



Species that share traits do not necessarily form distinct and universally applicable functional effect groups

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ABSTRACT: Recent studies considering the contribution of biodiversity to ecosystem functioning have emphasised the functional importance of individual species and, in so doing, have rekindled the use of categorical descriptors that group species according to their relative contribution to ecosystem processes or functioning. Such functional effect groupings, however, tend to be based on specific traits or contributory roles that are assumed to adequately characterise the functional importance of a species, rather than being based on direct measures of ecosystem processes and functions. This decoupling of organism–environment interaction is difficult to reconcile and, when applied widely, distorts understanding of the mediating role that species play in natural ecosystems. In this study, we begin to address this problem by characterising the functional contributions of 7 benthic invertebrate species for 2 ecosystem processes (particle reworking and bioirrigation) linked to 4 ecosystem functions (changing concentrations of NH₄-N, NO_x-N, PO₄-P and SiO₂-Si) and use these data to derive functional effect groupings. We show that whilst it is possible to categorise species according to how they influence ecosystem properties, the membership and number of functional effect groups depends on which ecosystem property is considered. Furthermore, we demonstrate that categorisations based on functional effects are not synonymous with species taxonomy and that they cannot be applied generically even when considering closely linked biogeochemical processes. Collectively, our findings call for a rethink of how functional effect groups are defined and emphasise the need to interrogate presumed links between species and ecosystem properties across a range of biodiversity–environment contexts.

KEY WORDS: Functional groups · Functional traits · Ecosystem function · Functional diversity · Bioturbation · Bioirrigation

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INTRODUCTION

A wealth of experiments examining the relationship between biodiversity and ecosystem functioning provide strong evidence that a change in biodiversity leads to concomitant changes in ecosystem functioning (Cardinale et al. 2012), and it is clear that the extent to which ecosystem properties change reflects the functional effect traits of the modified community

(Solan et al. 2004a). Classifying species by how they affect ecosystem properties has a long and well-established history (for reviews, see Wilson 1999, Pearson 2001, Hooper et al. 2002) and is fundamental to projecting the ecological consequences of uncertain environmental futures (Solan et al. 2004a, Bunker et al. 2005, McIntyre et al. 2007). Consequently, a number of approaches have been developed that allow species to be assigned to discrete

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functional groups (e.g. microbial: McGrady-Steed et al. 1997, Naeem & Li 1997; plant: Lavorel et al. 1997, Fry et al. 2014; soil: Brussaard 1998; and invertebrates: Pearson 2001), mostly based upon determining relative differences in the distribution of particular sets of traits within an assemblage of co-occurring species. A difficulty, however, is that the relevance of functional effect groups to specific ecosystem functions, such as nutrient cycling, decomposition or primary productivity, is not always known and may be assumed or inferred rather than objectively validated or explored empirically (Padilla & Allen 2000, Srivastava & Vellend 2005, Petchey & Gaston 2006, Teal et al. 2010). As such, the presupposed mechanistic link between species and ecosystem properties during trait selection are often weak or invalid (Luck et al. 2012). This unsatisfactory position is often overlooked, in spite of the widely accepted view that statements about the role of biodiversity need to be underpinned by a firm understanding of unambiguous functional parameters, especially when supporting evidence-based policy-making (Svancara et al. 2005, Hodapp et al. 2014).

A key problem in the application of functional effect groupings is that whilst broadly defined descriptors correlate well for many bulk ecosystem properties and so gain acceptance, when the same groupings are subsequently applied to more specific ecosystem processes or functions, these correlations weaken and become less compelling. This is because broad functional classifications overlook the intricacies of how (Godbold et al. 2009, Gilbertson et al. 2012), when (Solan & Kennedy 2002, Maire et al. 2010) and to what extent species affect multiple ecosystem properties. Such classifications remain appealing because they can be applied across dissimilar sets of species, often belonging to multiple trophic levels and systems, which is important when distantly related taxa provide similar contributions to an ecosystem, such as insects, nematodes and fungi contributing to decomposition (Blondel 2003), or diatoms, macrophytes and macro-invertebrates promoting sediment stability (Widdows & Brinsley 2002). However, where a diverse range of organisms have similar functional effects, or compete for a limited number of resources, establishing appropriate functional effect traits becomes more difficult because separation of species roles requires a finer level of detail. This is further complicated by the fact that closely related species can share physiological traits but are not necessarily functional equivalents (e.g. invertebrates: *Amphiura* spp., Nilsson 1999, *Marenzelleria* spp., Renz & Forster 2013; fish: *Enneacanthus*

spp., Resetarits & Chalcraft 2007), and distinguishing functional contributions under these circumstances necessitates meticulous investigation (e.g. nutritional niches, Godbold et al. 2009), which can be technically challenging and may result in classifications that are too specific to be applied more widely (Teal et al. 2013). Consequently, there are many types of functional groups, some based on single traits and some based on multiple traits, which will have different attributes with respect to how well they reflect specific functions. Getting this balance right is not trivial, has important interpretative connotations, and becomes increasingly important in species-rich ecosystems where the levels of functional redundancy and species interaction are elevated (Grman et al. 2010, Picard et al. 2012). Moreover, differences in the resolution at which functional groups are set may provide an alternate explanation for apparently contradictory assessments of the functional role of individual species (Petchey & Gaston, 2006). This problem is compounded when several functional traits are combined into multi-metrics or when variations in species performance are associated with changes in context (e.g. Spehn et al. 2002, Dyson et al. 2007, Nogaro et al. 2008, Bulling et al. 2010). Such difficulties are not insurmountable (e.g. fuzzy coding in biological trait analysis; Bremner et al. 2003) but are seldom acknowledged, and in practice, the influence of distinct categories of functional traits tends to be treated as equivalents (e.g. Törnroos & Bonsdorff 2012).

The challenges of assigning appropriate functional effect groups are particularly pertinent in studies of soft sediment benthic ecosystems. For these communities, the allocation of species to functional effect groups has, historically, relied on a limited set of species characteristics, such as body size (McIntyre 1978, Basset et al. 2004), location within a habitat (Rhoads & Young 1970), trophic level (Hunt 1925, Naeem et al. 1994), differences in bioturbation behaviour (François et al. 1997), or individual physiological and life history traits, including feeding guild (Yonge 1928, Auster & Link 2009) and morphotype (Rocha et al. 2011). Combinations of these with a wider range of traits, including feeding mode, locomotion and reproduction (e.g. Fauchald & Jumars 1979, Bremner et al. 2003, Swift 1993), form more comprehensive functional designations. These are touted as providing greater explanatory power, but they often lack methodological justification and are based on an assumed or incomplete understanding of the underlying mechanistic processes. Whilst the limitations of some functional

effect groups have been outlined and acknowledged (e.g. Queirós et al. 2013), correlative evidence can nevertheless be disappointing, even for the most established mechanisms that link species to the mediation of ecosystem functioning (e.g. bioturbation and nutrient generation, Solan et al. 2008). This is because levels of ecosystem process and functioning are a product of multiple variables (Teal et al. 2010), which also means that the extent and importance of biological mediation can inadvertently be misrepresented when only a subset is considered (Godbold & Solan 2009). This position is unlikely to change in the short to medium term, as extensive gaps in knowledge of basic trait data (Tyler et al. 2012), the phenomenological status of models describing species–environment interactions (Snelgrove & Butman, 1994) and the lack of critical assessment of assumed species roles are unlikely to be resolved rapidly.

Accepting the premise that the functional role of an individual species is a product of the way in which species interact with one another and the environment, it follows that the assignment of species to functional groupings based on traits (or sets of traits) alone falls short of incorporating the full span of known mechanisms that influence the extent to which species mediate ecosystem functioning. An alternative and parallel approach is to distinguish representative species contributions based on direct measures of ecosystem processes and functioning that are established under highly controlled representative conditions. From these data, the relative importance and functional standing of an inventory of species can be compiled, albeit for a limited set of species, ecosystem functions and circumstances, forming an operational baseline or standard important for building appropriate ecosystem models (Blackford 1997). In this study, our objective was to characterise the functional contributions of 7 common benthic invertebrate species for 2 ecosystem processes (particle reworking and bioirrigation) linked to 4 ecosystem functions (concentrations of $\text{NH}_4\text{-N}$, $\text{NO}_x\text{-N}$, $\text{PO}_4\text{-P}$ and $\text{SiO}_2\text{-Si}$) and use these data to derive functional effect groupings. We hypothesized that functional effect groups would be identifiable but that they would vary between response variables because of subtle differences in species–environment interactions that are imposed by differences in lifestyle. In addition, we predicted that similar functional effect groups would be identified for functions that are intrinsically linked, such as different components of the nitrogen cycle.

MATERIALS AND METHODS

Sediment and fauna collection

Sediment was collected from the Ythan Estuary mudflats ($57^\circ 20.085' \text{N}$, $02^\circ 0.206' \text{W}$) and adjacent dune systems ($57^\circ 18.464' \text{N}$, $01^\circ 59.430' \text{W}$) in Scotland. Mud was sieved (500 μm mesh) in a filtered (10 μm) seawater bath (salinity 24, 6°C) to remove macrofauna. After a settlement period of 24 h (to retain the fine sediment fraction, $<63 \mu\text{m}$), the supernatant seawater was siphoned off and the sediment was homogenised by stirring. Dune sand was dry-sieved (500 μm mesh) and mixed (1:1 by volume) to form standardised sediment representative of the habitats from which the species under study were collected. This is preferential to the use of sediment obtained from contrasting locations because it provides confidence that any differences in our response variables are related to species identity and not to subtle variations in habitat at the point of species collection. Macrofaunal invertebrates, representing a range of lifestyles commonly found in soft sediment systems (Queirós et al. 2013), were obtained from the Ythan Estuary (the polychaete *Hediste diversicolor*, the bivalve *Cerastoderma edule* and the decapod crustacean *Crangon crangon*) or the north Clyde Sea area around the Isles of Cumbrae (the decapod crustacean *Pagurus bernhardus*, the bivalve *Angulus tenuis* and the polychaete *Nephtys hombergii*). The polychaete *Alitta virens* was sourced from a commercial supplier (Dragon Baits).

Experimental setup

Sediment (10 cm depth, $\sim 1 \text{ l}$ per aquarium) was added to thin-walled (5 mm) transparent Perspex aquaria (10 \times 10 \times 33 cm, length \times width \times height), overlain with seawater (2 l, UV sterilised, 10 μm filtered, salinity 24, temperature 6°C), and allowed to settle for 24 h before seawater was replaced to remove excess nutrient release associated with aquarium assembly. Replicate ($n = 5$) aquaria containing no macrofaunal species were maintained to allow macrofaunal species contributions to ecosystem process and functioning to be separated from other faunal components, including the meiofauna (Piot et al. 2014). Species were added to each aquaria, in monoculture and at a replication level of $n = 5$, at a density equivalent to 500 ind. m^{-2} (i.e. 5 ind. per aquarium; *A. tenuis*, *C. edule*, *H. diversicolor* and *N. hombergii*), 300 ind. m^{-2} (i.e. 3 ind. per aquarium; *A. virens*) or

100 ind. m⁻² (i.e. 1 ind. per aquarium; *C. crangon* and *P. bernhardus*). These nominal densities (for biomass, see Table S1 in the Supplement at www-int-res.com/articles/suppl/m516p023_supp.pdf) are within the range encountered for the species under study in temperate regions (e.g. Solan et al. 2008). Aquaria were continually aerated and maintained in a temperature-controlled room (12°C) and in 24 h light. Species were acclimatised to laboratory conditions for a minimum of 5 d prior to the experiment. Due to space limitations, aquaria were randomly allocated to 1 of 6 consecutive experimental runs, each taking 6 d to complete (1 d to allow burrow construction + 5 d; following Bulling et al. 2010).

Measures of ecosystem process

Bioirrigation activity was estimated by measuring the change in water column concentrations of an inert tracer (sodium bromide, NaBr, dissolved in seawater [Br⁻] = 800 ppm, 5 mM). Filtered water samples (5 ml, 0.45 µm cellulose acetate membrane filter) were taken at intervals of 0, 1, 2, 4, 6, 8, 12 and 24 h on Day 4 of the experimental run (following Forster et al. 1999, Mermillod-Blondin et al. 2004) and immediately frozen (-18°C). Br⁻ concentration was analysed using colorimetric analysis (FIAstar 5000 flow injection analyzer, FOSS Tecator) for each time point. From these data, the maximal period of time for the redistribution of tracer prior to reaching equilibrium was determined to be 4 h, and therefore, the change in the relative concentration of Br⁻ ($\Delta[\text{Br}^-]$) was calculated over 4 h. Negative values indicate increased bioirrigation activity (transport of Br⁻ from the overlying water column into the sediment profile).

Particle reworking was measured non-invasively using fluorescent sediment profile imaging (f-SPI; Solan et al. 2004b) and fluorescent-dyed sediment particles (luminophores, 20 g per aquarium; Trace 2290 orange, size 125–355 µm, Partrac) housed in a UV-illuminated imaging box (Schiffers et al. 2011). This method allows the distribution of luminophores to be determined at high spatial resolution (66 µm) from images of the side of the aquarium. Luminophores were distributed across the sediment surface of each aquarium (mean ± 1 SD thickness of luminophore layer = 2.26 ± 0.77 mm) and imaged at 0 and 72 h. The camera (Canon 400D, 10.14 megapixels) was set to a shutter speed of 0.25 s, aperture f = 5.6, sensitivity equivalent to ISO 400, and was controlled using third party software (GB Timelapse, v.2.0.20.0). Image analysis was achieved using a custom-made

semi-automated macro in ImageJ (v. 1.44), a public domain Java-based software program (<http://rsbweb.nih.gov/ij/download.html>). Each image was opened and converted to a red-blue-green (RGB) stack. The user manually traced the sediment–water interface using the segmented line tool before adjusting an appropriate threshold level that distinguished the luminophores (excited by the UV light: $\lambda = 375\text{--}500$ nm) from the sediment. The image was converted to a bitmapped image where the user-defined sediment–water interface was flattened so that the sediment–water interface aligns with the top pixel row. This allows a binary data matrix for each image to be generated with each cell in the matrix corresponding to a pixel in the image. From these data, and following Murray et al. (2013), the maximum (Lum_{max}), mean (Lum_{mean}) and median (Lum_{med}) vertical distributions of luminophores were identified after 72 h. The rugosity of the lower extent of the mixed layer (Lum_{rug}) was calculated as the sum of the Euclidian distances between the deepest luminophores in adjacent columns across the width of the matrix. These descriptors provide an indication of the maximum (Lum_{max}) and typical (Lum_{mean}, Lum_{med}) extent of vertical particle redistribution, as well as the lateral extent of surficial infaunal activity (Lum_{rug}).

Measures of ecosystem functioning

Water samples (20 ml, 0.45 µm cellulose acetate membrane filtered) were taken to determine the change in nutrient concentrations over 6 d ($\Delta[\text{NH}_4\text{-N}]$, $\Delta[\text{NO}_x\text{-N}]$, $\Delta[\text{PO}_4\text{-P}]$ and $\Delta[\text{SiO}_2\text{-Si}]$) and analysed using colorimetric analysis and standard protocols (FIAstar 5000 flow injection analyzer, FOSS Tecator).

Statistical analysis

Species-specific differences in particle reworking, bioirrigation and nutrient concentrations were investigated using mixed effects regression models. Individual regression models were developed for each of the response variables examined (Lum_{max}, Lum_{mean}, Lum_{med} and Lum_{rug}, each based on data extracted from the 72 h images, and $\Delta[\text{Br}^-]$, $\Delta[\text{NH}_4\text{-N}]$, $\Delta[\text{NO}_x\text{-N}]$, $\Delta[\text{PO}_4\text{-P}]$ and $\Delta[\text{SiO}_2\text{-Si}]$), with species identity used as a nominal explanatory variable. Functional differences between species were determined by significance. Subsets of species that did not significantly differ ($p > 0.05$) were grouped together with

respect to their relative contribution (in absolute terms) to the ecosystem processes and functions under study. Species were only grouped together if every species did not significantly differ from every other species in that group. The aquaria containing no macrofauna provided confirmation that the effects we observed were related to macrofaunal activity, but were excluded from these analyses because our focus was to determine groupings of species that share similar contributions to ecosystem process and functioning, rather than to identify species presence versus absence effects.

In all of our statistical models, species identity was specified as a fixed effect and, to estimate and account for inter-run variance, experimental run was specified as a random effect. During the initial model-building phase of the analysis, diagnostic residual plots indicated the presence of heteroscedasticity due to differences in species-specific variances not accounted for by the fixed and random effects. Within the mixed effects modelling framework, variance functions can be explicitly included to model the variance structure, avoiding the need for data transformation. Therefore, where appropriate, a species-specific variance-covariate was included to model the variance for each species (Pinheiro & Bates 2000). Following the inclusion of species-specific variance covariates, diagnostic residual plots indicated homoscedasticity. Parameters in the final models were estimated using restricted maximum likelihood (REML; following West et al. 2007). REML was used in preference to maximum likelihood (ML) as it accounts for the loss of degrees of freedom in estimating the fixed effects, thus producing unbiased estimates of the covariance parameters (West et al. 2007). Details of the initial and minimum adequate models for each variable and the residual plots for each model are included as supplementary material (Models S1–S9, Figs. S1–S9). Following the identification of distinct faunal groupings, we tested the mechanistic link between infaunal mediated ecosystem process and functioning using Pearson's product moment correlations.

All mixed modelling analyses were carried out using the nlme package (v3.1-101; Pinheiro et al. 2011) within the R statistical and programming environment (version 2.15.0, R Development Core Team 2011).

RESULTS

We found evidence for distinct functional groupings based on measures of ecosystem processes and

measures of ecosystem functioning, but the composition of species within these groups was not necessarily consistent between closely associated faunal activities or biogeochemical processes, and it was not always possible to form discernable functional groups (Fig. 1).

Functional effect groupings based on ecosystem process

Our analyses of species contributions to particle reworking and bioirrigation revealed distinct functional effect groupings, but the composition of these groupings was dependent on subtle differences in organism–sediment interactions (Fig. 2). The extent of vertical particle reworking was confined to the uppermost layers of the sediment in treatments containing *Pagurus bernhardus*, *Angulus tenuis*, *Cragon crangon* and *Cerastoderma edule* (*Pb*, *At*, *Cc* and *Ce*, respectively), whilst discrete burrow systems were present at depth in treatments containing *Alitta virens*, *Hediste diversicolor* and *Nephtys hombergii* (*Av*, *Hd* and *Nh*, respectively). Inter-specific differences were detected for Lum_{max} ($F_{6,23} = 33.175$, $p < 0.001$, Fig. 2a, Model S1 in the Supplement) and 4 distinct functional effect groups could be identified (*At–Cc–Ce*, *Pb*, *Nh–Av* and *Hd*; Fig. 1). *P. bernhardus* did not differ from *C. edule* or *N. hombergii*; however, it could not be grouped with them as *C. edule* and *N. hombergii* were found to be different (Table S2 in the Supplement). Species differences for Lum_{mean} ($F_{6,23} = 4.384$, $p = 0.004$, Fig. 2b, Model S2) resulted in 2 main functional effect groups being identified (*Pb–At–Ce–Cc* and *Nh–Av–Hd*; Fig. 1, Table S3 in the Supplement), although there was evidence for an intermediate functional effect grouping (*Ce–Cc–Nh–Hd*) because the contributions of these 4 species were indistinguishable (Table S3). For Lum_{med} , there was no evidence of any significant differences between species ($F_{6,23} = 2.305$, $p = 0.069$; Model S3). There were inter-specific differences in Lum_{rug} ($F_{6,23} = 3.578$, $p = 0.012$; Fig. 2c, Model S4), and 2 functional effect groupings were identified (*Cc–At–Ce–Nh–Hd* and *Nh–Hd–Pb–Av*; Fig. 1, Table S4 in the Supplement). *Nephtys hombergii* and *H. diversicolor* contributed to both of these groups, but did not form a distinct grouping as the contribution of these species was variable. Finally, there were species differences for $\Delta[Br^-]$ ($F_{6,23} = 3.032$, $p = 0.025$; Fig. 2d, Model S5) and 2 main functional effect groups were identified (*Av* was distinct from *Pb–At–Ce–Cc–Nh–Hd*; Fig. 1, Table S5 in the Supplement),

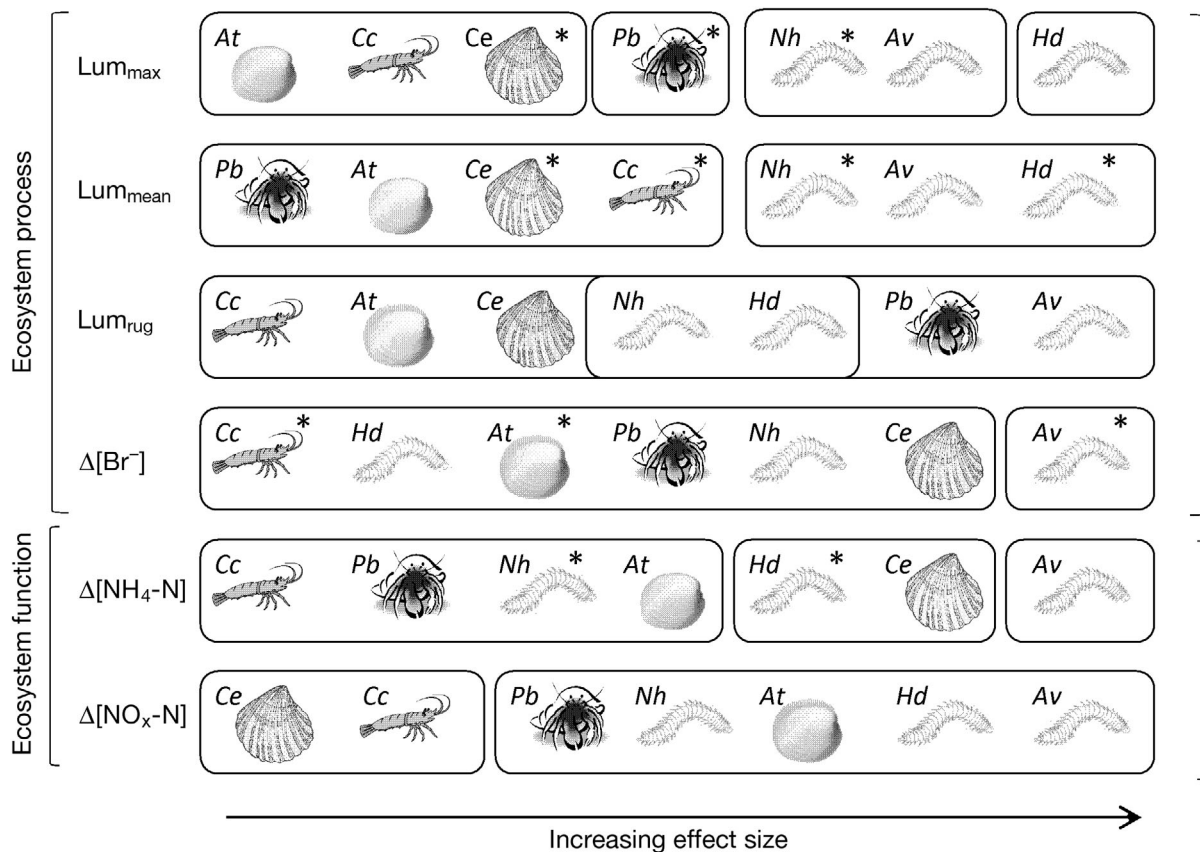


Fig. 1. Summary of functional effect groups identified based on aspects of sediment particle reworking, bioirrigation or nutrient concentrations. Boxes identify subsets of species that form a functional grouping based on the ecosystem process or function indicated for each row. Species were ascribed to groupings based on statistical differences in response variable and are positioned (from left to right) in order of increasing effect size. Boxes overlap with one another where the contribution of a species is assigned to more than one grouping. Species that are also functional equivalents of species in a different functional group are indicated by an asterisk. Lum_{max}, Lum_{mean}: maximum and mean vertical distributions of luminophores, respectively; Lum_{rug}, rugosity of the lower extent of the mixed layer; At: *Angulus tenuis*; Av: *Alitta virens*; Cc: *Crangon crangon*; Ce: *Cerastoderma edule*; Hd: *Hediste diversicolor*; Nh: *Nephtys hombergii*; Pb: *Pagurus bernhardus*

although there was an intermediate level grouping (Cc–At–Av) that exhibited contributions that overlapped with both of the main groupings. Whilst there were some consistencies across these functional effect groupings (e.g. At, Cc and Ce always shared the same functional grouping; see Tables S2–S5), the composition of the groupings was not necessarily constant (e.g. compare positioning of Av, Hd, Nh and Pb).

Functional effect groupings based on ecosystem functioning

Analysis of nutrient concentrations (Fig. 3) identified inter-specific differences resulting in distinct functional effect groups for Δ[NH₄-N] ($F_{6,23} = 92.200$, $p < 0.001$; Model S6) and Δ[NO_x-N] ($F_{6,23} = 4.879$, $p =$

0.003; Model S7). Species contributions to Δ[NH₄-N] were separable into 3 functional effect groupings (Av–Ce–Hd, At–Cc–Nh and Pb; Fig. 3a, Model S6, Table S6 in the Supplement). Interestingly, for the reciprocal function, Δ[NO_x-N], our analyses revealed only 2 different functional effect groups (Ce–Cc and Pb–Nh–At–Hd–Av; Fig. 3b, Model S7, Table S7 in the Supplement). Whilst there were also differences between species detected for Δ[PO₄-P] ($F_{6,23} = 3.619$, $p = 0.011$; Fig. 3c, Model S8) and Δ[SiO₂-Si] ($F_{6,23} = 2.669$, $p = 0.041$; Fig. 3d, Model S9), no functional groups could be identified. In this case, we were unable to form a single functional effect group comprising all of the species under study because there were some inter-specific differences within the species pool. *N. hombergii* differed from *A. virens* (coefficient = -0.035 , $t = -3.886$, $p = 0.001$; Table S8 in the Supplement) and *C. edule* (coefficient = -0.032 , $t =$

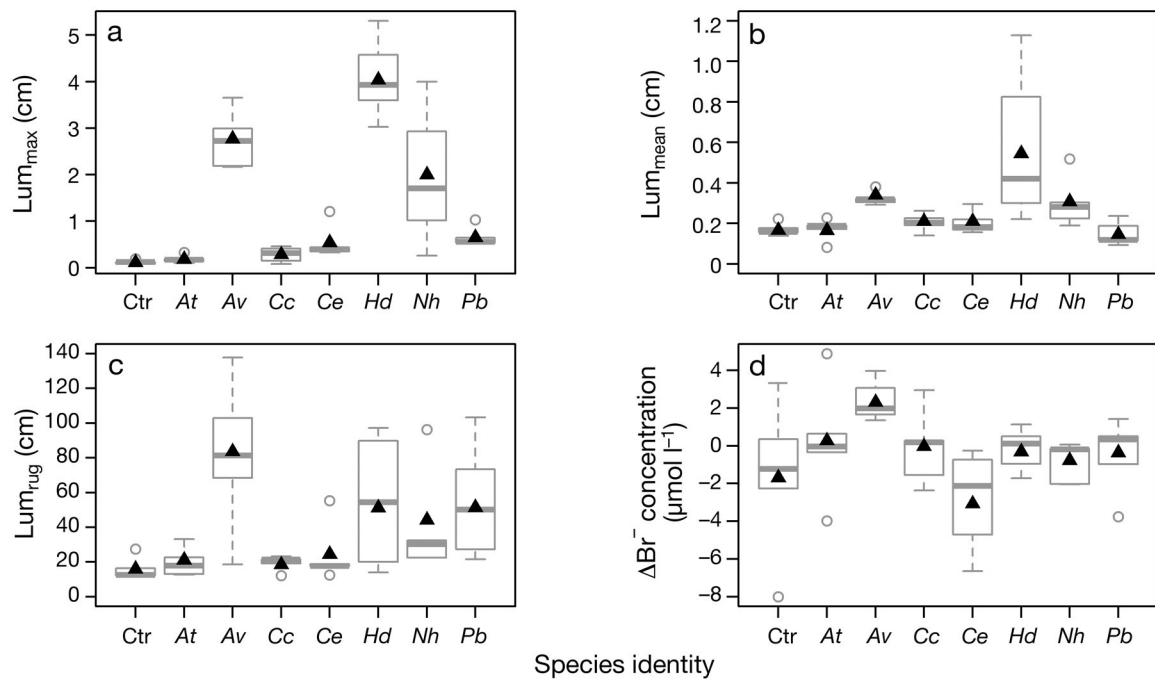


Fig. 2. Sediment reworking and bioirrigation associated with benthic invertebrates. Species-specific effects on the particle reworking metrics (a) maximum vertical luminophore distribution (Lum_{max}), (b) mean vertical luminophore distribution (Lum_{mean}), and (c) rugosity of the lower extent of the mixed layer (Lum_{rug}), and on bioirrigation (d) $\Delta[Br^-]$. Boxes are upper and lower quartiles; median indicated at the midpoint; whiskers represent the spread; open circles are outliers defined as $1.75 \times$ interquartile range. Black triangles represent the fitted values for each species from the mixed effects models. Ctr: no macrofauna; At: *Angulus tenuis*; Av: *Alitta virens*; Cc: *Crangon crangon*; Ce: *Cerastoderma edule*; Hd: *Hediste diversicolor*; Nh: *Nephtys hombergii*; Pb: *Pagurus bernhardus*

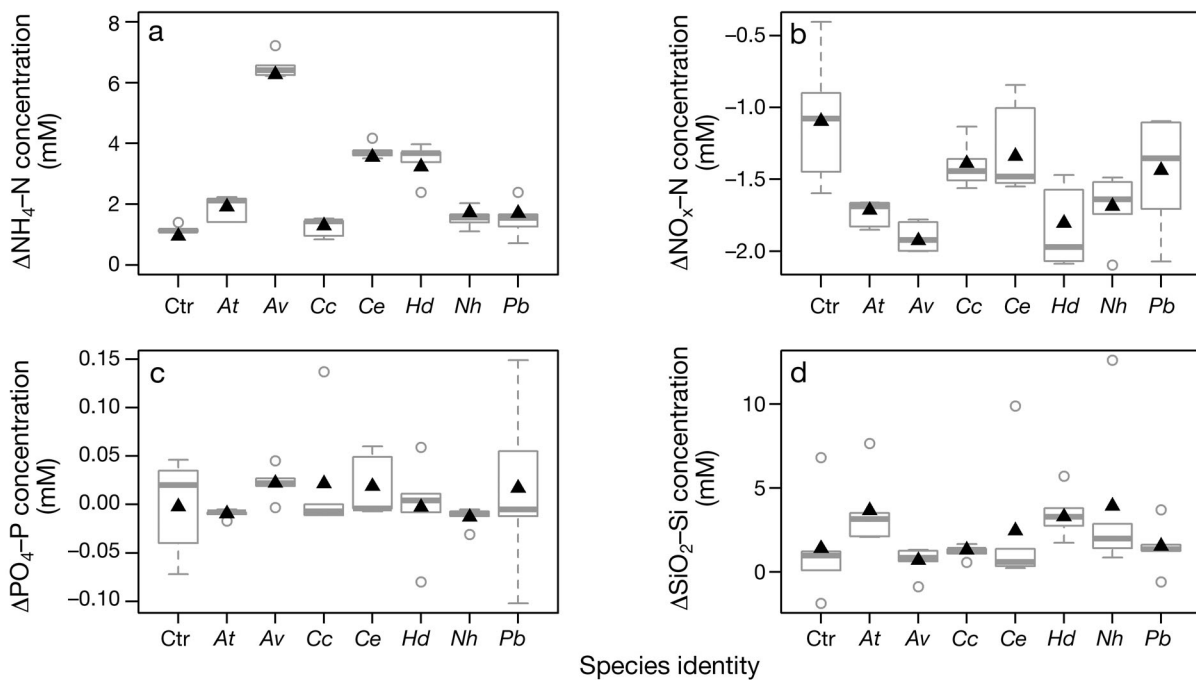


Fig. 3. Benthic invertebrate effects on (a) ammonium, (b) nitrate and nitrite, (c) phosphate, and (d) silicate concentrations. Boxes are upper and lower quartiles; median indicated at the midpoint; whiskers represent the spread; open circles are outliers defined as $1.75 \times$ interquartile range. Black triangles represent the fitted values for each species from the mixed effects models. Ctr: no macrofauna; At: *Angulus tenuis*; Av: *Alitta virens*; Cc: *Crangon crangon*; Ce: *Cerastoderma edule*; Hd: *Hediste diversicolor*; Nh: *Nephtys hombergii*; Pb: *Pagurus bernhardus*

Table 1. Pearson correlations between all pairwise combinations of the 8 response variables: maximum (Lum_{max}) and mean (Lum_{mean}) vertical distributions of luminophores, rugosity of the lower extent of the mixed layer (Lum_{rug}), $\Delta[Br^-]$, $\Delta[NH_4-N]$, $\Delta[NO_x-N]$, $\Delta[PO_4-P]$ and $\Delta[SiO_2-Si]$. Significant values and the level of significance are indicated (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Significant correlations between an ecosystem process and an ecosystem function are in **bold**

	Lum_{max}	Lum_{mean}	Lum_{rug}	$\Delta[Br^-]$	$\Delta[NH_4-N]$	$\Delta[NO_x-N]$	$\Delta[PO_4-P]$	$\Delta[SiO_2-Si]$
Lum_{max}	–	0.752***	0.552***	0.155	0.457**	-0.436**	-0.079	0.020
Lum_{mean}		–	0.489**	0.109	0.226	-0.154	-0.119	-0.035
Lum_{rug}			–	0.137	0.415**	-0.144	-0.003	-0.095
$\Delta[Br^-]$				–	0.326*	-0.300	0.162	-0.289
$\Delta[NH_4-N]$					–	-0.275	0.224	-0.157
$\Delta[NO_x-N]$						–	0.297	-0.261
$\Delta[PO_4-P]$							–	-0.189
$\Delta[SiO_2-Si]$								–

-2.064, $p = 0.050$; Table S8) for $\Delta[PO_4-P]$. *C. crangon* differed from *A. tenuis* (coefficient = -2.399, $t = -2.104$, $p = 0.046$; Table S9 in the Supplement) and *H. diversicolor* (coefficient = 2.029, $t = 2.863$, $p = 0.009$; Table S9) for $\Delta[SiO_2-Si]$. *H. diversicolor* also differed from *A. virens* (coefficient = 2.688, $t = 3.099$, $p = 0.005$; Table S9) for $\Delta[SiO_2-Si]$.

Linkage between ecosystem process and functioning

Despite having fundamentally different consequences for ecosystem functioning, alternative metrics of particle redistribution were highly correlated with one another (Table 1). There were no significant correlations between bioirrigation ($\Delta[Br^-]$) and the redistribution of particles, confirming that these processes can reflect different aspects of species behaviour. The redistribution of particles was positively correlated with increased levels of $\Delta[NH_4-N]$ and $\Delta[NO_x-N]$ but not $\Delta[PO_4-P]$ or $\Delta[SiO_2-Si]$, whilst bioirrigation activity was positively correlated with increases in $\Delta[NH_4-N]$ (Table 1).

DISCUSSION

Understanding concepts of species redundancy and the mechanisms that influence species contributions to ecosystem functioning has recently regained prominence but is reliant on an ability to identify groups of species that have similar effects on ecosystem functioning. A key constraint in achieving this goal is that many approaches for defining functional effect groups are based on establishing similarities in biological traits that ignore, or at least poorly integrate, organism–environment interactions

that are important in determining how traits are expressed and, in turn, species contributions to ecosystem functioning (Needham et al. 2011). Species that disproportionately contribute to particular processes are not necessarily ranked as highly for their contributions to ecosystem functioning (e.g. compare particle reworking coefficients to nutrient release in Bulling et al. 2010, Godbold et al. 2011), suggesting that direct assessments of ecosystem properties may be a more appropriate means of establishing the relative role of species. Indeed, the present study confirms that functional effect groups based on measurements of ecosystem processes (particle reworking and bioirrigation activity), ecosystem functioning (nutrient release) or both can be informative, but it also reveals that variation in species contributions can mean that functional effect group structures and compositions are difficult to apply more widely. For instance, our experimental design allowed us to test the common assumption that species regarded as being functionally dominant, or belonging to certain *a priori*-defined functional categories (e.g. bioturbation modes, François et al. 1997), will exert similar levels of influence across multiple ecosystem processes and functions. We were unable to support this view, even when species had a consistently high functional standing or when the ecosystem functions under study were closely related (e.g. reciprocal changes in NO_x-N following NH_4-N release during faunal-mediated nitrification–denitrification), as the performance ranking of each species varied across our response variables.

There were some consistencies across functional effect groupings (e.g. *Angulus tenuis*, *Crangon crangon* and *Cerastoderma edule* tended to share the same functional effect groupings), but group membership was not necessarily constant (e.g. compare the positioning of *Alitta virens*, *Hediste diversicolor*,

Nephtys hombergii and *Pagurus bernhardus* across functional effect groupings). Nevertheless, individual species were often important mediators of multiple ecosystem functions, indicating that functional effect groups should either be constrained in usage to specific functions and circumstances, or defined in a holistic way that can account for multi-functionality. A common outcome from the latter (Zavaleta et al. 2010, Mouillot et al. 2011, Maestre et al. 2012) is that more species are required to maintain ecosystem functioning than would otherwise be concluded from studying a reduced set of functionally prominent species. This is important because the mismatch between the subset of functionally dominant species derived (using functional group approaches that are based on a single or reduced set of species traits) and the full complement of species that contribute to ecosystem functioning increases the likelihood of species overlap between functional effect groups and will lead to overestimates of redundancy (Hector & Bagchi 2007). Such a position also ignores the role of rare species (Jain et al. 2014) that provide comparatively minor contributions to a functional effect group but which may be of importance to other ecosystem functions, other functional effect groups, or become more significant to either or both of these in an alternative context (e.g. Volkenborn & Reise 2007). Therefore, estimating redundancy from an inventory of functional effects requires caution. This is particularly true if multi-functionality is inferred rather than tested (Mouillot et al. 2011) or when estimates are based on a subset of functionally strong species that have been evaluated using an inadequate or inappropriate set of functional descriptors over a short period of time or in limited environmental circumstances.

To achieve a more defensible means of allocating species to functional effect groupings, it is important to understand the mechanisms by which species interact with their environment. This has been a central focus of benthic ecological research for several decades (for reviews, see Gray 1974, Rhoads 1974, Aller 1982, Snelgrove & Butman 1994, Pearson 2001), but, despite intimate knowledge of how benthic-dwelling invertebrates redistribute sediment particles and pore water fluids and affect biogeochemical cycling, a surprising difficulty is that grouping species based solely on bioturbation activity or mode is not a particularly good predictor of species functional effects. In the present study, for example, only changes in $\text{NH}_4\text{-N}$ concentrations were correlated with particle reworking and bioirrigation. Whilst these findings are consistent with expectations,

given previously documented poor process–function correlations (e.g. Solan et al. 2008) and the recognition that ecosystem functioning is dependent on multiple factors (Teal et al. 2010), they highlight a need to determine the most important traits for specific ecological functions. In this regard, we did find that species with higher biomass tended to be associated with the greatest changes in nutrient concentrations, but it is unclear whether changes in $\text{NH}_4\text{-N}$ concentrations were associated with the effects of infaunal activity on sediment microorganisms (Gilbertson et al. 2012) or driven by other processes, such as macrofaunal excretion (Gardner et al. 1993). Where biomass has been held constant elsewhere, larger species have been found to contribute both more (Michaud et al. 2006) and less (Solan et al. 2008) to specific ecosystem functions relative to smaller species, so body size is not necessarily an appropriate predictor of likely species contributions to benthic biogeochemical cycling; 2 similar sized species within the present study (the polychaetes *N. hombergii* and *H. diversicolor*) that are routinely regarded as being functional equivalents (Bremner et al. 2003) showed very different contributions to functioning. Importantly, these differences were only detected because direct measures of functioning were available, as these 2 species were generally indistinguishable based on their contributions to ecosystem process. Had we ascribed species to functional effect groupings without taking into account this mechanistic linkage (e.g. body size: $Av-Ce > At-Nh-Hd > Pb-Cc$; bioturbation mode: $Cc-Pb_{[epifaunal]}$, $At-Ce_{[surficial\ modifiers]}$, $Nh-Av-Hd_{[bioturbators]}$), concluding statements about the contributory role and relative importance of species would have been misleading and difficult to reconcile with observed levels of functioning.

It is clear that the classification of species into functional effect groups will remain inherently difficult because organisms respond to their environment as individuals. Species functional activities are not set at discrete levels but vary along a continuum (Picard et al. 2012) that reflects individual responses to the environment and each other. Although some behaviour patterns are highly stereotyped (e.g. *Amphiura filiformis* emergence in response to hypoxia, Nilsson 1999), and will be relatively consistent within a species, individuals are capable of displaying a range of responses to stimuli (Yang & Rudolf 2010) and will act based on their individual needs. Rather than perpetuating research foci towards the quantification of a few dominant and well-known species (MacGillivray et al. 1995, Tilman et al. 1997, Wardle

et al. 1997), efforts may be better directed towards the identification of how and when species contribute to functioning, irrespective of their proportional contribution. This last point is not trivial because there are some significant gaps in understanding, mainly with respect to the mechanisms that link biodiversity to specific ecosystem functions. In other systems where understanding is more advanced, such as terrestrial plant and soil communities, evidence suggests that a trait-based approach may be more appropriate in understanding the functional role of species than a species-based approach (Messier et al. 2010), particularly when traits are directly linked to the specific ecosystem functions under study (e.g. leaf surface area with primary production: Reich et al. 1998; actinorrhiza and nitrogen fixation: Zahran 1999). It is premature to draw similar conclusions for marine benthic systems, as there is a scarcity of information on which (and when) physiological, behavioural, ecological and morphological traits correlate with ecosystem properties and services. The immediate challenge for benthic ecologists is to close these significant gaps in the availability of such basic information and work towards building capability in predictive understanding of the links between species and ecosystem properties across a range of biodiversity–environment contexts.

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