

Non-linear effects of macrofauna functional trait interactions on biogeochemical fluxes in marine sediments change with environmental stress

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ABSTRACT: Biogeochemical fluxes in marine sediments are profoundly influenced by species that bioturbate and bioirrigate the sediments. However, functional traits associated with these activities encompass a wide range of behaviours that have different consequences for the movement of particles and solutes. Interactions between infaunal species of different functional groups and benthic biogeochemical fluxes may be context-specific, requiring multiple studies; yet, to date these experiments are rare. In a laboratory experiment, we incubated specimens of *Macomona liliana*, a facultative deposit-feeding bivalve, and *Macroclymenella stewartensis*, a head-down conveyor-belt feeding polychaete, both separately and together, and measured fluxes of nutrients and oxygen. Both species are common in New Zealand estuaries and often coexist. The addition of thin surface layers of mud generated 3 treatment levels (0, 3 and 6 mm thickness). The presence of *M. liliana* and *M. stewartensis* enhanced benthic fluxes compared to control treatments. Oxygen uptake and nitrogen cycling stimulation due to their interaction were modelled, based on the results of single-species treatments, and then compared to results of multiple-species treatments with no animals. The effect of the interaction of the 2 organisms proved to be stronger than the additive effect of each species. This study demonstrated the central role of functional trait interactions for ecosystem functioning and its non-linear nature, highlighting the importance of testing actual effects against prediction based on trait analysis and the incorporation of these community effects in future research and models of ecosystem function and service delivery across marine habitats.

KEY WORDS: Benthic fluxes · Bioturbation · Biogeochemistry · Ecosystem function · Functional trait · Nitrogen cycle

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1. INTRODUCTION

Soft sediments cover 70 % of the ocean seafloor and dominate estuarine and coastal habitats, where infaunal organisms profoundly influence biogeochemical processes and ecosystem functioning (Snelgrove 1997, Thrush et al. 2004). These habitats support primary production in coastal seas, and through remineralization can contribute between one-third and half of the nutrients required for primary producers

in the water column (Mortazavi et al. 2012). However, the human-induced decline in biodiversity and resulting loss of benthic bioturbators threatens the ecosystem services these habitats provide. Thus, it is critical to understand the role of these species in ecosystem functioning and the mechanisms through which they affect processes. This information is also fundamental to create more realistic mathematical models of biogeochemical processes. These models are often based on general assumptions and lack a

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real understanding and explanation of the role of the underlying biodiversity, leading to potentially biased results and misleading conclusions (Snelgrove et al. 2018).

The role of macrobenthic organisms' functional traits in marine ecosystem functioning has been addressed in previous studies (Mermillod-Blondin et al. 2004, Volkenborn et al. 2012, Dornhoffer et al. 2015, Woodin et al. 2016). Different bioturbation and bio-irrigation modes have been shown to affect ecosystem functions such as carbon mineralization (e.g. Banta et al. 1999) and nutrient cycling differently (Pelegrí & Blackburn 1995, Mermillod-Blondin et al. 2004). Michaud et al. (2005) demonstrated how different species representing 2 functional groups in a *Macoma balthica* community have different effects on the oxygen (O_2) uptake at the sediment–water interface and concluded that future studies should also account for the interactions among these species to fully understand their importance for ecosystem functioning. Despite the importance of the link between functional biodiversity and ecosystem processes, there are few specific and empirical studies. Previous studies have indicated that the effects of functional biodiversity on ecosystem processes are not additive and suggested that functional biodiversity and species-specific traits, rather than species richness per se, can be important in explaining ecosystem processes (Mermillod-Blondin et al. 2005, Ieno et al. 2006, Norling et al. 2007, Godbold et al. 2009, Harvey et al. 2013).

The combination of real-time pore-water pressure recording and O_2 imaging has improved our mechanistic knowledge of the behaviour-related hydraulic activity of a number of worms and bivalves (Volkenborn et al. 2010, 2012). The use of this technique has demonstrated the relationship between both positive and negative pressurizations, mostly due to feeding, excretion and burrowing, and the O_2 dynamics in the sediment. However, the link between the functional traits of macrofauna, their behaviours and the biophysical interaction of different species is often overlooked when predicting changes

in ecosystem functioning. Direct measurements of ecosystem functions in the presence of different species are especially important where synergistic effects are possible. This may explain the variability observed in field-measured ecosystem processes driven by bioturbation (Woodin et al. 2016) and help untangle the complex relationships between biodiversity and ecosystem functioning.

The aim of this study was to assess how the interaction between different functional traits affects nutrient cycling and ecosystem functioning. We hypothesized that when different functional groups coexist, the results may not be linear due to non-additive effects. Therefore, we chose 2 deposit feeders with very different traits (Fig. 1) that co-occur and are abundant in New Zealand intertidal sandflats: the bivalve *Macomona liliana*, a facultative deposit feeder and bio-irrigator, and the polychaete *Macroclyme-*

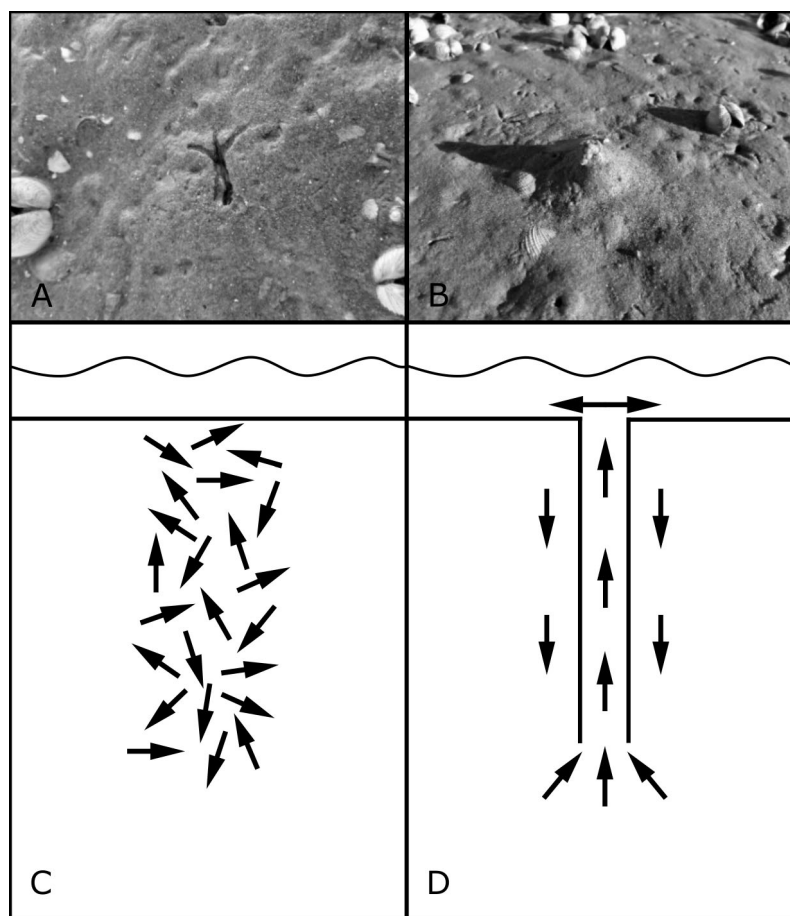


Fig. 1. Functional groups of the target species. (A) *Macomona liliana* feeds on the surface through a long inhalant siphon leaving bird-like feeding traces and (C) behaves as a biodiffuser. (B) *Macroclymenella stewartensis* creates volcano-like fecal mounds on the sediment surface and (D) behaves as an upward conveyor (modified from Kristensen et al. 2012)

nella stewartensis, a head-down conveyor-belt feeder. To assess how their interaction enhances biogeochemical processes, we measured nutrient and dissolved gas fluxes. In particular, due to the different mechanisms of bioturbation and bioirrigation exhibited by the 2 organisms, our hypothesis was that the interaction would be synergistic and would enhance benthic fluxes. Moreover, we investigated how the effect of surface mud deposition, one of the most common and important stressors in New Zealand estuaries (Thrush et al. 2004), alters this relationship. Recent studies have demonstrated that thick (>1 cm) deposits can reduce macrofauna-mediated ecosystem functioning (Cummings et al. 2003, Mestdagh et al. 2018) and impact the recovery of the macrobenthos, often leading to completely defaunated sediment and habitat change (Norkko et al. 2002, Hewitt et al. 2003, Thrush et al. 2003). Although often non-lethal, thinner (<1 cm) deposits also negatively affect macrobenthic community structure and modify the behaviour and functional role of benthic organisms (Lohrer et al. 2004, Cummings et al. 2009, Needham et al. 2010, Woodin et al. 2012, McCartain et al. 2017). The deposition of thin clay layers on the sediment surface can also impact the diffusion of nutrients and solutes across the sediment–water interface (Berkenbusch et al. 2002, Cummings et al. 2009); furthermore, it occurs with greater frequency and over greater spatial scales than the deposition of thicker layers (Foster & Carter 1997, Wheatcroft 2000). Hence, we determined whether the presence of a mud layer can alter the interaction between different species and its effect on benthic fluxes.

2. MATERIALS AND METHODS

2.1. Study species

Macomona liliana (tellinid bivalve) is a deposit feeder common in New Zealand intertidal sandflats, where adults live within the sediment to depths of 10 cm (Hewitt et al. 1996). Adult *M. liliana* alter the sediment and its biogeochemical properties, playing an important role in community dynamics and benthic fluxes (Thrush et al. 1992, Woodin et al. 2012). This species feeds through a long inhalant siphon to ingest surface deposits and excretes through an exhalant siphon at depth in the sediment (Pridmore et al. 1991).

The polychaete *Macroclomenella stewartensis* (mal-danid) is a conveyor-belt feeder that feeds head-

down at depth in the sediment and defecates at the sediment surface. It also irrigates its burrow, pumping in oxygenated water for respiratory purposes. This species is commonly found in New Zealand sandflats, both in subtidal (Thrush et al. 1995, Wong & O'Shea 2010) and intertidal (Thrush et al. 1989, Pridmore et al. 1990, Turner et al. 1995) habitats and naturally co-occurs with *M. liliana* (authors' pers. obs.).

2.2. Specimen collection and preparation

Sediment and target species were collected at low tide in the Whangateau Harbour (36° 18' 40" S, 174° 46' 42" E), on the north-east coast of New Zealand, between April and May 2017. The sediment at the collection site consists mainly of fine sand (median grain size: 211 µm; fine sand fraction: 50.6%; mud fraction: 3.9%) with an average organic content (% loss on ignition) of 0.71%. Both *M. liliana* and *M. stewartensis* are present and dominate the macrofaunal community. Specimens of both species were hand collected. The sediment was collected on 30 March 2017 and sieved through a 500 µm mesh to remove macrofauna. Sediments were homogenized prior to addition to experimental aquaria. Cylindrical buckets (25 cm diameter, 27 cm deep) were filled to a depth of 13 cm with sieved sediments and left for 4 wk with flow-through seawater to allow for equilibration. Prior to the 4 wk equilibration, the mud layer settled on top of the sediment was removed by feeding the aquaria with a seawater flow higher than the resuspension rate of mud and lower than that of underlying sandy sediment and allowing the mud to overflow for 24 h. This created uniform sediment conditions to which we could add our mud addition treatments (see next sub-section).

2.3. Experimental design

We used 4 species treatments: (1) *M. liliana* only; (2) *M. stewartensis* only; (3) a combination of the same density of the two and (4) a control without macrofauna. These animal treatments were crossed with 3 mud layer treatments (surface thickness levels: 0, 3 and 6 mm). The average animal length and wet weight were, respectively, 40 mm and 2.3 g for *M. liliana* and 103 mm and 0.2 g for *M. stewartensis*. Species density in the microcosms for both *M. liliana* and *M. stewartensis* was 101.9 ind. m⁻², which reflects the natural density of the 2 species observed

in the ecological monitoring of other intertidal sand-flats (Hailes & Hewitt 2012) and is consistent with density ranges found in previous studies of New Zealand estuaries (e.g. Thrush et al. 1989, Pridmore et al. 1990, Turner et al. 1995). The same density of each species was used in the combined treatment. To create the 3 mud level treatments, 3 and 6 mm mud layers were added to all medium and high mud treatments by adding, respectively, 150 and 300 ml of mud. The chosen thicknesses mimicked field conditions following depositional events, known to alter macrobenthic community structure (Lohrer et al. 2004). Mud ($<63\ \mu\text{m}$) was obtained by sieving sediment collected at Whangateau Harbour. For the duration of the experiment, microcosms were maintained under the same laboratory conditions (water temperature: 19°C ; salinity: 36). Organisms were left for 24 h in the experimental microcosms for acclimation before the first set of measurements was performed. Individuals that did not burrow within 30 min were replaced with new individuals. During 3 consecutive days, we randomly incubated 2 microcosms of each treatment per day ($n = 6$); all incubations lasted for 4 h in the dark. At the end of the experiment we recorded the wet weight (without shells) of the organisms in each microcosm.

2.4. Benthic flux measurements

O_2 , N_2 , dissolved inorganic nitrogen (DIN; $\text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$) and dissolved inorganic phosphorus (DIP; PO_4^{3-}) fluxes were measured using dark, dome-shaped plastic incubation chambers (17 cm diameter) placed on the sediment surface. All chambers had Luer stopcock ports for sample collection, and pressure was equilibrated using a vent port open to the surrounding reservoir. Water samples were collected at the beginning of each incubation and after 4 h, following the procedure described by O'Meara et al. (2017). O_2 and N_2 concentrations were determined by membrane-inlet mass spectrometry (MIMS) with a Pfeiffer Vacuum QMS 200 quadrupole mass spectrometer (Kana et al. 1994). Consumption and production rates were calculated from the concentration difference between initial and final samples. DIN and DIP concentrations were determined by flow injection analysis (FIA) with a Lachat Quick-Chem 8000 automated ion analyser (Thrush et al. 2017). The difference between the concentrations in the final and initial samples was used to calculate net DIN and DIP fluxes.

2.5. Data analysis

Preliminary analysis of the data was performed using 2-way ANOVA to investigate the effects of each species and sediment layer and their interaction on measured fluxes. Post hoc pairwise comparisons to identify the source of any significant differences were performed using Sidak's tests.

The effect of the interaction between the 2 species was then modelled based on the results of single-species treatments (hereafter called 'modelled'). To do so, for each sediment composition level (0, 3 and 6 mm surficial mud layer) the per gram (wet weight of animal tissue) rates of O_2 , N_2 and DIN change were calculated for the single-species treatments and then summed to match the biomass composition of the multiple-species treatment. A simple additive effect was assumed to represent the modelled interaction with no synergistic or antagonistic effect, which was then compared to the actual results of multiple-species treatments (hereafter called 'real'). Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences between the modelled interaction and the real interaction (source factor, 2 levels), the effect of increasing mud levels (treatment factor, 3 levels) and the interaction between the 2 factors. A post hoc test was then conducted using pairwise permutation MANOVAs to test the effect of the mud layer treatments within modelled and real. All analyses were conducted in R v.3.4.1 (R Core Team 2013). Semi-parametric tests were calculated using the R packages 'vegan' (Oksanen et al. 2013) and 'RVAideMemoire' (Hervé 2019). Results were considered significant at $p \leq 0.05$; however, in a few cases we obtained p -values between 0.05 and 0.08.

3. RESULTS

NO_2^- , NO_3^- and PO_4^{3-} levels were close to the detection limit of the instruments and therefore considered to be negligible. For the statistical analysis of DIN fluxes, only NH_4^+ was taken into account. Preliminary analysis indicated that the presence of macrofauna stimulated benthic fluxes compared to control treatments (Fig. 2 and the Supplement at www.int-res.com/articles/suppl/m624p013_supp.pdf). The presence of a thick mud layer also had a positive effect on fluxes in single-species treatments. NH_4^+ efflux and sediment O_2 uptake were higher with a 6 mm mud layer than with 0 and 3 mm layers. NH_4^+ efflux, however, decreased with the increasing mud layer thickness in the multi-species combination.

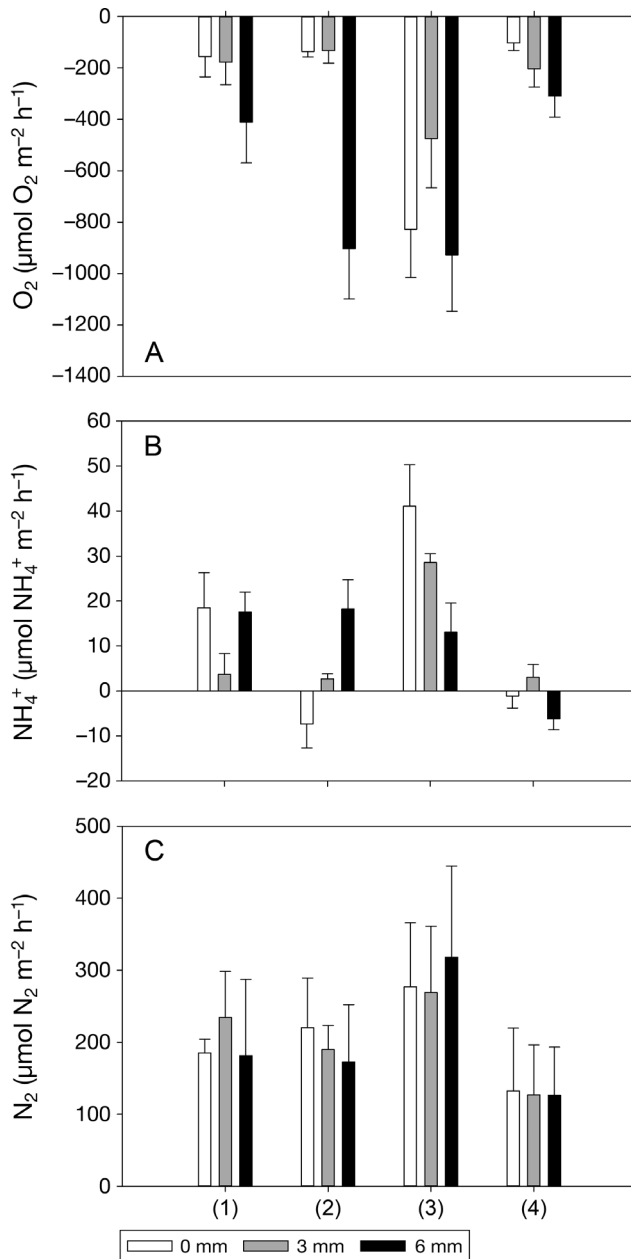


Fig. 2. Measured rates of benthic processes expressed as mean (\pm SD) changes in the concentrations of (A) oxygen, (B) ammonium and (C) nitrogen. Numbers on the x-axis correspond to: (1) *Macomona liliana*; (2) *Macroclymenella stewartensis*; (3) combination of both *M. liliana* and *M. stewartensis*; (4) control

Denitrification rates were consistent between treatments. Furthermore, when the rates were normalized for biomass, the effect of *Macroclymenella stewartensis* on fluxes was always found to be stronger than that of *Macomona liliana* (Table 1).

Comparison between the modelled and real interaction (source factor) showed differences with sedi-

ment composition (Fig. 3, Table 2). The analysis of variance indicated a significant treatment ($p = 0.001$) and source \times treatment ($p = 0.001$) effect on sediment O_2 uptake. Pairwise multiple comparison analyses showed that the difference between modelled and real was only significant in the 0 mm treatment ($p = 0.037$). Source and source \times treatment had a significant effect on NH_4^+ efflux ($p = 0.003$ and $p = 0.001$ respectively). However, both measured O_2 and NH_4^+ fluxes changed from being higher (in the 0 and 3 mm mud treatments) to being lower (in the 6 mm treatment) than those predicted. Real denitrification rates instead were lower than modelled rates, and the difference was statistically significant ($p = 0.07$).

Within the modelled interaction, O_2 uptake and NH_4^+ efflux were significantly higher in 6 mm compared to both 0 and 3 mm but no significant differences were observed for denitrification rates. Within the real interaction, however, NH_4^+ efflux followed an opposite path, with rates in the 6 mm treatment significantly lower than those in both 0 and 3 mm. Sediment O_2 uptake and denitrification rates, on the contrary, were not different between treatments.

4. DISCUSSION

Through the manipulation of sediment and macrofauna composition in a controlled laboratory setup, it is possible to detect the effects of single species on benthic fluxes (e.g. Bertics et al. 2010, 2012, Volkenborn et al. 2007). The present study, however, differed from previous studies in the literature as it directly addressed the interaction between species with different functional traits on biogeochemical fluxes. Although microcosm experiments are a simplified representation of natural conditions and are carried out in a highly controlled setup, they provide a mechanistic understanding of ecosystem functioning, thus being a pivotal tool to untangle the relationship between ecological processes and the underlying biodiversity.

Our study confirmed the well-documented stimulation of sediment biogeochemical processes caused by burrowing infauna. Mermillod-Blondin et al. (2004) compared the influences of bioturbation activities by 3 dominant species of shallow-water habitats on sediment processes and found amphipods and polychaetes had a stronger effect than bivalves, due to the creation of irrigated biogenic structures. Another study (Braeckman et al. 2010), comparing the role of 2 polychaete and 1 bivalve species in biogeochemical fluxes, showed similar results, suggesting that the mal-

Table 1. Mean (\pm SD) measured fluxes of O_2 , NH_4^+ and N_2 in the single-species incubations normalized to faunal biomass (g wet weight, excluding shell material) for the 3 different mud level treatments

Treatment	O_2 (μmol $O_2 \text{ g}^{-1} \text{ h}^{-1}$)	NH_4^+ (μmol $NH_4^+ \text{ g}^{-1} \text{ h}^{-1}$)	N_2 (μmol $N_2 \text{ g}^{-1} \text{ h}^{-1}$)
0 mm			
<i>Macomona liliana</i>	-12.8 ± 6.5	1.5 ± 0.6	15.2 ± 1.6
<i>Macrocliyomenella stewartensis</i>	-123.5 ± 18.4	-6.6 ± 4.8	200 ± 62.4
3 mm			
<i>M. liliana</i>	-15 ± 7.3	0.3 ± 0.4	19.7 ± 5.4
<i>M. stewartensis</i>	-125.2 ± 46.4	2.5 ± 1.1	179.2 ± 31.6
6 mm			
<i>M. liliana</i>	-35.5 ± 13.7	1.51 ± 0.4	15.7 ± 9.2
<i>M. stewartensis</i>	-870.4 ± 189.5	17.6 ± 6.3	166.4 ± 77

danid polychaetes stimulated benthic respiration, nutrient release and denitrification more than bivalves. In agreement with these findings, our study indicated that the per gram effects of *Macrocliyomenella stewartensis* on sediment O_2 uptake, denitrification and NH_4^+ efflux were always greater than those of *Macomona liliana*. This difference can be explained by the different behaviours of the 2 organisms. *M. stewartensis* is a tube builder and periodically flushes its burrow with overlaying water. Because of this characteristic, according to Levin et al. (1997) maldanid worms also have the capacity to redistribute labile organic matter deep within the sediment column. The biodiffuser *M. liliana* instead creates oxygenated pockets at depths of around 10 cm in the sediment, bringing oxygenated fluids into contact with suboxic or anoxic sediment and pressurizing the surrounding porewater (Volkenborn et al. 2012). Moreover, based on previous literature (Meyhöfer 1985, Volkenborn et al. 2010) and the direct observation of the surface features created by the 2 species in our experimental aquaria, *M. stewartensis* is likely to exhibit higher activity rates than *M. liliana*. Observed benthic respiration and denitrification rates are within the range of those observed in other New Zealand estuaries (e.g. Gongol & Savage 2016) although, to the best of our knowledge, no other studies have directly measured the specific effect of the polychaete *M. stewartensis* on sediment biogeochemistry. However, literature on nereid polychaetes (e.g. Pelegrí & Blackburn 1995) reported denitrification rates similar to those of *M. stewartensis* in our study.

The analysis of the interaction between our 2 species produced context-dependent outcomes. The PERMANOVA indicated differences between the

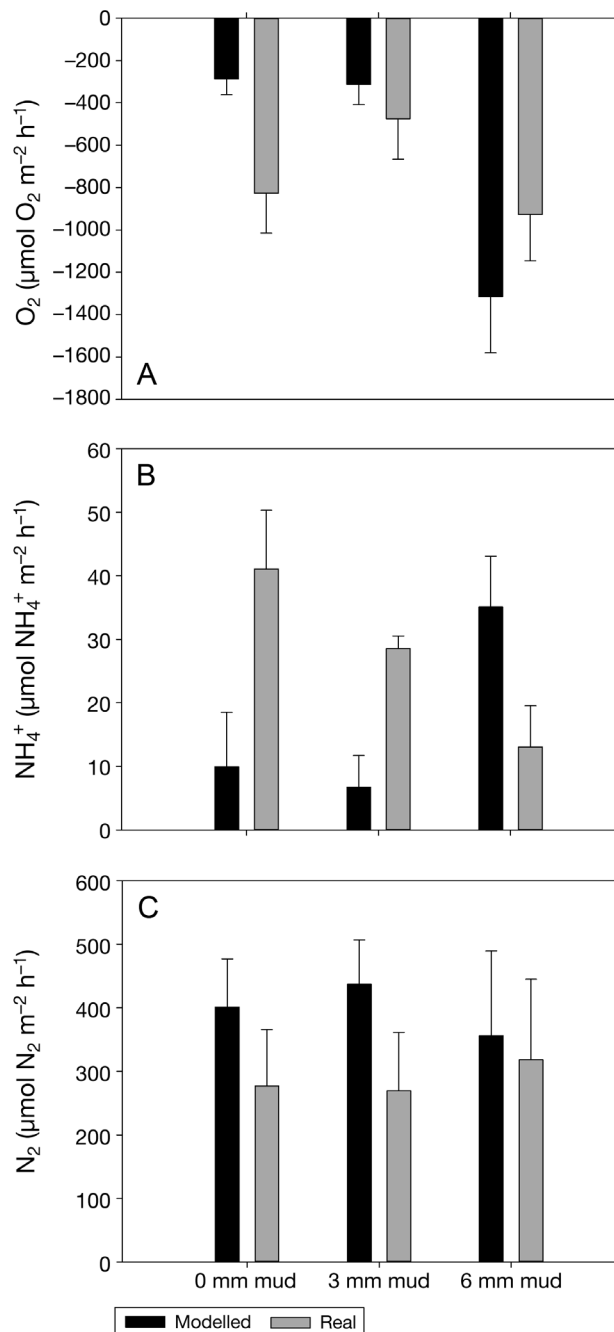


Fig. 3. Mean (\pm SD) rates of change in the concentrations of (A) oxygen, (B) ammonium and (C) nitrogen. Black bars: results from the calculated interaction; grey bars: real interaction. The x-axis refers to the thickness of the added mud layer in the treatment

modelled (additive) and real interaction for all of the measured variables. Excluding denitrification rates, which seemed to be unaffected by the different mud layers, the 2 sets of data also showed different responses to the increasing mud contents. Modelled rates, predicted from the single-species results, in-

Table 2. Results of the PERMANOVA showing the differences between ‘modelled’ and ‘real’ interactions. Significant results ($p \leq 0.05$) are indicated in **bold**

Factor	df	SS	MS	F model	R ²	p-value
O₂						
Source	1	590	589.5	2.406	0.01605	0.138
Treatment	2	20953	10476.3	42.750	0.57030	0.001
Source × treatment	2	7845	3922.7	16.007	0.21654	0.001
Residuals	30	7352	245.1		0.20011	
Total	35	36739			1	
NH₄⁺						
Source	1	1856.6	1865.6	16.278	0.11942	0.003
Treatment	2	823.3	411.7	3.609	0.05295	0.047
Source × treatment	2	9445.7	4722.8	41.407	0.60754	0.001
Residuals	30	3421.8	114.1		0.22009	
Total	35	15547.4			1	
N₂						
Source	1	651.45	651.45	8.9466	0.21685	0.007
Treatment	2	11.04	5.52	0.0758	0.00368	0.933
Source × treatment	2	157.2	78.60	1.0794	0.05233	0.355
Residuals	30	2184.47	72.82		0.72715	
Total	35	3004.15			1	

creased greatly in the 6 mm treatment compared to the 0 and 3 mm treatments. The higher input of organic matter due to the higher mud concentration can, in fact, be responsible for the increased O₂ consumption and NH₄⁺ efflux rates observed in the modelled interaction (Williams et al. 1985, Provoost et al. 2013); however, this increase was not present in the real interaction. As a result of the interaction, real NH₄⁺ efflux decreased with increasing mud content and sediment O₂ uptake did not change. These results support our hypothesis, demonstrating that the nature of the interaction between different functional traits is not additive and thus cannot be predicted from the sum of the components. In agreement with our predictions, this interaction was found to be synergistic, with the exception of denitrification rates, which showed antagonistic effects. This is in contrast to previous studies on the effects of functional biodiversity on ecosystem processes, which reported lower fluxes of both benthic O₂ and nutrients for multiple-species than for additive single-species treatments (Waldbusser et al. 2004, Mermillod-Blondin et al. 2005, Ieno et al. 2006, Norling et al. 2007). Our study, however, not only focused on the interaction between very functionally different organisms, but also demonstrated how the presence of a stressor (the deposition of a mud layer on the sediment surface) can change the nature of the interaction to such an extent as to shift it from synergistic to antagonistic. In addition, our results indicate that the deposition of a mud layer has different effects on processes that occur at different depths in the sed-

iment. While eliciting a strong effect on O₂ uptake in single-species treatments, it had no detectable effect on the multiple-species treatment, leading to the conclusion that the interaction provides some resilience to this stressor. Denitrification rates in both single- and multiple-species treatments, however, were not affected, suggesting that denitrification may not have been carbon-limited during our experiment and that the organic carbon was more rapidly utilized in aerobic processes. Furthermore, we demonstrated that simple additive models of functional trait effects on nitrogen cycling could largely underestimate the processes involved, such as denitrification and remineralization, by not including interactions in the models.

This study was limited to 2 species and constant densities in a highly controlled environment, and it is therefore necessary to use caution when extrapolating the results to explain real-world ecosystem functioning. The nature and the degree of the interactions could be affected both by abiotic factors, such as water flow and sediment grain size and porosity (Biles et al. 2003), and biotic factors, such as the functional traits involved and patchiness of the organisms (McIntosh 1991). Plasticity in the behaviours of the animals (i.e. switching feeding modes) may also have played an important role. In fact, similar to other tellinid bivalves, *M. liliana* may have the potential to suspension feed under some circumstances. However, this behaviour has not been observed in previous studies—and was not observed in the context of the experiment—and feeding traces on the sediment–water interface highlight the importance of surface deposit feeding. To understand the importance of the interactions between different functional traits at large scales, it is of critical importance to further investigate the role of species density. By controlling the distance between the organisms and therefore the probability and extent of their interaction, species density is likely to control the strength of the effect of the interaction on ecosystem functioning. However, our results provide mechanistic insight into the nature of ecological processes. This information is critical to mathematical models, which often underestimate the role and importance of biodiversity, and to the formulation of new theories and studies that address ecosystem functioning. This may be particu-

larly important for ecological boundaries and habitat transition areas, the contributions of which to overall functioning are still unclear and poorly studied (Cadenasso 2003). Lohrer et al. (2013) demonstrated that habitat transitions influence facilitation in a marine soft-sediment ecosystem and suggested that these areas should be included in future studies rather than avoided. Our findings agree with this concept and support the importance of ecological boundaries and the interaction between functional traits for ecosystem functioning. Moreover, they suggest that the loss of functional diversity can have significant consequences for ecosystem function.

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