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Realistic scenarios of environmental disturbance lead to functionally important changes in benthic species-environment interactions

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A R T I C L E I N F O

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A B S T R A C T

Changes in community structure concurrent with environmental forcing often form a precursor to changes in species diversity, and can have substantive consequences for ecosystem functioning. Here, we assess the effects of altered levels of evenness that are representative of different levels of eutrophication and changes in salinity associated with altered precipitation patterns, on the mediation of nutrient release by sediment-dwelling invertebrate communities. We find that an adjustment towards a more even distribution of species corresponds with an increase in sediment particle reworking that, in general, translates to increased levels of nutrient release. This response, however, is dependent on the functional role of each species in the community and is influenced by concomitant changes in salinity, especially when salinity extends beyond the range typically experienced by the community. Overall, our findings highlight the dynamic nature of species contributions to functioning and reinforce the importance of understanding when, and how, the mechanistic basis of species-environment interactions are modified as the influence of abiotic and biotic factors flex under periods of directional forcing.

1. Introduction

Coastal and estuarine systems provide many ecosystem services essential for society (Costanza et al., 2014; Barbier, 2017), but intensification of human activity, combined with the modifying effects of various aspects of climate change (Dolbeth et al., 2011; Godbold and Solan, 2013; Smale et al., 2019), can lead to changes in diversity that impair the efficiency at which ecosystems function (Gamfeldt et al., 2015; Strong et al., 2015). This, in turn, can lessen the likelihood of delivering benefits to society (Doney et al., 2012; Bennett et al., 2015; Culhane et al., 2019). However, whilst the functional significance of changes in biodiversity are generally accepted (Cardinale et al., 2012), both theory (Thomsen et al., 2017) and empirical and observational data (Hale et al., 2017; Sciberras et al., 2017; Thomsen et al., 2019) along environmental and anthropogenic gradients of disturbance (Dolbeth et al., 2011, 2014; Pan et al., 2016) confirm that the relative importance of species richness (Godbold and Solan, 2009), and the realised level of ecosystem function, often depart from expectation (Avolio et al., 2014; Wohlgemuth et al., 2016, 2017; Daam et al., 2019). Such a position is not a very satisfactory grounding on which to base management or planning decisions (Lundquist et al., 2016), especially with regard to anticipating the sort of ecosystem responses that can be mitigated (Dolbeth et al., 2016; Thomsen et al., 2017; Guerra et al., 2019) or the most likely effect size and confidence for specific levels or types and/or combinations of directional change (Hewitt et al., 2016; O'Meara et al., 2017; Nicholls et al., 2018; Snelgrove et al., 2018). Further work is required to elucidate how local temporal and spatial dynamics influence ecosystem responses to disturbance, and to distinguish whether any observed ecological outcomes that relate to ecosystem functioning are a product of long-term historical trends or short-term context-specific shocks within this history (Whitfield et al., 2019).

Changes in species evenness and the rank order of dominant species are common responses to directional forcing in estuarine systems (Wohlgemuth et al., 2016) and, coupled with the spectrum of variation in abiotic-biotic conditions (Elliott and Whitfield, 2011; Dolbeth et al., 2013), can provide opportunity for existing and invading species to

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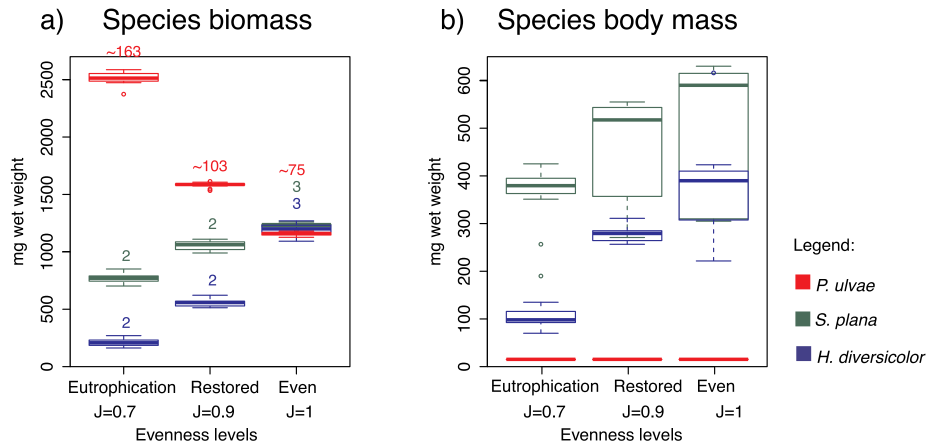

Fig. 1. Summary of a) total population biomass for species within each aquaria, and b) the mean body mass of individuals for each species across each of the evenness levels (*Eutrophication, Restored* and *Even*) under study. For *Peringia ulvae*, mean body mass was estimated with the shell. Integers indicate abundance.

outcompete or otherwise improve their standing (Langenheder et al., 2012; Simberloff et al., 2013; Crespo et al., 2018). Recent work confirms that these responses can be population-specific and dependent on habitat configuration, as well as on other attributes of the environmental setting (Godbold et al., 2011; Wohlgemuth et al., 2017). Whilst the effects of species composition and the arrangement of dominance hierarchies remain under-studied in an estuarine context (but see Altieri et al., 2009; Wohlgemuth et al., 2016), an emerging realisation is that the best performing species in a community prior to disturbance (Strong et al., 2015; Daam et al., 2019) are not necessarily the most important contributors to functioning post disturbance (Hale et al., 2014, 2017; Murray et al., 2014; Gamfeldt et al., 2015; Thomsen et al., 2019). This is because the functional role of a species reflects the responses of individuals to disturbance, including exploitation of new opportunity (Hicks et al., 2011), and the nature of species-environment interactions in the surviving community (Godbold and Solan, 2013; Thomsen et al., 2017, 2019; Wohlgemuth et al., 2017; Crespo et al., 2018). Motivated by the requirement to place more emphasis on relevant environmental scenarios (Bracken et al., 2008; Naeem, 2008), here we measure the effect of changes in evenness that are representative of those observed during altered levels of eutrophication combined with salinity associated with deviations in precipitation patterns (floods and drought) on estuarine ecosystem functioning. Our rationale and experimental design is informed by long-term background information on the influence of disturbance on macrobenthic communities of the Mondego estuary (e.g. Dolbeth et al., 2011, 2014). We anticipate that the way in which realistic changes in diversity affect estuarine processes and functions, such as bioturbation and nutrient generation, will differ from what is presently anticipated based on the form of the generalised biodiversity-function curve (Thomsen et al., 2017). Hence, our expectation is that any observed disparity will reflect subtle and context dependent changes in functionally important aspects of species behaviour.

2. Material and methods

2.1. Aquaria setup

We collected sediment from the polyhaline mudflats on the Mondego estuary (40°9′47.91″N, 8°40′12.42″W), which ordinarily experience a mean annual salinity of 25.6 ± 7.1 (Verdelhos et al., 2014). The sediment was sieved (0.5 mm) in a seawater bath to remove macrofauna, and left to settle for 24 h to retain the fine fraction of sediment. Excess water was removed and the sediment slurry was homogenized and distributed in glass aquaria (12 × 12 × 35 cm, internal dimensions) containing sediment (~10 cm depth) overlain with 20 cm of water (~2.88 L) for a period of 12 days.

We collected individuals of *Peringia ulvae* (Pu)*, Hediste diversicolor* (Hd) and *Scrobicularia plana* (Sp)*,* all dominant species of intertidal estuarine flats (Dolbeth et al., 2011) and representative of different functional groups (epifaunal, gallery biodiffuser and surficial modifier, respectively; Dolbeth et al., 2013, 2014). Rather than adopt an approach where multiple arrangements of species dominance patterns are examined to establish the generality of any evenness effects per se (as in Wohlgemuth et al., 2016), our experimental design is minimised to include all possible permutations of four different evenness levels (based on biomass) that reflect observed historical responses to disturbance in the Mondego estuary (Dolbeth et al., 2011, 2014): 1) *No macrofauna*, to distinguish the contribution of the micro- and meiofauna from that of the macrofauna; 2) *Eutrophication*, where the proportional representation of species reflects assemblage structure observed during periods of eutrophication ($J = 0.7$; ratio of 73:7:20% for Pu, Hd and Sp, respectively); 3) *Restored*, where the proportional representation of species reflects assemblage structure after a recovery period following restoration measures ($J = 0.9$; ratio of 53:16:31% for Pu, Hd and Sp, respectively); and 4) *Even,* where the biomass of all species are distributed equally ($J = 1$; ratio of 33:33:33% for Pu, Hd and Sp, respectively). Hence, the evenness levels we have used in scenarios 1-3 are indicative of those observed during relevant disturbance events, rather than an attempt to replicate a specific set of generic circumstances (as in 4). This design allows us to separate the effects of changes in evenness from the confounding effects of other physico-chemical parameters on ecosystem functioning. To ensure that any observed treatment effects were not confounded by changes in the distribution of biomass, total biomass was fixed to a constant (3.5 ± 0.2 g wet weight per $0.0144\ \mathrm{m}^{-2}$ aquaria^{-1}) equivalent to the total biomass observed in the field under the *Restored* condition. By fixing total biomass whilst adhering to the proportional representation of species in our treatments, abundance levels of each species varied (Fig. 1a). In general higher body mass of *H. diversicolor and S. plana* was included with increasing evenness levels (Fig. 1b).

We tested the response of our communities across three salinity levels, representative of hydrological changes following different precipitation patterns: a) 35, representing salinity levels that occur mostly in summer, or during drought events (34.8 ± 1.0, Verdelhos et al., 2014); b) 25, the mean salinity observed at the sampling location and typical for the species under study (25.6 ± 7.1, Verdelhos et al., 2014); and c) 5, the salinity achieved in mesohaline areas during high precipitation periods (4.6 ± 3.1, Verdelhos et al., 2014). Water for each salinity level (Ozone-sterilized, 11 μm pre-filtered) was replaced after 24 h to remove the effect of nutrient pulses associated with assembly, ensuring that changes in nutrients could be attributable to species activity during the experimental period. Hence, our design requires a total of 60 aquaria (4 evenness levels x 3 salinity x 5 replicates) that were continually aerated and kept under ambient light conditions. Due to practical constraints, aquaria were randomly allocated to one of two consecutive experimental runs (12 days).

2.2. *Measurement of particle reworking and nutrient concentrations*

The extent of particle reworking was measured non-invasively using fluorescent sediment profile imaging (f-SPI, Solan et al., 2004). This method allows dyed sediment particles that fluoresce under UV light (luminophores: 30 g aquaria^{-1}, 125–250 μm diameter, pink colour; Brian Clegg, Ltd, UK), to be visualised under UV illumination (Schiffers et al., 2011). The distribution of luminophores was determined from one side of the aquaria, taken with a Canon EOS 350D single lens reflex digital CMOS camera (8.0 megapixels; exposure, 10 s; f = 6.3 aperture; and a film equivalent speed - light sensitivity - of ISO 200). Given the mobility of the organisms under study, using a single side was sufficient to provide an indication of overall activity. Images were analysed using a custom-made plugin that runs within ImageJ (Version 1.48c), a java-based public domain program developed at the US National Institutes of Health (available at http://imagej.nih.gov/ij/). We quantified the occurrence and distribution of luminophore pixels from the binary data matrix of bitmapped images (0 = background sediment, 1 = luminophore). Following Hale et al. (2014), we quantified several descriptors of faunal mediated sediment particle reworking that reflect subtly different aspects of invertebrate behaviour: 1) surface boundary roughness (SBR), which describes the distance between the highest and lowest points of elevation along the sediment-water interface, a proxy for surficial activity; 2) mean luminophore depth ($^{f-SPI}L_{mean,}$ cm), the relative balance between minimum and maximum depth, representing a time dependent indication of mixing; 3) median luminophore depth ($^{f-SPI}L_{median,}$ cm), which largely reflects short-term mixing activity; and 4) the maximum depth of mixing ($^{f-SPI}L_{max,}$ cm), which reflects the maximum extent of mixing integrated over the long-term (Hale et al., 2014).

Nutrient concentrations (NH_3–N, NO_3–N, PO_4–P) were determined from water samples at the end of the experiment, day 12 (at least 3 replicates per evenness × salinity level, 10 mL, 0.45 μm filtered) using a Continuous Flow Analyzer Skalar Sanplus with Segmented Flow Analysis (SFA), following Skalar methodology: M461-318 (EPA 353.2), M155-008R (EPA 350.1) and M503-555R (Standard Method 450-P I). Over the duration of the experiment (12 days), salinity, temperature, pH and oxygen levels were monitored in all aquaria every 3 days.

2.3. *Statistical data analyses*

We used independent regression models for each of our dependent variables of particle reworking (SBR, $^{f-SPI}L_{mean,}$ $^{f-SPI}L_{median}$, $^{f-SPI}L_{max}$) and nutrient concentrations (NH_3–N, NO_3–N, PO_4–P) to examine the full factorial effect of our independent variables (evenness and salinity). We treated evenness and salinity as a fixed effect and, where necessary, included experimental run as a random effect. As our data showed evidence of heteroscedasticity in the residuals, analyses were extended to include the appropriate variance-covariate structure (Minimal adequate model summary, Supplementary Material) using a generalised least squares (GLS) estimation procedure (Pinheiro et al., 2017). The GLS allows the residual spread to vary with the explanatory variables and avoids the need to transform data. We used backward selection by Akaike Information Criteria (AIC) and visual comparison of residual patterns to determine the optimal fixed-effects structure. For GLS, the optimal variance-covariate structure was determined using restricted maximum-likelihood (REML) estimation by comparing the initial regression model without a variance-covariate structure to alternative regression models that include specific variance-covariate structures. The optimal fixed structure was then determined using backward selection using the maximum likelihood ratio (L-ratio) test and the minimal adequate model was re-expressed using REML (Zuur et al., 2009). All analyses were performed using the R statistical and programming environment (R Development Core, 2012) and the packages nlme (Pinheiro et al., 2017) and mvtnorm (Genz et al., 2011). All data are provided in the electronic supplementary material, Appendix S1-S2.

3. Results

When introduced to the aquaria, the polychaete *H. diversicolor* and bivalve *S. plana* buried immediately into the sediment, whilst *P. ulvae* remained at the sediment surface at intermediate and high levels of salinity. At low levels of salinity, a few *H. diversicolor* remained at the surface for extended periods of time before burying. Nevertheless, in general, we found that faunal activity and associated levels of nutrient concentrations tended to increase with evenness, but the form and extent of response was most often influenced by an interaction between evenness and salinity.

3.1. *Effects on sediment particle reworking*

We found that surface boundary roughness (SBR) was dependent on an independent effect of evenness, whilst the minimal adequate models for $^{f-SPI}L_{mean,}$ $^{f-SPI}L_{median}$ and $^{f-SPI}L_{max}$ were a linear regression with a generalised least squares (GLS) extension incorporating a two-way interaction between evenness and salinity (Table 1). For $^{f-SPI}L_{mean}$ and $^{f-SPI}L_{max,}$ evenness was the most influential variable ($^{f-SPI}L_{mean,}$ L-ratio = 62.4, d.f. = 9 = $p < 0.001$; $^{f-SPI}L_{max,}$ L-ratio = 115.7, d.f. = 9 = $p < 0.001$) followed by salinity ($^{f-SPI}L_{mean,}$ L-ratio = 20.5, d.f. = 8 = $p < 0.01$; $^{f-SPI}L_{max,}$ L-ratio = 24.5, d.f. = 8 = $p < 0.01$), but the reverse was true for $^{f-SPI}L_{median}$ (evenness, L-ratio = 33.0, d.f. = 9 = $p < 0.001$; salinity, L-ratio = 60.7, d.f. = 8 = $p < 0.01$). The allocation of aquaria to multiple experimental runs had no discernible effect on our observations of particle reworking and was excluded from our statistical analyses (Supporting Information models S1 – S4, raw data Table).

Table 1
Summary of regression models to examine the effects of evenness and salinity on the response variables for bioturbation and nutrients. For each model, we list the main terms, variance-covariate, degrees of freedom (d.f), test statistic (L-ratio) and level of significance (p).

Dependent variable	Main terms	Variance–covariate	d.f.	L-ratio	p
Bioturbation					
SBR	Evenness	Evenness x Salinity	3	26.93792	< 0.001
$^{f-SP}L_{mean}$	Evenness x Salinity	Evenness x Salinity	6	15.96642	0.014
$^{f-SPI}L_{median}$	Evenness x Salinity	Evenness x Salinity	6	13.78341	0.032
$^{f-SPI}L_{max}$	Evenness x Salinity	Evenness x Salinity	6	22.71589	< 0.001
Nutrients					
PO_4–P	Evenness x Salinity	Evenness x Salinity	6	23.82743	< 0.001
NH_3–N	Evenness x Salinity	Evenness x Salinity	6	22.08974	0.001
NO_3–N	Evenness	Salinity	3	13.41387	0.004

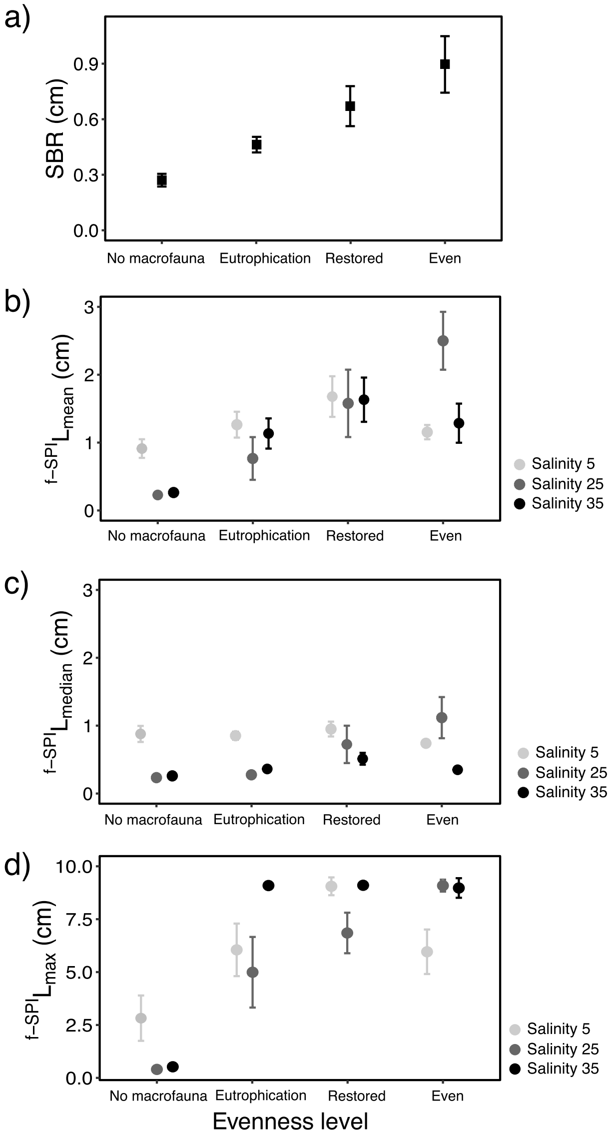

Fig. 2. The independent effect of evenness on (a) sediment surface boundary roughness and the interactive effects of evenness and salinity on (b) mean ($^{f-SPI}L_{mean}$), (c) median ($^{f-SPI}L_{median}$) and (d) maximum ($^{f-SPI}L_{max}$) depth of invertebrate mediated sediment particle mixing. Data are presented as mean ± s.e.

In the broadest terms, all of our descriptors for sediment particle reworking were lowest in the absence of fauna (*No macrofauna* treatment, mean ± s.e.; SBR, 0.27 ± 0.03; $^{f-SPI}L_{mean}$, 0.47 ± 0.094; $^{f-SPI}L_{median}$, 0.46 ± 0.09; and $^{f-SPI}L_{max}$, 1.25 ± 0.45 cm) and increased as the community became more even (through *Eutrophication, Restored* and *Even* treatments). The greatest amount of sediment particle reworking tended to occur under *Restored* and *Even* conditions, but the overall pattern was influenced by changes in salinity (Fig. 2). When salinity was close to typical values of the study site (Salinity 25, 26.3 ± 0.4 after 12 days), all particle reworking response variables showed a linear relationship trend with increasing evenness (Fig. 2). However, when salinity was markedly lower (*Salinity 5*, 10.2 ± 1.3 after 12 days) or higher (*Salinity 35*, 34.6 ± 0.5 after 12 days), the relationship between particle reworking and evenness became less evident (Fig. 2). Yet, highest values were generally observed for the *Restored* and *Even* treatments, which exhibited the deepest level of sediment mixing across all salinity treatments ($^{f-SPI}L_{max}$, mean ± s.e.: *Restored* = 8.33 ± 0.43; *Even* = 8.01 ± 0.53 cm). We experienced some mortality at low salinity (1 individual of *H. diversicolor* in one aquaria and 1 individual of *S. plana* in each of two aquaria), but this was insufficient to explain the difference in particle reworking behaviour as the values were within the range of the those measured for the aquaria without mortality. Overall, the mean (± s.e.) maximum extent of faunal mediated vertical particle reworking ($^{f-SPI}L_{max}$, Fig. 2d) ranged from 4.99 ± 1.67 cm (*Eutrophication* × *Salinity 25*) to 9.10 ± 0.15 cm (*Restored* × *Salinity 35*).

3.2. Effects on water column nutrient concentration (ecosystem functioning)

Our analyses reveal that NO_3–N was dependent on an independent effect of evenness (Table 1, Supplementary material, Model S5), whilst the minimal adequate models for NH_3–N and PO_4–P were a linear regression with a generalised least squares (GLS) extension incorporating a two-way interaction between evenness and salinity and experimental Run as a random effect (Table 1, Supplementary material, Models S6–S7). For NH_3–N and PO_4–P, evenness was the most influential variable (NH_3–N, L-ratio = 30.9, d.f. = 9, $p < 0.001$; PO_4–P, L-ratio = 43.7, d.f. = 9, $p < 0.001$) followed by salinity (NH_3–N, L-ratio = 28.9, d.f. = 8, $p < 0.001$; PO_4–P, L-ratio = 22.9, d.f. = 8, $p < 0.01$).

For NO_3–N, mean (± s.e.) concentrations were lower in the absence of fauna (*No macrofauna*, 0.17 ± 0.04 mg/L) and, with the exception of the *Restored* condition (0.18 ± 0.05 mg/L), increased as the community became more even (*Eutrophication*, 0.29 ± 0.05 mg/L; *Even*, 0.34 ± 0.05 mg/L, Fig. 3a). Closer examination of the coefficients reveals that NO_3–N concentrations (coefficient ± s.e.; electronic supplementary material, Table S2) were no different between *No macrofauna* and the evenness levels typically found during *Restored* conditions (0.049 ± 0.025, t = 1.945, p = 0.061), or between evenness levels typically found during *Eutrophication* and *Even* communities

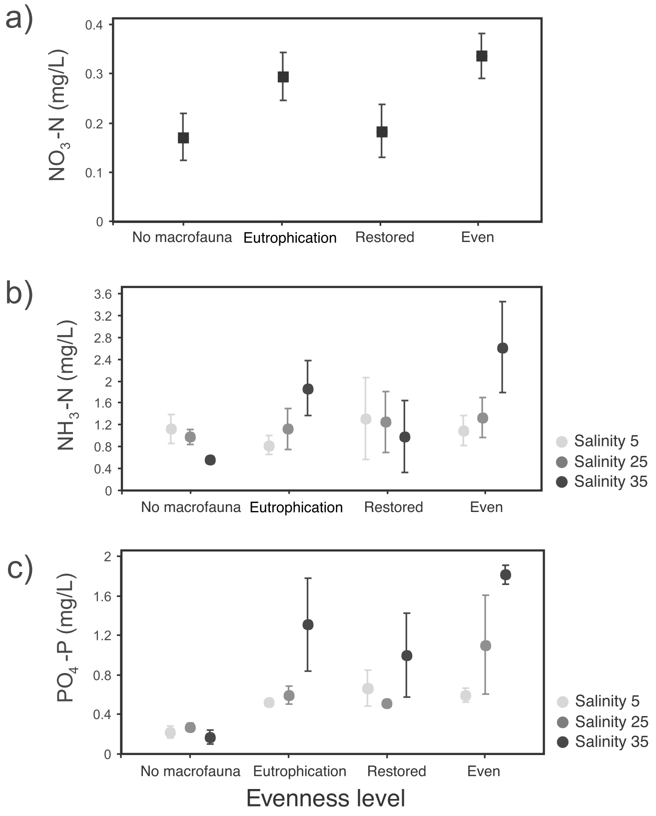

Fig. 3. The independent effect of evenness on the mean (± s.e.) change in nutrient concentrations (mg/L) over the experimental period (12 days) for (a) NH_3–N, and the interactive effects of evenness and salinity on (b) NO_3–N and (c) PO_4–P.

(0.047 ± 0.026, t = 1.791, p = 0.083).

The trend in concentrations observed for NO_3–N was echoed across all salinity levels for NH_3–N (Fig. 3b), with greater mean (± s.e.) concentrations in evenness levels typically realised during *Eutrophication* (with salinity 5, 0.82 ± 0.17; salinity 25, 1.13 ± 0.37; salinity 35, 1.87 ± 0.50 mg/L) and in *Even* communities (with salinity 5, 1.10 ± 0.27; salinity 25, 1.33 ± 0.36; salinity 35, 2.61 ± 0.83 mg/L) and lower concentrations under *No macrofauna* (with salinity 5, 1.12 ± 0.26; salinity 25, 0.97 ± 0.14; salinity 35, 0.55 ± 0.05 mg/L) and *Restored* conditions (with salinity 5, 1.32 ± 0.75; salinity 25, 1.25 ± 0.56; salinity 35, 0.99 ± 0.66 mg/L). Hence, increasing salinity had a negative effect on NH_3–N concentrations under the *No macrofauna* and *Restored* conditions, but a positive effect on NH_3–N concentrations under *Eutrophication* and *Even* conditions (Fig. 3).

A different pattern was observed for PO_4–P concentrations which, in general, were positively affected by increasing salinity and by increasing levels of evenness (Fig. 3c). This was particularly marked at the highest level of salinity as evenness levels increased (compare widening disparity between salinity treatment levels as evenness increases, Fig. 3c). Mean (± s.e.) concentrations of PO_4–P were lowest in the absence of macrofauna (with salinity 5, 0.22 ± 0.06; salinity 25, 0.28 ± 0.03; salinity 35, 0.17 ± 0.07 mg/L), but similar at evenness levels typical of *Eutrophication* (with salinity 5, 0.52 ± 0.03; salinity 25, 0.60 ± 0.09; salinity 35, 1.31 ± 0.47 mg/L), *Restored* conditions (with salinity 5, 0.67 ± 0.18; salinity 25, 0.51 ± 0.03; salinity 35, 1.00 ± 0.42 mg/L) or in *Even* communities (with salinity 5, 0.60 ± 0.07; salinity 25, 1.10 ± 0.50; salinity 35, 1.81 ± 0.09 mg/L).

4. Discussion

There is a great deal of interest and effort in establishing the most likely response of species, communities and ecosystems to environmental forcing, but there is also mounting evidence that the formulation of many predictive models does not recognize and embrace the modifying effects of context on system performance (Wohlgemuth et al., 2017; Crespo et al., 2018; Snelgrove et al., 2018; Thomsen et al., 2019). It is known, for instance, that the way in which species interact with one another and with the environment is altered following a change in circumstance and that these changes can have functional consequences (Godbold and Solan, 2013; Hale et al., 2017; Crespo et al., 2018). In this study, following the ideology of Bracken et al. (2008), we tested a scenario of local diversity loss linked to levers of forcing that have precedent (Dolbeth et al., 2013) in order to understand the functional consequences of realistic biodiversity change (Naeem, 2008). Our findings indicate that the changes in evenness have a directional impact on subtle aspects of bioturbation behaviour that are important in mediating macronutrient cycles. Whilst these changes reflect the rearrangement of species traits and changes in dominance patterns within the post-disturbance community, as has been documented elsewhere empirically (Wohlgemuth et al., 2016) and in the field (Godbold et al., 2017; Hale et al., 2017), it is clear that other changes that occur simultaneously (here, salinity) further modify the species-environment couple and lead to additional indirect changes in functioning (Crespo et al., 2018). This point is not trivial, because the vast majority of biodiversity-ecosystem function experiments (Cardinale et al., 2012) do not incorporate the environmental changes that accompany the circumstances that lead to an alteration to diversity and/or a change in species behaviour (exceptions include Bracken et al., 2008; O'Meara et al., 2017).

Our study was not designed to establish the mechanistic basis of changing species-environment interactions, but the variation in our data suggest that generic explanations (e.g. stimulating microbial activity, Gilbertson et al., 2012, Bonaglia et al., 2014; metabolism, Norkko et al., 2013; biomass, Séguin et al., 2014) are insufficient to explain the subtleties of the observed responses. Whilst species with larger body mass and greater bioturbation potential (e.g. *H. diversicolor*, Queirós et al., 2013) were disproportionately represented in communities with higher evenness, the relative role of changes in biogenic structures (Hale et al., 2014), ventilation behaviour (Ouellette et al., 2004) and other aspects of mediation (gut passage, Dale et al., 2019a; mucus production, Dale et al., 2019b) in relation to specific typologies of disturbance remain largely unresolved or unknown. Hence, our findings lend support to the growing view that species that show plasticity to highly variable environmental conditions, such as *H. diversicolor*, can exhibit significant changes in their functional contribution (Murray et al., 2017). However, it is also important to acknowledge the role of changes in biogeochemical conditions and microbial responses across the salinity gradient (nitrogen: Herbert, 1999, Rysgaard et al., 1999, Yu et al., 2019; phosphate: Huang and Morris, 2005, Jordan et al., 2008), noting that observed levels of nutrient exchange reflect complex interactions between the overlying water, physicochemical environment, sediment type, faunal composition and the relative role of bioturbation (Long et al., 2018). In most cases, the likelihood is that these influences will act in concert, but the net functional effects and responses are unlikely to be additive and may amplify or negate the effect of disturbance through the community (Griffith et al., 2019).

A consistent feature of our analyses is the influential role of evenness across all of our response variables, irrespective of contextual changes in the remainder of the system (Godbold and Solan, 2013). However, for our model estuarine sub-systems, this strong effect of evenness was modified by salinity changes that reflect hydrological changes that might occur during flood and drought conditions or hydrological management and which, in turn, have the potential to alter the extent and distribution of suitable habitat for species (Olsen, 2019). This finding presents the possibility that non-linear effects are more likely in the presence of multiple stressors (Paerl et al., 2006; Ellis et al., 2017) and suggests that uncertainty around projections will remain high because species may change their behaviour and expression of traits alongside environmental change (Verberk et al., 2013; Murray et al., 2014; Godbold and Solan, 2013). These changes in species contributions can be abrupt. As our study demonstrates, the decline in salinity routinely experienced during flood events is sufficient to reduce sediment particle reworking in communities with the highest potential for bioturbation, to values that lie within the same range of those observed for communities that lack significant bioturbators and experience eutrophication. All of the species in our study have physiological mechanisms capable of tolerating diurnal variations in salinity (Mouneyrac et al., 2010), yet, when continually exposed to low salinity, a different pattern of behaviour, which has functional connotations, is expressed. Indeed, a general decrease in activity associated with low levels of salinity has been observed for *S. plana*, possibly as a mean to minimise osmotic stress (Verdelhos et al., 2015). Similarly, when salinity increases, which may occur during drought periods or when freshwater runoff decreases as a result of hydrological management (e.g. Dolbeth et al., 2011), sediment particle reworking activities also decline, except for the maximum depth of burrowing, as observed in our study. Burrowing deeper is a known stress response (e.g. Maire et al., 2010) and a mean to avoid osmotic stress from a higher salinity (Hauton, 2016), and it is tempting to attribute any change in bioturbation to the primary drivers of change. However, a reduction in bioturbation may also reflect the introduction (or change in relative importance) of other variables that constrain the capacity of the system to respond (Tomašovych et al., 2018).

5. Conclusion

Our study confirms that changes in community structure concurrent with environmental forcing can have substantive consequences for ecosystem functioning, but demonstrates that the magnitude and direction of change is highly influenced by context. Patterns of response can vary across a range of forcing intensities, to the inclusion of abrupt changes in trait expression and species behaviour, especially at the fringes of typically encountered conditions. Overall, our findings highlight the fluid nature of species contributions to functioning and reinforce the importance of simultaneously understanding, and accounting for, the direct and indirect influence of multiple abiotic and biotic attributes that contribute to the circumstances that lead to altered biodiversity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2019.104770.

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