 -9.855 **<0.0001**	-0.322 ± 0.031 -10.350 **<0.0001**	-0.381 ± 0.044 -8.588 **<0.0001**
Ulva	0.361 ± 0.037 9.855 **<0.0001**	**/**	0.040 ± 0.047 0.854 0.396	-0.020 ± 0.056 -0.350 0.727
Fucus	0.322 ± 0.031 10.350 **<0.0001**	-0.040 ± 0.047 -0.854 0.396	**/**	-0.060 ± 0.053 -1.125 0.264
Ulva + Fucus	0.381 ± 0.044 8.588 **<0.0001**	0.020 ± 0.056 0.350 0.727	0.060 ± 0.053 1.125 0.264	/

Coefficient table: Intercept ± SE (For baseline ID = HU_{HDMB} and not enriched with algae): 0.073 ± 0.008 t-value = 9.069 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

HU	**No algae**	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	/	-0.208 ± 0.037 -5.682 **<0.0001**	-0.222 ± 0.031 -7.145 **<0.0001**	-0.190 ± 0.044 -4.287 **<0.0001**
Ulva	0.208 ± 0.037 5.682 **<0.0001**	/	-0.014 ± 0.047 -0.291 0.771	0.018 ± 0.056 0.321 0.749
Fucus	0.222 ± 0.031 7.145 **<0.0001**	0.014 ± 0.047 0.291 0.771	/	0.032 ± 0.053 0.599 0.551
Ulva + Fucus	0.190 ± 0.044 4.287 **<0.0001**	-0.018 ± 0.056 -0.321 0.749	-0.032 ± 0.053 -0.599 0.551	/

Coefficient table: Intercept ± SE (For baseline ID = MB_{HDHU} and not enriched with algae): 0.066 ± 0.008 t-value = 8.210 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

MB	**No algae**	***Ulva***	***Fucus***	***Ulva + Fucus***
No algae	/	-0.281 ± 0.037 -7.674 **<0.0001**	-0.231 ± 0.031 -7.435 **<0.0001**	-0.298 ± 0.044 -6.706 **<0.0001**
Ulva	0.281 ± 0.037 7.674 **<0.0001**	/	0.050 ± 0.047 1.080 0.283	-0.016 ± 0.056 -0.287 0.775
Fucus	0.231 ± 0.031 7.435 **<0.0001**	-0.050 ± 0.047 -1.080 0.283	/	-0.067 ± 0.053 -1.258 0.212
Ulva + Fucus	0.298 ± 0.044 6.706 **<0.0001**	0.016 ± 0.056 0.287 0.775	0.067 ± 0.053 1.258 0.212	/

Table A2.2 Summary of data used for statistical analysis. Data in the absence of macrofauna (ctrl) is shown for comparison but was not included in the analyses. ID = dominant species identity, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, MB = *Macoma balthica*, enrichment: 0 = no enrichment, F = *Fucus serratus*, U = *Ulva lactuca*, UF = 50:50 mixture of *Ulva lactuca* + *Fucus serratus*, rep = replicate

ID	*C.crangon presence*	Enrichment	rep	SBR	$^{fSPI}L_{mean}$ (cm)	$^{fSPI}L_{median}$ (cm)	$^{fSPI}L_{max}$ (cm)	Δ[Br⁻] (mg L^{-1})	[NH_4-N] (mg L^{-1})	[NO_x-N] (mg L^{-1})	[PO_4-P] (mg L^{-1})
cntrl	0	0	ctrl	0.529	0.156	0.150	0.796	58.244	6.896	0.818	0.062
cntrl	0	F	ctrl	0.503	0.149	0.073	0.879	-2.656	6.386	0.480	0.093
cntrl	0	U	ctrl	1.001	0.071	0.000	1.054	7.214	7.372	0.089	0.558
cntrl	0	UF	ctrl	0.838	0.090	0.085	0.504	7.552	2.261	0.285	0.116
cntrl	1	0	ctrl	0.780	0.065	0.000	1.392	24.797	2.141	1.578	0.063
cntrl	1	F	ctrl	1.237	0.115	0.000	1.969	-18.648	2.327	0.520	0.088
cntrl	1	U	ctrl	1.050	0.191	0.000	0.646	27.109	2.222	0.630	0.102
cntrl	1	UF	ctrl	1.607	0.109	0.000	2.314	79.259	2.105	0.523	0.219
HD	0	F	1	1.040	0.529	0.000	8.380	-39.462	16.819	0.121	0.517
HU	0	F	1	0.765	0.545	0.178	8.549	-24.640	10.594	0.132	0.346
MB	0	F	1	1.473	0.561	0.297	8.255	-12.429	10.972	0.049	0.297
HD	0	U	1	0.741	0.499	0.069	9.064	-25.556	16.241	0.077	0.520
HU	0	U	1	0.873	0.408	0.082	8.174	-26.211	9.301	0.215	0.237
MB	0	U	1	0.717	0.496	0.000	8.241	8.449	5.408	0.062	0.389
HD	0	UF	1	1.056	0.357	0.000	7.936	-30.755	6.930	0.143	0.508
HU	0	UF	1	0.876	0.262	0.146	8.128	-6.999	4.410	0.161	0.190
MB	0	UF	1	0.979	0.427	0.172	7.752	-25.005	5.607	0.107	0.239
HD	0	0	1	0.613	0.536	0.187	8.054	160.95	7.456	0.558	0.069
HU	0	0	1	1.128	0.927	0.319	8.126	-14.194	5.812	1.135	0.085
MB	0	0	1	1.282	1.002	0.710	8.417	-52.550	6.024	0.251	0.072
HD	1	F	1	1.276	0.385	0.000	8.484	-39.624	9.201	0.290	0.562
HU	1	F	1	1.216	0.166	0.000	7.212	-43.386	4.604	0.170	0.094
MB	1	F	1	1.074	0.370	0.000	8.696	-4.125	6.745	0.103	0.400
HD	1	U	1	1.751	0.259	0.000	6.741	-18.461	7.187	0.205	0.523
HU	1	U	1	1.732	0.368	0.000	8.884	-7.467	9.035	0.070	0.391
MB	1	U	1	0.734	0.374	0.000	8.704	4.148	9.353	0.120	0.319
HD	1	UF	1	0.824	0.361	0.000	8.715	15.298	10.745	0.141	0.531
HU	1	UF	1	0.855	0.382	0.114	8.901	-9.508	6.892	0.406	0.259
MB	1	UF	1	1.414	0.203	0.000	4.444	-47.221	7.280	0.341	0.432
HD	1	0	1	1.152	0.841	0.000	8.322	-22.931	10.732	0.510	0.079
HU	1	0	1	1.017	0.234	0.141	7.434	7.841	5.513	1.210	0.082
MB	1	0	1	1.061	0.208	0.000	8.573	3.903	7.651	0.534	0.083

cntrl	0	0	ctrl	0.900	0.059	0.027	0.873	-18.242	4.847	1.098	0.068
cntrl	0	F	ctrl	0.511	0.067	0.055	0.506	31.530	9.718	0.207	0.165
cntrl	0	U	ctrl	0.620	0.086	0.000	0.552	-13.365	9.822	0.092	0.781
cntrl	0	UF	ctrl	1.102	0.077	0.059	2.777	2.984	9.128	0.225	0.138
cntrl	1	0	ctrl	0.764	0.105	0.000	0.727	57.816	7.851	1.733	0.059
cntrl	1	F	ctrl	1.914	0.111	0.000	1.509	-39.141	9.893	0.857	0.105
cntrl	1	U	ctrl	0.690	0.072	0.000	0.669	17.152	9.266	0.735	0.131
cntrl	1	UF	ctrl	1.021	0.128	0.000	0.850	-15.799	8.508	0.572	0.135
HD	0	F	2	1.453	0.577	0.043	8.689	16.858	17.037	0.227	0.394
HU	0	F	2	0.480	0.273	0.160	6.296	2.021	16.370	0.329	0.257
MB	0	F	2	0.519	0.777	0.378	8.621	-34.651	17.044	0.035	0.253
HD	0	U	2	1.268	0.506	0.000	8.618	-32.660	16.467	0.154	0.472
HU	0	U	2	1.423	0.347	0.146	3.029	-28.659	15.187	0.119	0.337
MB	0	U	2	0.873	0.595	0.259	8.682	-54.322	17.241	0.071	0.450
HD	0	UF	2	0.663	0.562	0.000	8.390	-74.899	16.332	0.111	0.599
HU	0	UF	2	0.547	0.702	0.234	8.798	-25.209	15.816	0.131	0.337
MB	0	UF	2	0.698	0.376	0.187	4.750	-2.621	13.241	0.061	0.336
HD	0	0	2	0.728	0.200	0.000	7.112	-25.963	14.907	0.437	0.123
HU	0	0	2	0.507	1.105	0.315	8.807	-35.537	13.434	1.291	0.096
MB	0	0	2	0.806	0.796	0.601	6.167	-33.850	14.296	0.154	0.077
HD	1	F	2	0.843	0.361	0.000	7.466	-40.119	15.083	0.107	0.307
HU	1	F	2	0.803	0.295	0.000	4.447	-29.789	12.354	0.266	0.261
MB	1	F	2	1.042	0.186	0.000	3.709	-24.295	17.741	0.113	0.610
HD	1	U	2	0.914	0.404	0.000	8.203	-6.955	18.080	0.090	0.518
HU	1	U	2	0.767	0.120	0.000	1.986	-18.645	14.596	0.280	0.295
MB	1	U	2	1.856	0.226	0.000	6.919	-9.035	15.550	0.113	0.451
HD	1	UF	2	1.259	0.504	0.000	7.660	-12.436	15.764	0.241	0.543
HU	1	UF	2	0.978	0.329	0.137	7.462	8.616	12.465	0.328	0.306
MB	1	UF	2	0.768	0.569	0.000	8.332	-49.452	13.639	0.210	0.533
HD	1	0	2	1.424	0.604	0.000	8.228	-38.673	16.121	0.292	0.082
HU	1	0	2	1.123	0.464	0.000	7.982	115.78	13.613	1.063	0.092
MB	1	0	2	1.307	0.633	0.537	7.485	1.769	15.335	0.206	0.053
cntrl	0	0	ctrl	0.690	0.111	0.068	0.563	-8.502	9.054	0.892	0.045
cntrl	0	F	ctrl	0.738	0.108	0.096	0.738	-19.716	10.104	0.304	0.125

cntrl	0	U	ctrl	0.774	0.107	0.041	2.478	-63.241	11.043	0.082	0.653
cntrl	0	UF	ctrl	0.835	0.031	0.009	0.330	-22.157	9.721	0.200	0.245
cntrl	1	0	ctrl	1.470	0.180	0.145	2.769	-27.550	9.093	1.652	0.080
cntrl	1	F	ctrl	0.962	0.184	0.150	0.940	-16.190	9.504	0.183	0.220
cntrl	1	U	ctrl	0.948	0.063	0.000	2.151	-62.746	2.724	0.140	0.070
cntrl	1	UF	ctrl	1.070	0.107	0.000	0.743	13.487	1.716	0.601	0.085
HD	0	F	3	0.695	0.771	0.055	8.673	-81.047	6.138	0.107	0.397
HU	0	F	3	0.695	0.669	0.215	9.173	58.487	4.169	0.211	0.345
MB	0	F	3	0.550	0.456	0.174	5.271	10.697	5.546	0.075	0.297
HD	0	U	3	0.867	0.640	0.000	8.662	-86.305	6.336	0.100	0.550
HU	0	U	3	0.705	0.478	0.146	9.220	-24.554	5.297	0.124	0.350
MB	0	U	3	0.574	0.366	0.118	8.300	-54.994	4.156	0.049	0.231
HD	0	UF	3	0.947	0.514	0.000	8.485	-8.547	6.324	0.134	0.562
HU	0	UF	3	0.561	0.470	0.196	8.647	-4.852	3.797	0.385	0.473
MB	0	UF	3	0.663	0.445	0.200	8.963	-5.355	4.525	0.051	0.509
HD	0	0	3	0.963	1.301	0.303	8.117	21.632	6.506	0.547	0.218
HU	0	0	3	2.208	0.510	0.284	9.135	-159.17	4.355	0.912	0.207
MB	0	0	3	0.610	0.710	0.483	8.659	-44.397	5.247	0.219	0.188
HD	1	F	3	1.236	0.466	0.078	8.375	-3.497	6.109	0.174	0.440
HU	1	F	3	1.026	0.280	0.000	6.536	22.034	4.860	0.137	0.404
MB	1	F	3	1.351	0.762	0.069	9.521	23.469	6.336	0.188	0.552
HD	1	U	3	1.577	0.260	0.000	9.008	-2.123	8.346	0.122	0.436
HU	1	U	3	1.004	0.194	0.080	7.521	-18.548	3.858	0.261	0.188
MB	1	U	3	1.127	0.275	0.000	8.995	-16.514	5.568	0.091	0.414
HD	1	UF	3	0.782	0.363	0.000	7.704	-20.598	6.487	0.087	0.252
HU	1	UF	3	1.269	0.139	0.041	1.305	92.500	3.239	0.466	0.112
MB	1	UF	3	1.419	0.303	0.000	7.591	-9.519	4.289	0.211	0.269
HD	1	0	3	2.136	0.683	0.000	8.620	-8.241	9.085	0.290	0.085
HU	1	0	3	1.194	0.228	0.000	4.897	-19.216	5.550	0.746	0.069
MB	1	0	3	1.472	0.206	0.000	7.323	-5.290	6.350	0.214	0.064
cntrl	0	0	ctrl	1.512	0.045	0.000	2.479	-14.790	1.539	0.758	0.000
cntrl	0	F	ctrl	0.927	0.079	0.011	1.139	-5.294	1.270	0.249	0.064
cntrl	0	U	ctrl	0.459	0.084	0.000	0.623	2.661	2.265	0.096	0.294
cntrl	0	UF	ctrl	0.914	0.062	0.000	1.094	35.006	0.589	0.127	0.093
cntrl	1	0	ctrl	0.765	0.099	0.000	1.827	-22.094	1.866	1.421	0.059

cntrl	1	F	ctrl	1.293	0.073	0.000	0.844	-173.23	2.552	0.103	0.153
cntrl	1	U	ctrl	1.411	0.078	0.000	0.906	-52.292	2.229	0.102	0.062
cntrl	1	UF	ctrl	0.698	0.062	0.000	1.386	34.648	2.180	0.249	0.080
HU	0	F	4	0.836	0.373	0.150	8.741	-24.980	5.253	0.112	0.272
MB	0	F	4	0.632	0.495	0.000	9.254	33.263	5.034	0.042	0.230
HD	0	F	4	0.749	0.636	0.000	9.804	-22.395	5.667	0.117	0.289
HD	0	U	4	1.052	0.395	0.000	7.706	-205.75	14.032	0.126	0.252
HU	0	U	4	1.132	0.300	0.000	6.582	-43.259	11.363	0.137	0.245
MB	0	U	4	0.513	0.400	0.000	5.594	14.774	12.154	0.046	0.150
HD	0	UF	4	0.984	0.391	0.000	7.775	-35.923	13.298	0.103	0.278
HU	0	UF	4	0.683	0.118	0.000	2.927	5.789	11.185	0.078	0.346
MB	0	UF	4	0.724	0.330	0.000	5.138	-35.529	11.468	0.051	0.278
HD	0	0	4	0.899	1.102	0.000	9.514	-55.227	14.442	0.134	0.033
HU	0	0	4	0.583	0.482	0.173	8.896	-16.349	12.458	0.324	0.043
MB	0	0	4	0.794	0.517	0.175	8.041	-43.408	11.686	0.109	0.035
HD	1	F	4	1.171	0.380	0.000	6.610	-17.145	13.531	0.108	0.271
HU	1	F	4	0.589	0.142	0.000	4.917	13.941	11.541	0.112	0.184
MB	1	F	4	0.713	0.218	0.000	3.968	-35.376	11.128	0.070	0.299
HD	1	U	4	0.908	0.347	0.000	8.375	16.250	14.055	0.037	0.248
HU	1	U	4	0.627	0.203	0.137	2.938	51.516	11.362	0.089	0.221
MB	1	U	4	0.657	0.355	0.000	5.487	16.361	10.837	0.063	0.330
HD	1	UF	4	0.765	0.413	0.000	9.140	-7.594	14.935	0.094	0.406
HU	1	UF	4	0.986	0.100	0.000	2.889	-35.029	10.052	0.203	0.118
MB	1	UF	4	0.549	0.210	0.000	6.023	18.490	12.234	0.058	0.304
HD	1	0	4	1.355	0.617	0.000	9.045	-37.387	15.617	0.206	0.055
HU	1	0	4	0.986	0.292	0.000	8.804	-6.835	13.292	0.225	0.042
MB	1	0	4	0.980	0.184	0.000	6.757	-16.711	12.513	0.170	0.059

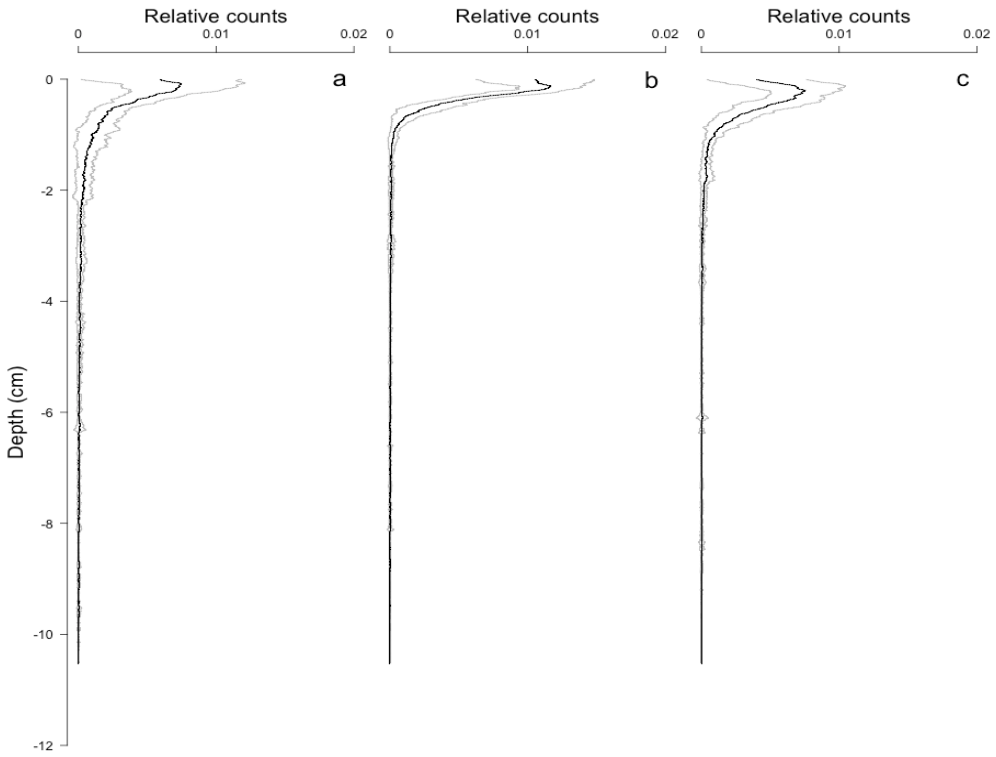

Figure A2.1: Sediment particle reworking profiles with relative particle counts (n = 4) derived from the f-SPI images for dominant species identity. a = *Hediste diversicolor*, b = *Hydrobia ulvae*, c = *Macoma balthica*

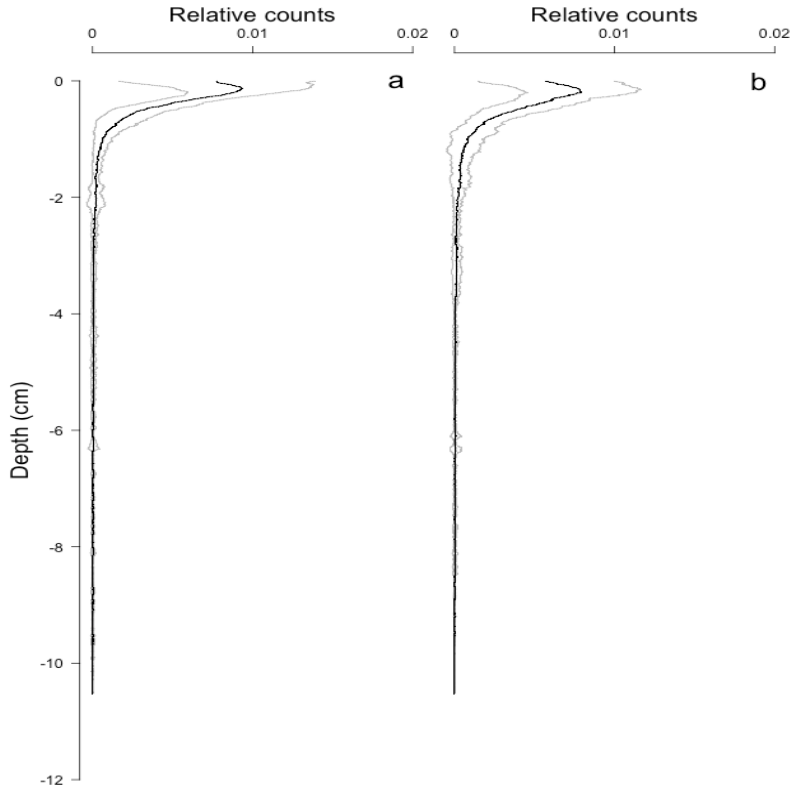

Figure A2.2: Sediment particle reworking profiles with relative particle counts (n = 4) derived from the f-SPI images for predator presence (a) and absence (b).

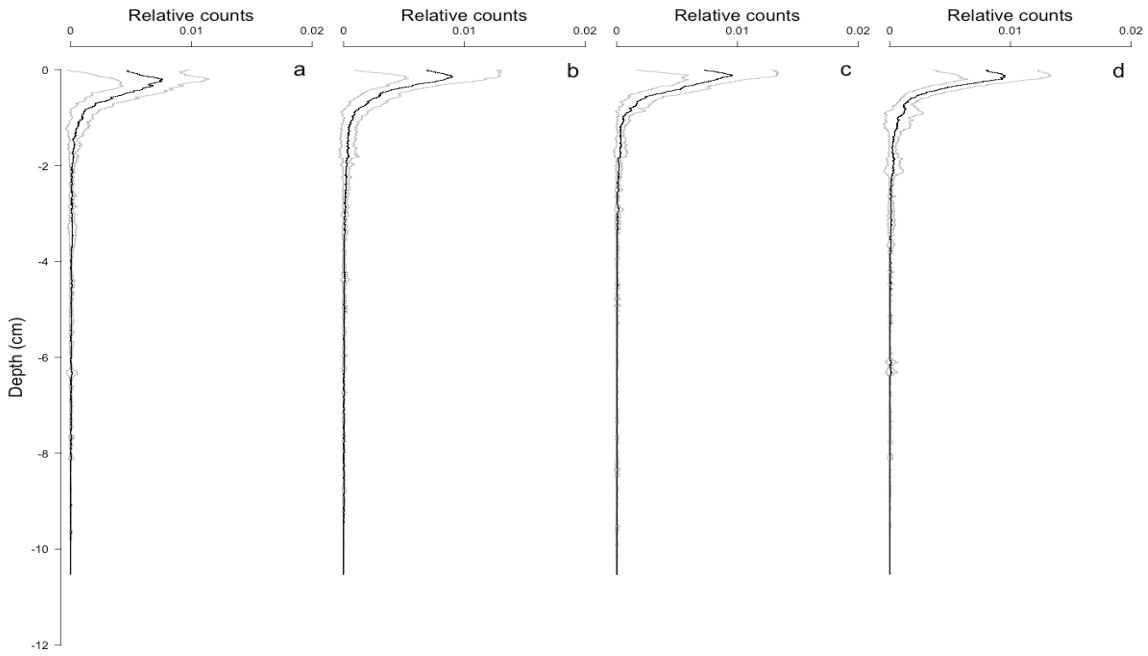

Figure A2.3: Sediment particle reworking profiles with relative particle counts (n = 4) derived from the f-SPI images for algal enrichment (a = no enrichment,

b = *Ulva lactuca*, c = *Fucus serratus*, d = a mixture of *Ulva lactuca* and *Fucus serratus*)

Appendix 3

Table A3.1: Utilized biomass for the different community dominance compositions. Values show mean ± standard deviation. HD = *Hediste diversicolor*, CV = *Corohpium volutator*, HU = *Hydrobia ulvae*

Community composition	Biomass (g) *H. diversicolor*	Biomass (g) *C. volutator*	Biomass (g) *H. ulvae*	Biomass (g) total
$J^{1.00}$ HD=CV=HU	0.678 ± 0.028	0.672 ± 0.004	0.669 ± 0.002	2.019 ± 0.028
$J^{0.64}$ HD>CV=HU	1.560 ± 0.032	0.229 ± 0.003	0.228 ± 0.002	2.017 ± 0.033
$J^{0.64}$ CV>HD=HU	0.228 ± 0.030	1.561 ± 0.007	0.228 ± 0.002	2.016 ± 0.029
$J^{0.64}$ HU>CV=HD	0.231 ± 0.037	0.229 ± 0.003	1.558 ± 0.010	2.019 ± 0.043

Table A3.2: parameters for calculated wave functions of the type f(t)= (A × cos(w × t + p))+y; A = Amplitude, w = Angular frequency, p = Phase offset, y = Intercept correction

Tidal regime	A	w	p	y
6:6	1	0.5067	1.5708	0
9:3	1	0.5067	1.5708	0.7

Statistical model summary

Summary of the statistical models S1-S7. For each model, the initial linear regression model and the minimal adequate model are listed. Where it was necessary to account for a violation of homogeneity of variance, a linear regression with GLS estimation was used and a summary of the coefficient tables is provided. As the experiment was separated across two successive experimental runs because of limited space in the experimental system, experimental run was included as a random factor if a model improvement was indicated by AIC (Akaike Information Criterion). The coefficients indicate the relative performance of each treatment level relative to the relevelled baseline (as indicated). Coefficients ± SE, t-values and respective significance values are presented. Abbreviations: CID = community composition (table A3.1; HD = *Hediste diversicolor*, CV = *Corophium volutator*, HU = *Hydrobia ulvae*), tide = tidal regime (0, constant immersion; 6:6, 6 hours 12 minutes immersion followed by 6 hours 12 min emersion; 9:3, 9 hours 18 minutes immersion followed by 3 hours 6 min emersion), run = experimental run

Model S1: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{mean}$~ tide × CID)

Minimal adequate model:

lme($^{f\text{-}SPI}L_{mean}$~ CID, weights = varIdent (form = ~1|CID), random=~1|experimental run, method = 'REML')

Coefficient table: Intercept ± SE (For baseline CID = „$J^{1.00}$"): 1.045 ± 0.25 t-value = 4.18 p-value = 0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

CID	$J^{1.00}$ HD=CV=HU		
$J^{0.64}$ HD>CV=HU	0.325 ± 0.086 3.759 **<0.001**	$J^{0.64}$ HD>CV=HU	
$J^{0.64}$ CV>HD=HU	-0.07 ± 0.086 -0.804 0.426	-0.596 ± 0.169 -3.525 **0.001**	$J^{0.64}$ CV>HD=HU
$J^{0.64}$ HU>HD=CV	0.216 ± 0.086 2.504 **0.016**	-0.191 ± 0.193 -0.987 0.329	0.406 ± 0.138 -2.948 **0.005**

Model S2: Median mixed depth of particle reworking ($^{f\text{-}SPI}L_{median}$, cm)

Initial linear regression model:

$Lm(^{f\text{-}SPI}L_{median} \sim tide \times CID)$

Minimal adequate model:

$Lme(^{f\text{-}SPI}L_{median} \sim tide + CID, random=\sim 1|run, method = 'REML')$

Coefficient tables: Intercept ± SE (For baseline CID = „$J^{1.00}$" and "no tides"): 1.22 ± 0.233 t-value = 5.225 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

CID	**$J^{1.00}$ HD=CV=HU**			
J0.64 HD>CV=HU	0.265 ± 0.097 2.731 **0.009**	**J0.64 HD>CV=HU**		
$J^{0.64}$ CV>HD=HU	-0.125 ± 0. 097 -1.286 0.206	-0.39 ± 0. 097 -4.017 0.404	**$J^{0.64}$ CV>HD=HU**	
$J^{0.64}$ HU>HD=CV	0.265 ± 0. 097 2.723 **0.009**	-0.001 ± 0. 097 -0.008 0.994	0.389 ± 0. 097 4.01 **<0.001**	**$J^{0.64}$ HU>HD=CV**

Tide	**No tide**		
6:6	-0.329 ± 0.084 -3.909 **<0.001**	**6:6**	
3:9	-0.332 ± 0. 084 -3.952 **<0.001**	-0.004 ± 0. 084 -0.042 0.966	**3:9**

Model S3: Max mixed depth of particle reworking ($^{f\text{-}SPI}L_{nax}$, cm)

Initial linear regression model:

Lm($^{f\text{-}SPI}L_{max}$~ tide × CID)

Minimal adequate model:

Lm($^{f\text{-}SPI}L_{max}$~ CID)

Coefficient table: Intercept ± SE (For baseline CID = „$J^{1.00}$"): 7.796 ± 0.553 t-value = 14.1 p-value < 0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

CID	**$J^{1.00}$ HD=CV=HU**		
$J^{0.64}$ HD>CV=HU	1.114 ± 0.782 1.425 1.161	**$J^{0.64}$ HD>CV=HU**	
$J^{0.64}$ CV>HD=HU	-1.062 ± 0. 782 -1.358 0.181	-2.176 ± 0. 782 -2.783 **0.008**	**$J^{0.64}$ CV>HD=HU**
$J^{0.64}$ HU>HD=CV	-0.643 ± 0. 782 -0.822 0.415	-1.757 ± 0. 782 -2.247 **0.03**	0.419 ± 0. 782 0.536 0.595

Model S4: Surface boundary roughness (SBR, cm)

Initial linear regression model:

Lm(SBR ~ tide × CID)

Minimal adequate model:

Lm(SBR ~ tide)

Coefficient table: Intercept ± SE (For baseline "no tides"): 0.813 ± 0.045 t-value = 17.996 p-value < 0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

Tide	**No tide**		
6:6	-0.405 ± 0.064 -6.338 **<0.0001**	**6:6**	
3:9	-0.317 ± 0. 064 -4.957	0.088 ± 0. 064 1.381	**3:9**

<0.0001	0.174

Model S5: Δ[Br^-] (mg l^{-1})

Initial linear regression model:

Lm(Δ[Br^-] ~ tide × CID)

Minimal adequate model:

lme(Δ[Br^-] ~ CID + tide, weights = varIdent (form = ~1|CID×tide), method = 'REML')

Coefficient tables: Intercept ± SE (For baseline CID = „$J^{1.00}$" and "no tides"): -14.338 ± 1.697 t-value = -8.449 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

CID	**$J^{1.00}$ HD=CV=HU**			
J0.64 HD>CV=HU	-24.931 ± 8.492 -2.936 **0.005**	**J0.64 HD>CV=HU**		
$J^{0.64}$ CV>HD=HU	11.083 ± 8.544 1.297 0.202	36.014 ± 7.187 5.011 **<0.0001**	**$J^{0.64}$ CV>HD=HU**	
$J^{0.64}$ HU>HD=CV	-21.866 ± 7.027 -3.112 **0.003**	3.065 ± 10.282 0.298 0.767	-32.949 ± 10.446 -3.154 **0.003**	**$J^{0.64}$ HU>HD=CV**

Tide	**No tide**	
6:6	26.859 ± 8.46 3.175 **0.003**	**6:6**

39.079 ± 9.185 4.255 **0.0001**	12.22 ± 7.868 1.553 0.128	**3:9**

Model S6: NH_4-N concentration (NH_4-N, mg l^{-1})

Initial linear regression model:

Lm(NH_4-N ~ tide × CID)

Minimal adequate model:

lm(NH_4-N ~ CID + tide)

Coefficient tables: Intercept ± SE (For baseline CID = „$J^{1.00}$" and "no tides"): 5.829 ± 0.534 t-value = 10.915 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

CID	**$J^{1.00}$ HD=CV=HU**			
J0.64 HD>CV=HU	-1.779 ± 0.617 -2.885 **0.006**	**J0.64 HD>CV=HU**		
$J^{0.64}$ CV>HD=HU	0.595 ± 0.617 0.965 0.34	2.374 ± 0.617 3.85 **<0.001**	**$J^{0.64}$ CV>HD=HU**	
$J^{0.64}$ HU>HD=CV	-1.746 ± 0.617 -2.831 **0.007**	0.033 ± 0.617 0.054 0.957	-2.341 ± 0.617 -3.797 **<0.001**	**$J^{0.64}$ HU>HD=CV**

Tide	**No tide**	
6:6	-1.936 ± 0.534 -3.625 **<0.001**	**6:6**

	-2.835 ± 0.534	-0.899 ± 0.534	
3:9	-5.309	-1.684	**3:9**
	0.0001	0.1	

Model S7: NO_x-N concentration (NO_x-N, mg l^{-1})

Initial linear regression model:

Lm(NO_x-N ~ tide × CID)

Minimal adequate model:

Lme(NO_x-N ~ CID, weights = varIdent(form = ~ 1|CID×tide), random=~1| run, method = "REML")

Coefficient table: Intercept ± SE (For baseline CID = „$J^{1.00}$"): 0.645 ± 0.072 t-value = 8.994 p-value = <0.0001. Order in table from top to bottom: Intercept ± SE, t-value, p-value

CID	**$J^{1.00}$ HD=CV=HU**			
J0.64 HD>CV=HU	-0.535 ± 0.062 -8.604 **<0.0001**	**J0.64 HD>CV=HU**		
$J^{0.64}$ CV>HD=HU	-0.233 ± 0.061 -8.049 **0.007**	0.303 ± 0.067 5.026 **<0.0001**	**$J^{0.64}$ CV>HD=HU**	
$J^{0.64}$ HU>HD=CV	-0.49 ± 0.617 -2.831 **<0.0001**	0.045 ± 0.024 1.854 0.071	-0.258 ± 0.059 -4.376 **0.0001**	**$J^{0.64}$ HU>HD=CV**

Model S8: PO_4-P concentration (PO_4-P, mg l^{-1})

Initial linear regression model:

Lm(PO_4-P ~ tide × CID)

No minimal adequate model, intercept only (CID, F= 1.634, d.f. = 3, p = 0.195)

Table A3.3: Summary of data used for statistical analysis. Data in the absence of macrofauna is shown for comparison but was not included in the analyses. CID = community composition, HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, CV = *Corophium volutator*; T = tidal regime (0, constant immersion; 9:9, hours 18 min immersion; 6:6, 6 hours 12 min immersion)

T	CID	rep	SBR	$^{f\text{-}SPI}L_{mean}$ (cm)	$^{f\text{-}SPI}L_{median}$ (cm)	$^{f\text{-}SPI}L_{max}$ (cm)	Δ[Br^-] (mg L^{-1})	[NH_4-N] (mg L^{-1})	[NO_x-N] (mg L^{-1})	[PO_4-P] (mg L^{-1})
0	/	CTRL	0.327	0.241	0.211	1.325	33.026	5.418	0.301	0.068
0	HD=HU=CV	1	0.788	1.583	1.577	8.981	-13.021	5.236	1.811	0.112
0	HD>HU=CV	1	0.796	1.546	1.805	8.773	-59.440	8.462	0.081	0.042
0	HU>HD=CV	1	0.748	1.593	1.890	4.686	-39.233	6.003	0.550	0.102
0	CV+HD=HU	1	1.033	1.257	1.722	4.421	8.738	5.261	2.165	0.094
9	/	CTRL	0.270	0.228	0.231	0.809	21.011	2.351	0.171	0.000
9	HD=HU=CV	1	0.321	1.263	1.170	8.739	39.577	5.373	0.654	0.081
9	HD>HU=CV	1	0.429	1.309	0.877	8.695	16.756	2.732	0.130	0.056
9	HU>HD=CV	1	0.894	1.668	1.476	9.441	44.145	3.569	0.039	0.061
9	CV+HD=HU	1	0.485	1.270	0.854	6.347	30.954	4.465	1.214	0.047
6	/	CTRL	0.216	0.368	0.372	0.588	84.538	2.674	0.470	0.000
6	HD=HU=CV	1	0.292	0.847	0.759	6.263	50.821	6.263	0.953	0.065
6	HD>HU=CV	1	0.246	1.659	1.191	9.263	-6.356	5.367	0.130	0.057
6	HU>HD=CV	1	0.348	1.745	1.458	9.233	-5.798	4.782	0.232	0.058
6	CV+HD=HU	1	0.542	0.714	0.696	1.412	40.908	6.265	0.498	0.071
0	/	CTRL	0.263	0.351	0.357	0.734	35.902	5.250	0.105	0.000
0	HD=HU=CV	2	0.559	1.176	1.464	7.342	-18.363	8.509	0.401	0.080
0	HD>HU=CV	2	0.827	1.823	1.870	9.073	0.098	7.414	0.424	0.076
0	HU>HD=CV	2	0.877	1.530	1.890	7.464	-54.213	7.844	0.185	0.074
0	CV+HD=HU	2	0.592	1.146	1.382	8.625	-18.373	8.671	1.219	0.099
9	/	CTRL	0.368	0.364	0.387	1.433	-19.418	3.376	0.169	0.000
9	HD=HU=CV	2	0.444	0.931	0.907	6.096	-15.356	7.083	0.867	0.063
9	HD>HU=CV	2	0.469	1.566	1.269	9.334	-24.928	5.338	0.129	0.059
9	HU>HD=CV	2	0.344	1.618	1.528	8.729	-105.54	2.567	0.023	0.061
9	CV+HD=HU	2	0.408	1.005	0.914	8.107	37.432	6.403	1.535	0.074
6	/	CTRL	0.440	0.315	0.320	0.740	32.499	1.960	0.429	0.000
6	HD=HU=CV	2	0.451	1.789	1.128	9.420	158.374	5.841	0.437	0.067
6	HD>HU=CV	2	0.412	2.896	1.944	9.129	-11.017	4.573	0.089	0.057
6	HU>HD=CV	2	0.267	1.839	1.315	7.568	78.989	4.197	0.166	0.065
6	CV+HD=HU	2	0.587	0.654	0.625	8.044	0.240	8.762	0.478	0.119
0	/	CTRL	0.367	0.315	0.309	0.658	-0.433	1.111	0.253	0.000
0	HD=HU=CV	3	1.238	0.920	0.857	8.248	-15.353	7.416	0.354	0.073
0	HD>HU=CV	3	0.884	1.100	1.248	8.797	-27.523	5.802	0.136	0.072
0	HU>HD=CV	3	0.892	1.104	1.169	7.888	-38.451	6.936	0.222	0.070
0	CV+HD=HU	3	1.142	1.018	1.085	7.711	1.875	8.590	0.204	0.072
9	/	CTRL	0.153	0.172	0.172	0.479	-21.135	0.216	0.230	0.000

9	HD=HU=CV	3	0.489	0.865	0.846	9.367	34.040	2.486	0.557	0.000
9	HD>HU=CV	3	0.881	1.219	0.998	9.436	-2.336	2.149	0.122	0.106
9	HU>HD=CV	3	0.405	0.907	0.925	6.940	23.299	3.157	0.285	0.117
9	CV+HD=HU	3	0.627	0.785	0.549	7.683	37.037	5.484	0.223	0.111
6	/	CTRL	0.469	0.340	0.313	0.802	-101.23	0.135	0.002	0.000
6	HD=HU=CV	3	0.292	0.891	0.915	4.284	27.944	6.127	0.966	0.107
6	HD>HU=CV	3	0.285	1.048	0.892	8.696	-21.231	3.718	0.255	0.135
6	HU>HD=CV	3	0.347	0.886	0.848	2.254	-5.200	2.650	0.106	0.000
6	CV+HD=HU	3	0.175	0.627	0.564	5.623	29.191	4.309	0.397	0.000
0	/	CTRL	0.412	0.217	0.206	1.123	-17.010	0.104	0.000	0.000
0	HD=HU=CV	4	0.480	0.612	0.595	7.942	-10.338	9.170	0.276	0.103
0	HD>HU=CV	4	0.670	1.231	0.926	9.635	-5.461	1.787	0.115	0.000
0	HU>HD=CV	4	0.891	0.745	0.871	8.171	-19.069	7.247	0.120	0.084
0	CV+HD=HU	4	0.591	0.653	0.788	4.587	-41.843	8.164	0.566	0.094
9	/	CTRL	0.194	0.251	0.233	0.777	-8.653	0.473	0.134	0.000
9	HD=HU=CV	4	0.600	0.961	0.988	8.426	-17.968	5.078	0.472	0.072
9	HD>HU=CV	4	0.483	0.815	0.832	6.169	15.686	2.100	0.024	0.000
9	HU>HD=CV	4	0.268	0.874	0.901	3.508	-16.699	1.641	0.060	0.000
9	CV+HD=HU	4	0.393	0.871	0.787	9.380	96.509	7.523	0.835	0.114
6	/	CTRL	0.551	0.267	0.256	0.532	-5.655	0.640	0.290	0.000
6	HD=HU=CV	4	0.695	0.811	0.789	8.439	9.211	5.508	0.315	0.077
6	HD>HU=CV	4	0.594	1.558	1.326	9.913	-14.650	3.298	0.000	0.000
6	HU>HD=CV	4	0.486	0.971	0.898	9.948	70.613	2.545	0.111	0.000
6	CV+HD=HU	4	0.511	0.613	0.530	8.862	26.484	7.334	0.180	0.093

Appendix 4

Sediment parameters

Sediment parameters were measured by the department of geography, University of Cambridge, United Kingdom, after standard protocol (http://www.geog.cam.ac.uk/facilities/laboratories/techniques/) using a laser particle sizer (Malvern Mastersizer 2000) and particle size parameters were calculated using logarithmic graphical measures (Blott & Pye 2001).

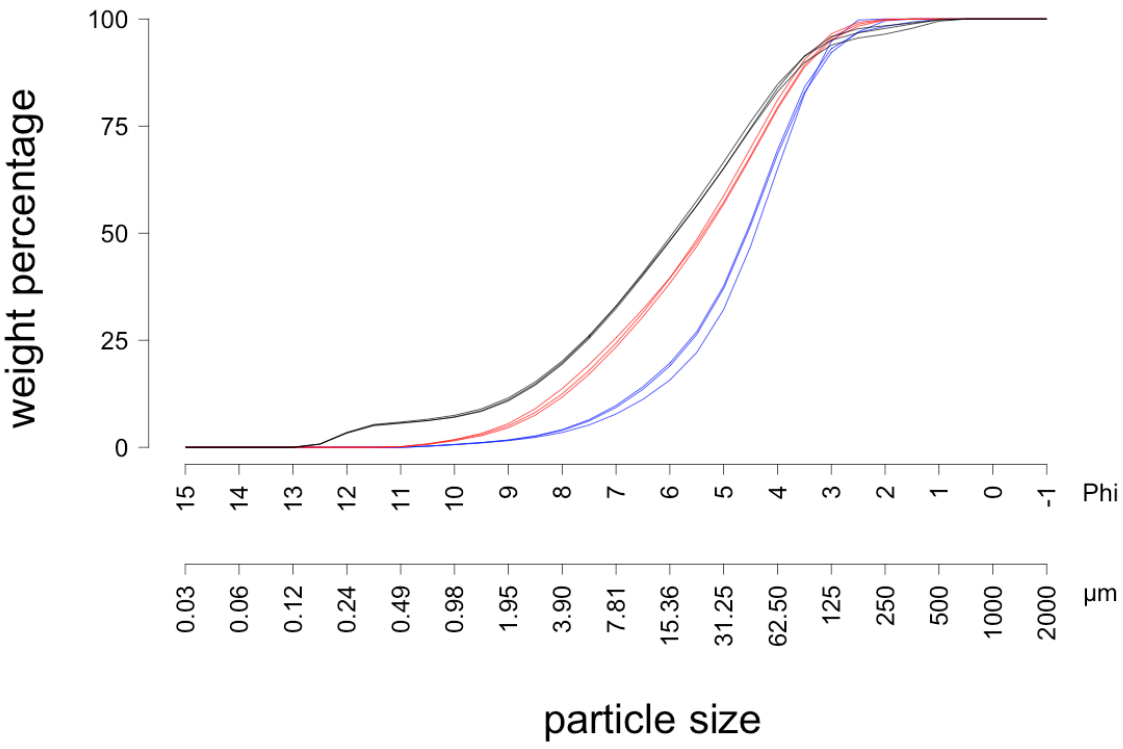

Figure A4.1: Accumulative sediment particle size distributions for the environmental setting of the Ythan Estuary (blue), Humber Estuary (red) and Hamble Estuary (black).

Table A4.1: Sediment parameters (mean ± sd, n=3) for the three environmental settings used in the experiment.

Source of sediment	Mz (µm)	Mz (Phi)	Sorting (µm)	Sorting (Phi)	Kurtosis (µm)	Kurtosis (Phi)	Skeweness (µm)	Skeweness (Phi)	Results below 63 µm (%)	TOC (%)
Ythan Estuary	49.4 ± 2	4.7 ± 0.1	375.8 ± 21.4	1.4 ± 0.08	451.7 ± 3.6	1.1 ± 0.01	1208.8 ± 27.1	-0.3 ± 0.03	68.8 ± 2.3	9.3 ± 2.6
Humber Estuary	33.6 ± 1.1	5.6 ± 0.1	274.3 ± 7.2	1.9 ± 0.04	540.9 ± 5.7	0.9 ± 0.02	1151.4 ± 12.2	-0.2 ± 0.02	80.1 ± 1.1	10.2 ± 2.2
Hamble Estuary	27.5 ± 0.9	6.1 ± 0.04	189.1 ± 4.6	2.4 ± 0.04	449.7 ± 9.55	1.2 ± 0.03	1167.6 20.4	-0.2 ± 0.03	84.0 ± 0.9	6.8 ± 0.1

Statistical model summary

Summary of the analyses including species identity (Table A3.2) and the statistical models analysing each species separately, while the species mixture was treated as a unique species identity (Model S1 to S23). For each model, the initial linear regression model and the minimal adequate model are list. When variance homogeneity was violated a linear regression with GLS estimation was used. A summary of the coefficient tables for single terms is presented. The coefficients indicate the relative performance of each treatment level relative to the re-levelled baseline (as indicated). Coefficients ± SE, t-values and respective significance values are presentment.

Abbreviations: SID, species identity; EnvSet, environmental setting; Pop, population

Model S1: Surface boundary roughness (SBR, cm) - *Hydrobia ulvae*

Initial linear regression model:

lm(SBR ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls(SBR ~ EnvSet, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary): 0.364 ± 0.026, t = 14.010, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	-0.226 ± 0.067 3.361 **0.003**	0.093 ± 0.043 -2.149 **0.042**
Humber	0.226 ± 0.067 3.361 **0.003**	/	0.319 ± 0.071 -4.491 **<0.001**
Hamble	-0.093 ± 0.043 -2.149 **0.042**	-0.319 ± 0.071 -4.491 **<0.001**	/

Model S2: Surface boundary roughness (SBR, cm) - *Corophium volutator*

Initial linear regression model:

lm(SBR ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls(SBR ~ EnvSet+Pop, weights = varIdent(form = ~1|Pop), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 0.552 ± 0.082, t = 6.764, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	0.120 ± 0.100 -1.198 0.244	-0.305 ± 0.100 3.040 **0.006**
Humber	-0.120 ± 0.100 -1.198 0.244	/	-0.425 ± 0.100 4.239 **<0.001**
Hamble	0.305 ± 0.100 3.040 **0.006**	0.425 ± 0.100 4.239 **<0.001**	/

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-0.399 ± 0.149 2.679 **0.014**	-0.056 ± 0.086 0.653 0.521
Humber	0.399 ± 0.149 2.679 **0.014**	/	0.343 ± 0.152 -2.260 **0.034**
Hamble	0.056 ± 0.086 0.653 0.521	-0.343 ± 0.152 -2.260 **0.034**	/

Model S3: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm) - *Hediste diversicolor*

Initial linear regression model:

lm($^{f\text{-}SPI}L_{mean}$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm($^{f\text{-}SPI}L_{mean}$ ~ EnvSet+Pop)

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 1.987 ± 0.119, t = 16.818, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	0.909 ± 0.129 7.025 **<0.0001**	0.734 ± 0.129 5.668 **<0.0001**
Humber	-0.909 ± 0.129 -7.025 **<0.0001**	/	-0.176 ± 0.129 -1.356 0.189
Hamble	-0.734 ± 0.129 -5.668 **<0.0001**	0.176 ± 0.129 1.356 0.189	/

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	**/**	-0.450 ± 0.129 -3.474 **0.002**	0.374 ± 0.129 2.891 **0.008**
Humber	0.450 ± 0.129 3.474 **0.002**	/	0.824 ± 0.129 6.364 **<0.0001**
Hamble	-0.374 ± 0.129 -2.891 **0.008**	-0.824 ± 0.129 -6.364 **<0.0001**	/

Model S4: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm) - *Hydrobia ulvae*

Initial linear regression model:

$lm(^{f\text{-}SPI}L_{mean} \sim EnvSet+Pop+EnvSet:Pop)$

Minimal adequate model:

$lm(^{f\text{-}SPI}L_{mean} \sim EnvSet+Pop)$

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 0.294 ± 0.014, t = 21.541, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	0.100 ± 0.150 6.694 **<0.0001**	0.046 ± 1.150 3.054 **0.006**
Humber	-0.100 ± 0.150 -6.694 **<0.0001**	/	-0.054 ± 0.150 -3.640 **0.001**
Hamble	-0.046 ± 1.150 -3.054 **0.006**	0.054 ± 0.150 3.640 **0.001**	/

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-0.036 ± 0.150 -2.411 **0.025**	0.028 ± 0.150 1.852 0.078
Humber	0.036 ± 0.150 2.411 **0.025**	/	0.064 ± 0.150 4.263 **0.0003**
Hamble	-0.028 ± 0.150 -1.852 0.078	-0.064 ± 0.150 -4.263 **0.0003**	/

Model S5: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm) - *Corophium volutator*

Initial linear regression model:

lm($^{f\text{-}SPI}L_{mean}$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm($^{f\text{-}SPI}L_{mean}$ ~ EnvSet+Pop+EnvSet:Pop)

Model S6: Mean mixed depth of particle reworking ($^{f\text{-}SPI}L_{mean}$, cm) - species mixture

Initial linear regression model:

lm($^{f\text{-}SPI}L_{mean}$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls($^{f\text{-}SPI}L_{mean}$ ~ EnvSet+Pop+EnvSet:Pop, weights = varIdent(form = ~1|Pop), method = 'REML'))

Model S7: Maximum mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm) - *Hediste diversicolor*

Initial linear regression model:

lm($^{f\text{-}SPI}L_{max}$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls($^{f\text{-}SPI}L_{max}$ ~ EnvSet, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary): 10.627 ± 0.151, t = 70.244, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	1.313 ± 1.028 1.277 0.214	0.771 ± 0.205 3.768 **0.001**
Humber	-1.313 ± 1.028 -1.277 0.214	/	-0.542 ± 1.026 -0.529 0.602
Hamble	-0.771 ± 0.205 -3.768 **0.001**	0.542 ± 1.026 0.529 0.602	/

Model S8: Maximum mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm) - *Hydrobia ulvae*

Initial linear regression model:

lm($^{f\text{-}SPI}L_{max}$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls($^{f\text{-}SPI}L_{max}$ ~ EnvSet+Pop, weights = varIdent(form = ~1|EnvSet×Pop), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 2.245 ± 0.345, t = 6.516, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	0.026 ± 0.220 0.118 0.907	0.873 ± 0.181 4.815 **0.0001**
Humber	-0.026 ± 0.220 -0.118 0.907	/	0.847 ± 0.134 6.304 **<0.0001**
Hamble	-0.873 ± 0.181 -4.815 **0.0001**	-0.847 ± 0.134 -6.304 **<0.0001**	/

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	0.632 ± 0.317 1.992 0.059	0.755 ± 0.315 2.399 **0.025**
Humber	-0.632 ± 0.317 -1.992 0.059	/	0.123 ± 0.058 2.119 **0.046**
Hamble	-0.755 ± 0.315 -2.399 **0.025**	-0.123 ± 0.058 -2.119 **0.046**	/

Model S9: Maximum mixed depth of particle reworking ($^{f\text{-}SPI}L_{max}$, cm) - species mixture

Initial linear regression model:

lm($^{f\text{-}SPI}L_{max}$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls($^{f\text{-}SPI}L_{max}$ ~ EnvSet+Pop+EnvSet:Pop, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Model S10: Burrow ventilation ($\Delta[Br^-]$, mg L^{-1}) - *Hediste diversicolor*

Initial linear regression model:

lm($\Delta[Br^-]$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm($\Delta[Br^-]$ ~ Pop)

Intercept ± SE (when baseline is for Ythan Estuary for Pop): -69.213 ± 10.654, t = -6.496, p < 0.0001

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-9.302 ± 15.067 -0.617 0.543	-37.849 ± 15.067 -2.512 **0.019**
Humber	9.302 ± 15.067 0.617 0.543	/	-28.548 ± 15.067 -1.895 0.070
Hamble	37.849 ± 15.067 2.512	28.548 ± 15.067 1.895	/

	0.019	0.070	

Model S11: Burrow ventilation ($\Delta[Br^-]$, mg L^{-1}) - *Corophium volutator*

Initial linear regression model:

lm($\Delta[Br^-]$ ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm($\Delta[Br^-]$ ~ Pop)

Intercept ± SE (when baseline is for Ythan Estuary for Pop): -45.270 ± 10.520, t = -4.303, p = 0.0002

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-37.600 ± 14.881 -2.527 0.019	-27.270 ± 14.881 -1.833 0.079
Humber	37.600 ± 14.881 2.527 0.019	/	10.325 ± 14.881 0.694 0.494
Hamble	27.270 ± 14.881 1.833 0.079	-10.325 ± 14.881 -0.694 0.494	/

Model S12: NH_4-N concentration ([NH_4-N], mg L^{-1}) - *Hediste diversicolor*

Initial linear regression model:

lm([NH_4-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm([NH_4-N] ~ EnvSet+Pop)

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 5.658 ± 0.869, t = 6.508, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	-5.502 ± 0.952 -5.778 **<0.0001**	1.720 ± 0.952 1.805 0.085
Humber	5.502 ± 0.952 5.778 **<0.0001**	/	7.222 ± 0.952 7.582 **<0.0001**
Hamble	-1.720 ± 0.952 -1.805	-7.222 ± 0.952 -7.582	/

	0.085	**<0.0001**	

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-2.114 ± 0.952 -2.220 **0.037**	-2.577 ± 0.952 -2.706 **0.013**
Humber	2.114 ± 0.952 2.220 **0.037**	/	-0.463 ± 0.952 -0.486 0.632
Hamble	2.577 ± 0.952 2.706 **0.013**	0.463 ± 0.952 0.486 0.632	/

Model S13: NH_4-N concentration ([NH_4-N], mg L^{-1}) - *Hydrobia ulvae*

Initial linear regression model:

lm([NH_4-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([NH_4-N] ~ EnvSet+Pop+EnvSet:Pop, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Model S14: NH_4-N concentration ([NH_4-N], mg L^{-1}) - *Corophium volutator*

Initial linear regression model:

lm([NH_4-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([NH_4-N] ~ EnvSet+Pop, weights = varIdent(form = ~1| EnvSet×Pop), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 2.414 ± 0.141, t = 17.100, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	-4.442 ± 0.235 -18.886 **<0.0001**	-3.483 ± 0.148 -23.483 **<0.0001**
Humber	4.442 ± 0.235 18.886 **<0.0001**	/	0.960 ± 0.184 5.223 **<0.0001**

Hamble	3.483 ± 0.148 23.483 **<0.0001**	-0.960 ± 0.184 -5.223 **<0.0001**	/

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-0.801 ± 0.073 -11.026 **<0.0001**	-0.699 ± 0.215 -3.246 **0.004**
Humber	0.801 ± 0.073 11.026 **<0.0001**	/	0.103 ± 0.216 0.475 0.640
Hamble	0.699 ± 0.215 3.246 **0.004**	-0.103 ± 0.216 -0.475 0.640	/

Model S15: NH_4-N concentration ([NH_4-N], mg L^{-1}) - species mixture

Initial linear regression model:

lm([NH_4-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([NH_4-N] ~ EnvSet+Pop, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary for EnvSet and Pop): 3.950 ± 0.385, t = 10.271, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	-5.604 ± 1.020 -5.493 **<0.0001**	-2.574 ± 0.366 -7.041 **<0.0001**
Humber	5.604 ± 1.020 5.493 **<0.0001**	/	3.030 ± 0.976 3.104 **0.005**
Hamble	2.574 ± 0.366 7.041 **<0.0001**	-3.030 ± 0.976 -3.104 **0.005**	/

Coefficient table for Pop

	Ythan	Humber	Hamble
Ythan	/	-0.771 ± 0.333 -2.317 **0.030**	0.324 ± 0.333 0.973 0.341
Humber	0.771 ± 0.333 2.317 **0.030**	/	1.095 ± 0.333 3.290 **0.003**
Hamble	-0.324 ± 0.333 -0.973 0.341	-1.095 ± 0.333 -3.290 **0.003**	/

Model S16: NO_x-N concentration ([NO_x-N], mg L^{-1}) - *Hediste diversicolor*

Initial linear regression model:

lm([NO_x-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm([NO_x-N] ~ EnvSet)

Intercept ± SE (when baseline is for Ythan Estuary): 9.678 ± 1.170, t = 8.269, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	6.306 ± 1.655 3.810 **<0.001**	1.674 ± 1.655 1.012 0.322
Humber	-6.306 ± 1.655 -3.810 **<0.001**	/	-4.632 ± 1.655 -2.799 **0.01**
Hamble	-1.674 ± 1.655 -1.012 0.322	4.632 ± 1.655 2.799 **0.01**	/

Model S17: NO_x-N concentration ([NO_x-N], mg L^{-1}) - *Hydrobia ulvae*

Initial linear regression model:

lm([NO_x-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

lm([NO_x-N] ~ EnvSet)

Intercept ± SE (when baseline is for Ythan Estuary): 17.689 ± 0.618, t = 28.54, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	11.063 ± 0.874 12.660 **<0.0001**	5.023 ± 0.874 5.750 **<0.0001**
Humber	-11.063 ± 0.874 -12.660 **<0.0001**	/	-6.040 ± 0.874 -6.914 **<0.0001**
Hamble	-5.023 ± 0.874 -5.750 **<0.0001**	6.040 ± 0.874 6.914 **<0.0001**	/

Model S18: NO_x-N concentration ([NO_x-N], mg L^{-1}) - *Corophium volutator*

Initial linear regression model:

lm([NO_x-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([NO_x-N] ~ EnvSet, weights = varIdent(form = ~1| EnvSet×Pop), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary): 30.744 ± 3.893, t = 7.896, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	17.960 ± 4.443 4.042 **<0.001**	25.648 ± 3.939 6.512 **<0.0001**
Humber	-17.960 ± 4.443 -4.042 **<0.001**	/	7.689 ± 2.222 3.460 **0.002**
Hamble	-25.648 ± 3.939 -6.512 **<0.0001**	-7.689 ± 2.222 -3.460 **0.002**	/

Model S19: NO_x-N concentration ([NO_x-N], mg L^{-1}) - species mixture

Initial linear regression model:

lm([NO_x-N] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([NO_x-N] ~ EnvSet, weights = varIdent(form = ~1|EnvSet×Pop), method = 'REML'))

Intercept ± SE (when baseline is for Ythan Estuary): 21.514 ± 0.177, t = 121.518, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	16.630 ± 0.757 21.980 **<0.0001**	18.643 ± 0.411 45.379 **<0.0001**
Humber	-16.630 ± 0.757 -21.980 **<0.0001**	/	2.013 ± 0.824 2.444 **0.022**
Hamble	-18.643 ± 0.411 -45.379 **<0.0001**	-2.013 ± 0.824 -2.444 **0.022**	/

Model S20: PO_4-P concentration ([PO_4-P], mg L^{-1}) - *Hediste diversicolor*

Initial linear regression model:

lm([PO_4-P] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([PO_4-P] ~ EnvSet, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary): 1.530 ± 0.157, t = 9.741, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	1.008 ± 0.159 6.337 **<0.0001**	0.990 ± 0.163 6.064 **<0.0001**
Humber	-1.008 ± 0.159 -6.337 **<0.0001**	/	0.018 ± 0.051 0.356 0.725
Hamble	-0.990 ± 0.163 -6.064 **<0.0001**	0.018 ± 0.051 0.356 0.725	/

Model S21: PO_4-P concentration ([PO_4-P], mg L^{-1}) - *Hydrobia ulvae*

Initial linear regression model:

lm([PO_4-P] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([PO_4-P] ~ EnvSet, weights = varIdent(form = ~1|Pop), method = 'REML')

Intercept ± SE (when baseline is for Ythan Estuary): 0.620 ± 0.013, t = 46.206, p < 0.0001

Coefficient table for EnvSet

	Ythan	Humber	Hamble
Ythan	/	0.119 ± 0.019 6.277 **<0.0001**	0.300 ± 0.019 15.778 **<0.0001**
Humber	-0.119 ± 0.019 -6.277 **<0.0001**	/	0.180 ± 0.019 9.501 **<0.0001**
Hamble	-0.300 ± 0.019 -15.778 **<0.0001**	-0.180 ± 0.019 -9.501 **<0.0001**	/

Model S22: PO_4-P concentration ([PO_4-P], mg L^{-1}) - *Corophium volutator*

Initial linear regression model:

lm([PO_4-P] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([PO_4-P] ~ EnvSet+Pop+EnvSet:Pop, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Model S23: PO_4-P concentration ([PO_4-P], mg L^{-1}) - species mixture

Initial linear regression model:

lm([PO_4-P] ~ EnvSet+Pop+EnvSet:Pop)

Minimal adequate model:

gls([PO_4-P] ~ EnvSet+Pop+EnvSet:Pop, weights = varIdent(form = ~1|EnvSet), method = 'REML')

Table A4.2: Summary of data used for statistical analysis. Data in the absence of macrofauna is shown for comparison but was not included in the analyses. EnvSet = environmental setting, Pop = population, SID = species identity (HD = *Hediste diversicolor*, HU = *Hydrobia ulvae*, CV = *Corophium volutator,* Mix = species mixture, cntrl = no macrofauna), Ha = Hamble Estuary, Hu = Humber Estuary, Y = Ythan Estuary

Env Set	Pop	SID	Repli-cate	$^{f\text{-}SPI}L_{mean}$ (cm)	$^{f\text{-}SPI}L_{max}$ (cm)	SBR (cm)	$\Delta[Br^-]$ (mg L^{-1})	$[NH_4\text{-}N]$ (mg L^{-1})	$[NO_x\text{-}N]$ (mg L^{-1})	$[PO_4\text{-}P]$ (mg L^{-1})
Ha	Ha	HD	1	0.915	10.465	0.850	-20.160	6.552	5.443	0.358
Ha	Ha	HD	2	1.126	10.438	0.514	-24.325	7.743	5.024	0.683
Ha	Ha	HD	3	0.965	9.608	0.746	-36.740	5.745	7.501	0.596
Ha	Ha	HU	1	0.236	0.605	0.384	1.218	1.096	12.395	0.322
Ha	Ha	HU	2	0.208	0.575	0.316	-11.459	1.384	10.972	0.329
Ha	Ha	HU	3	0.230	0.668	0.063	-5.637	0.655	10.825	0.209
Ha	Ha	CV	1	0.928	2.839	0.969	7.622	6.697	6.403	0.268
Ha	Ha	CV	2	1.018	2.606	0.917	-1.636	6.089	5.051	0.248
Ha	Ha	CV	3	0.821	2.380	0.467	-8.667	6.817	2.664	0.175
Ha	Ha	Mix	1	0.638	4.650	0.422	-70.389	6.499	1.537	0.203
Ha	Ha	Mix	2	0.744	8.680	1.237	-7.093	6.007	2.427	0.230
Ha	Ha	Mix	3	0.819	7.751	0.776	-34.825	6.096	3.115	0.204
Ha	Hu	HD	1	1.667	9.746	0.831	-76.752	4.782	9.260	0.657
Ha	Hu	HD	2	1.868	9.639	0.638	15.830	7.952	1.348	0.731
Ha	Hu	HD	3	1.454	9.392	0.775	-62.558	4.637	9.104	0.456
Ha	Hu	HU	1	0.279	0.780	0.302	-22.948	0.765	10.868	0.293
Ha	Hu	HU	2	0.291	0.807	0.271	-44.985	0.491	13.403	0.332

Ha	Hu	HU	3	0.242	0.638	0.139	33.476	0.769	12.829	0.345
Ha	Hu	CV	1	0.550	2.731	1.010	-12.575	6.604	3.818	0.260
Ha	Hu	CV	2	0.927	3.941	1.280	20.377	6.797	7.401	0.310
Ha	Hu	CV	3	0.815	3.443	2.052	-18.774	6.704	7.868	0.265
Ha	Hu	Mix	1	1.521	10.379	1.459	-33.554	6.807	5.439	0.337
Ha	Hu	Mix	2	0.872	8.576	0.998	46.851	7.767	1.192	0.406
Ha	Hu	Mix	3	1.072	9.474	0.864	-11.443	7.481	3.466	0.440
Ha	Y	HD	1	1.129	9.499	0.723	-78.203	3.732	11.983	0.536
Ha	Y	HD	2	1.366	10.251	1.004	-64.653	2.532	15.152	0.423
Ha	Y	HD	3	1.015	9.671	0.524	-33.694	5.848	7.226	0.426
Ha	Y	HU	1	0.254	1.489	0.290	31.824	0.607	14.640	0.341
Ha	Y	HU	2	0.208	1.012	0.348	-23.202	0.774	13.803	0.332
Ha	Y	HU	3	0.313	5.103	0.329	-3.210	0.667	14.254	0.335
Ha	Y	CV	1	0.824	3.554	0.972	-24.510	5.960	3.963	0.215
Ha	Y	CV	2	0.700	2.960	1.008	-34.489	5.803	5.004	0.223
Ha	Y	CV	3	0.784	2.488	0.796	-51.996	5.930	3.697	0.227
Ha	Y	Mix	1	1.053	9.917	0.714	-43.169	6.995	2.653	0.324
Ha	Y	Mix	2	0.962	9.837	1.349	-58.581	5.856	4.556	0.277
Ha	Y	Mix	3	0.881	9.018	1.078	-47.269	6.558	2.997	0.338
Ha	Ha	/	cntrl	0.059	0.690	0.418	-17.355	0.085	3.621	0.031
Ha	Ha	/	cntrl	0.091	0.498	0.542	-8.946	0.023	3.547	0.065

Ha	Ha	/	cntrl	0.072	0.652	0.443	-64.054	1.117	7.760	0.205
Ha	Hu	/	cntrl	0.059	0.690	0.418	-17.355	0.085	3.621	0.031
Ha	Hu	/	cntrl	0.091	0.498	0.542	-8.946	0.023	3.547	0.065
Ha	Hu	/	cntrl	0.072	0.652	0.443	-64.054	1.117	7.760	0.205
Ha	Y	/	cntrl	0.059	0.690	0.418	-17.355	0.085	3.621	0.031
Ha	Y	/	cntrl	0.091	0.498	0.542	-8.946	0.023	3.547	0.065
Ha	Y	/	cntrl	0.072	0.652	0.443	-64.054	1.117	7.760	0.205
Hu	Ha	HD	1	0.797	10.977	0.900	-13.598	13.251	1.475	0.545
Hu	Ha	HD	2	0.073	1.324	0.933	-50.119	13.222	1.825	0.395
Hu	Ha	HD	3	0.641	9.609	1.069	-17.423	13.097	2.605	0.492
Hu	Ha	HU	1	0.190	1.682	0.398	0.838	4.778	11.101	0.493
Hu	Ha	HU	2	0.169	1.181	0.810	-13.943	6.031	5.846	0.509
Hu	Ha	HU	3	0.134	1.478	0.581	-28.530	5.797	6.525	0.492
Hu	Ha	CV	1	0.275	2.014	0.537	-11.058	8.048	0.971	0.674
Hu	Ha	CV	2	0.591	2.867	0.646	-16.046	6.637	19.963	1.031
Hu	Ha	CV	3	0.582	2.500	0.504	-24.338	9.185	11.724	0.923
Hu	Ha	Mix	1	0.540	10.592	0.518	-11.429	12.001	2.153	0.721
Hu	Ha	Mix	2	0.876	9.505	0.720	-31.978	6.774	8.402	0.781
Hu	Ha	Mix	3	0.625	9.507	0.423	-37.974	8.853	4.080	0.752
Hu	Hu	HD	1	1.719	10.709	1.752	-7.928	14.848	1.120	0.483
Hu	Hu	HD	2	2.041	10.998	0.807	-58.768	14.534	4.129	0.603

Hu	Hu	HD	3	1.212	9.835	1.318	-61.465	13.341	4.734	0.625
Hu	Hu	HU	1	0.214	1.631	0.866	-32.199	6.881	3.512	0.501
Hu	Hu	HU	2	0.193	1.044	0.297	-44.373	5.770	6.935	0.470
Hu	Hu	HU	3	0.269	2.734	0.564	-16.736	6.181	4.560	0.519
Hu	Hu	CV	1	0.240	3.382	0.595	-37.403	7.939	11.586	0.970
Hu	Hu	CV	2	0.231	1.467	0.434	-23.721	7.592	14.185	1.038
Hu	Hu	CV	3	0.290	4.041	1.068	4.033	7.296	17.111	1.021
Hu	Hu	Mix	1	1.441	10.092	0.416	-55.431	13.182	2.506	0.622
Hu	Hu	Mix	2	0.837	9.332	0.921	-52.307	12.040	5.327	0.760
Hu	Hu	Mix	3	1.046	9.221	0.491	-60.298	12.240	5.491	0.876
Hu	Y	HD	1	0.903	10.218	0.491	-36.421	13.287	4.101	0.493
Hu	Y	HD	2	1.247	10.675	0.592	-80.054	12.922	3.069	0.475
Hu	Y	HD	3	1.294	9.483	0.758	-82.670	6.013	7.286	0.592
Hu	Y	HU	1	0.194	2.373	0.598	-136.94	6.315	5.640	0.486
Hu	Y	HU	2	0.227	1.498	0.478	-38.950	5.939	6.444	0.496
Hu	Y	HU	3	0.181	2.680	0.722	-82.200	7.629	9.077	0.790
Hu	Y	CV	1	0.438	2.952	0.460	-66.684	4.948	21.875	0.867
Hu	Y	CV	2	0.745	3.159	0.379	-119.99	8.386	9.748	0.821
Hu	Y	CV	3	0.612	2.123	0.347	-65.441	9.277	7.896	0.764
Hu	Y	Mix	1	0.668	9.990	0.908	-43.966	10.626	4.976	0.689

Hu	Y	Mix	2	0.748	7.347	0.876	-78.148	7.913	4.629	0.766
Hu	Y	Mix	3	0.649	8.135	1.164	-60.011	3.708	10.269	0.455
Hu	Ha	/	cntrl	0.106	1.023	0.429	-48.926	4.384	8.519	0.437
Hu	Ha	/	cntrl	0.093	1.158	0.654	-54.156	4.264	8.269	0.424
Hu	Ha	/	cntrl	0.047	1.158	0.541	14.475	1.762	17.420	0.459
Hu	Hu	/	cntrl	0.106	1.023	0.429	-48.926	4.384	8.519	0.437
Hu	Hu	/	cntrl	0.093	1.158	0.654	-54.156	4.264	8.269	0.424
Hu	Hu	/	cntrl	0.047	1.158	0.541	14.475	1.762	17.420	0.459
Hu	Y	/	cntrl	0.106	1.023	0.429	-48.926	4.384	8.519	0.437
Hu	Y	/	cntrl	0.093	1.158	0.654	-54.156	4.264	8.269	0.424
Hu	Y	/	cntrl	0.047	1.158	0.541	14.475	1.762	17.420	0.459
Y	Ha	HD	1	1.703	10.289	0.372	-13.602	4.844	17.614	1.189
Y	Ha	HD	2	1.546	9.971	1.371	-19.159	12.495	6.559	0.664
Y	Ha	HD	3	1.821	11.172	0.549	-87.152	8.516	7.327	1.476
Y	Ha	HU	1	0.305	2.862	0.378	-89.941	0.775	19.450	0.833
Y	Ha	HU	2	0.278	2.327	0.183	-31.893	0.258	18.003	0.620
Y	Ha	HU	3	0.211	1.331	0.366	-49.582	0.209	17.491	0.636
Y	Ha	CV	1	0.393	2.336	0.579	-51.354	1.868	43.017	1.165
Y	Ha	CV	2	0.554	1.810	0.801	-15.599	2.339	40.733	1.078
Y	Ha	CV	3	0.388	3.396	0.606	-40.912	7.085	8.426	0.817
Y	Ha	Mix	1	1.052	10.244	0.970	4.442	3.421	21.981	1.242

Y	Ha	Mix	2	1.066	11.091	0.669	-69.082	4.295	20.561	1.091
Y	Ha	Mix	3	1.231	10.651	1.347	-40.063	3.178	22.061	1.436
Y	Hu	HD	1	2.178	10.017	0.678	-68.074	6.039	9.706	1.451
Y	Hu	HD	2	2.189	10.898	1.055	-115.62	7.793	4.652	2.087
Y	Hu	HD	3	2.672	10.789	1.385	-103.86	7.374	9.858	2.267
Y	Hu	HU	1	0.344	1.162	0.398	-43.434	0.238	18.308	0.638
Y	Hu	HU	2	0.332	1.770	0.419	15.983	0.380	16.503	0.602
Y	Hu	HU	3	0.370	1.703	0.397	-8.297	0.268	17.281	0.597
Y	Hu	CV	1	0.473	1.925	1.063	-68.062	4.015	30.940	1.642
Y	Hu	CV	2	0.573	3.057	0.411	24.636	4.447	29.398	1.501
Y	Hu	CV	3	0.632	2.042	1.195	42.424	1.696	44.617	1.869
Y	Hu	Mix	1	1.918	11.131	0.378	-46.170	4.806	21.148	1.573
Y	Hu	Mix	2	2.924	10.777	0.719	14.968	4.194	21.554	1.586
Y	Hu	Mix	3	2.364	10.593	0.921	-83.518	3.576	21.857	1.517
Y	Y	HD	1	2.296	10.995	1.041	-43.345	7.181	6.746	1.518
Y	Y	HD	2	1.602	10.470	1.172	-86.256	5.794	10.152	1.409
Y	Y	HD	3	2.101	11.045	0.931	-117.62	4.961	14.487	1.713
Y	Y	HU	1	0.271	1.386	0.443	-40.121	0.493	14.004	0.545
Y	Y	HU	2	0.298	3.655	0.304	-58.421	0.538	18.759	0.685
Y	Y	HU	3	0.263	1.085	0.391	58.650	0.552	19.404	0.696
Y	Y	CV	1	0.357	4.600	0.498	0.439	2.177	34.452	1.368
Y	Y	CV	2	0.360	2.786	0.253	5.696	2.676	21.899	1.065

Y	Y	CV	3	0.341	2.622	0.807	-50.479	2.349	23.214	1.326
Y	Y	Mix	1	1.767	10.024	0.818	-67.061	3.966	18.581	1.088
Y	Y	Mix	2	1.326	10.343	0.378	-61.574	6.171	8.849	0.878
Y	Y	Mix	3	1.327	10.758	0.378	-39.049	3.288	22.172	1.445
Y	Ha	/	cntrl	0.258	1.190	0.405	-20.218	0.217	17.000	0.600
Y	Ha	/	cntrl	0.305	2.561	0.967	-30.673	0.223	15.020	0.548
Y	Ha	/	cntrl	0.346	1.289	0.461	-89.555	0.424	17.186	0.582
Y	Hu	/	cntrl	0.258	1.190	0.405	-20.218	0.217	17.000	0.600
Y	Hu	/	cntrl	0.305	2.561	0.967	-30.673	0.223	15.020	0.548
Y	Hu	/	cntrl	0.346	1.289	0.461	-89.555	0.424	17.186	0.582
Y	Y	/	cntrl	0.258	1.190	0.405	-20.218	0.217	17.000	0.600
Y	Y	/	cntrl	0.305	2.561	0.967	-30.673	0.223	15.020	0.548
Y	Y	/	cntrl	0.346	1.289	0.461	-89.555	0.424	17.186	0.582

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