**Trait-mediated processes and *per capita* contributions to ecosystem functioning depend on conspecific density and climate conditions**

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**Abstract**

**The ecological consequences of environmental change are highly dependent on the functional contributions of the surviving community, but categorical descriptors commonly used to project ecosystem futures fail to capture context dependant response variability. Here, we show that intraspecific variability for a range of sediment-dwelling marine invertebrates is moderated by changes in the density of conspecifics and/or climatic conditions. Although these trait-mediated changes result in modifications to ecosystem properties, we find that the contributions of individuals to functioning are not necessarily additive but, instead, are a result of alterations to *per capita* performance. Our findings also indicate that trait variation within species can exert a greater influence on functioning than that of trait variation between species. Hence, projections of likely functional outcomes that scale from mean trait values are unlikely to be robust, highlighting a need to account for how and when intraspecific variability results in context-dependent community responses to change.**

**Introduction**

Grouping species by their functional traits - morphological, biochemical, physiological, structural, phenological or behavioural1,2 - to infer or explain their influence on ecosystem functioning has a well-established history3,4, but trait-ecosystem function relationships are often built from fragmented information and seldom consider intraspecific variation in trait expression. Species that share traits do not necessarily form universally applicable functional effect groups5, as trait expression can depend on environmental and biotic setting6,7. Consequently, trait designations can lack relevance to, and be distinct from, what is observed in natural systems8-10. This oversight is surprising, as intraspecific trait variation is not only an important source of variation for species coexistence11, environmental filtering12 and community assembly13, but some continuous traits, such as body size14, can determine an individual's contribution to ecosystem functioning15 and extinction risk16. In addition, variation within a species can be as important as variation between species12,17-20 and populations with greater genotypic variability can outperform those with fewer genotypes21, and enhance both ecosystem functioning and biodiversity of other trophic levels22. It is known that species’ can modify their traits in response to environmental context (e.g. current velocity23, habitat configuration24-26, climate27,28) and/or biotic interactions (e.g., predation29,30, density19,31) which can disproportionately influence how a community moderates ecosystem properties19,32-34. However, considerable gaps in understanding remain of how, when, and under what circumstances, differences in trait expression occur and lead to alternative functional outcomes35.

In response to changing abiotic and/or biotic conditions, species are also known to switch behaviour36, make physiological adjustments37, or undergo compensatory responses38 as a precursor to39, and following, local alterations in species richness. Whilst the ecological consequence of altered diversity remains a strong focus in ecology40 including how the presence or absence of interspecific interactions promotes niche differentiation and ecosystem functioning41, comparatively little is known about how shifts in community structure, dominance, and species abundance in surviving communities moderate effect trait expression, defined here as traits that mediate one or more ecosystem functions35,42-45. Temporal shifts in species abundance46,47 can modify effect trait expression through altered synergistic or antagonistic conspecific interactions and consequential shifts in body mass and size48. While progress has been made in recent years on characterising the relevance of intraspecific trait variability to ecosystem functioning49,50, the extent to which abiotic (climate) and biotic (conspecific interactions) factors contribute to intraspecific effect trait variability and related ecosystem processes is still poorly constrained, frustrating the inclusion of trait-variation in biodiversity-function research11.

Here, we determine the effect of conspecific density (11-486 ind. m-2) and near-term climate change (550 ppm pCO2, + 2 °C warming) on trait expression and trait-driven processes assumed to be important in the mediation of nutrient cycling51 in six sediment-dwelling marine invertebrates. Our *a priori* expectation was that *per capita* contributions to trait-driven processes would differ between species and/or with biotic (density7) and environmental conditions (climate27), but that the effect of individuals within a species would not be consistent as individual sensitivities to novel conditions vary19. Consequently, we anticipated that associated changes in ecosystem functioning (nutrient cycling and sediment properties) would reflect intraspecific variation in functionally important behaviour which could, in turn, be sufficient to alter the functional role of a species. In this study, we find that future climate conditions and naturally occurring densities of conspecifics can elicit substantial changes in ecological processes mediated by behavioural effect traits, that lead to differences in the functional performance of populations. Our experiments reveal that these changes are driven by alterations to *per capita* functional contributions, rather than additive density effects, as species contributions did not increase linearly with individual density. These findings indicate that trait variation within species can exert a greater influence on functioning than that of trait variation between species, supporting the idea that the coarseness of the functional group approach when based on mean performance is likely to lead to the over or underestimation of biodiversity mediated ecosystem functioning under changing conditions.

**Results**

We observed that conspecific density (11-486 ind. m-2) and future climate (ambient: 12 °C, 410 ppm pCO2 vs future: 14 °C, 550 ppm pCO2) alters trait-mediated processes in marine benthic macrofauna, particularly for those related to sediment particle mixing. Increases in trait-driven particle reworking depths, correlated with changes in the depth of the apparent sediment redox potential discontinuity (aRPD, and indicator of the extent of sediment turnover) and *per capita* contributions to seawater nutrient concentrations, confirming that intraspecific variability in individual contributions to ecosystem processes can have measurable consequences for ecosystem functioning.

**Effects of density and climate on individual burial traits**

The time taken to start burying log(Burialstart) ranged from three seconds (*Turritellinella tricarinata,* ambient, 208 ind. m-2, 3 ind. aquarium-1) to ~2 days (*Paraleptopentacta elongata*, ambient, 11 ind. m-2, 1 ind. aquarium-1), but depended on the interaction between species density and climate treatment (ANCOVA, F1,354 = 4.32, p = 0.038; Figure 1a). Closer inspection of model coefficients indicated that, irrespective of species identity, log(Burialstart) decreased as conspecific density increased under future climate conditions (coef = -1.53, t = -2.08, p = 0.038) whilst under ambient conditions, density had no effect on log(Burialstart) (coef = 0.04, t = 0.79, p = 0.149; Supplementary Figure 1). Kernel smoothing to derive probability density estimations (KDE), to visualise the distribution of intraspecific trait values, revealed species differences in log(Burialstart) variability (interquartile range, from 2.73 in *P. elongata* to 1.12 in *Sternaspis scutata*, Figure 1b).

**Effects of density and climate on particle reworking depth and bioirrigation**

In general, faunally driven particle reworking activity was dependent on both conspecific density and climate treatment, but the magnitude of these effects varied between different aspects of species activities and depended on complex interactions between our explanatory variables. Surface boundary roughness (SBR) was dependent on an interaction between density and climate treatment (ANCOVA: F1,95 = 6.18, p = 0.015) with SBR decreasing with increasing density under future climate conditions (Figure 2a). When species identity is treated as a random factor, the mean mixed depth of particle redistribution (f-SPI*L*mean) increases with conspecific density (ANCOVA: F1,95 = 3.98, p = 0.049), but we identified species-specific responses of f-SPI*L*mean to density (L-ratio: 36.92, d.f. = 2, p < 0.001). f-SPI*L*mean was deeper with increasing *Amphiura chiajei* (slope = -0.110) and *Nepthys hombergii* (slope = -0.050) density but showed little change with increasing *S. scutata* density (slope = 0.001). We also found a weak effect of climate treatment, with shallower f-SPI*L*mean values in future climate treatments relative to those in ambient treatments (ANCOVA: F1,95 = 3.68, p = 0.058; Figure 2b). The maximum mixed depth of particle redistribution (f-SPI*L*max) increased linearly with species density (ANCOVA: F1,96 = 7.93, p = 0.010; Figure 2c), but there were species-specific differences in variability, ranging from 0.53 - 1.45 cm (*P. elongata*) to 0.60 - 10.23 cm (*A. chiajei*). Inspection of model coefficients revealed that f-SPI*L*max was ~0.6 cm shallower in future climate treatments compared to ambient conditions (ANCOVA: F1,96 = 2.92, p = 0.091; Supplementary Figure 2). KDE for ventilatory activity (∆[Br-]) provide evidence, in absolute terms, for active ventilatory activity (negative values, Figure 2d), although this behaviour was not affected by conspecific density (ANCOVA: F1,91 = 0.58; p = 0.447) or climate treatment (ANCOVA: F1,91 = 0.73, p = 0.397).

**Effects of density and climate on ecosystem functioning**

In the broadest terms, changes in climate conditions had a greater effect on nutrient concentrations than differences in species or density. We find [NH4-N] was dependent on climate treatment (ANCOVA: F1,95 = 50.82, p < 0.001), but not conspecific density (ANCOVA: F1,95 = 1.09, p = 0.298; Fig 3a). Overall, mean (± SE) [NH4-N] was lower under future climate conditions (10.80 ± 0.26 µmol L-1) relative to ambient conditions (12.67 ± 0.31 µmol L-1). Similarly, there was no effect of conspecific density on [NOx-N] (ANCOVA: F1,96 = 2.27, p = 0.135) but, irrespective of species identity, [NOx-N] was lower under future climate conditions (ANCOVA: F1,96 = 9.65, p = 0.003; Figure 3b). Comparing model slopes using an L-ratio test revealed, for some species, weak effects of density on [NOx-N] (L-ratio: 7.97, d.f. = 2, p = 0.019; Figure 3b). In contrast, [PO4-P] was not dependent on species density (ANCOVA: F1,96 = 0.31, p = 0.577) or climate treatment (ANCOVA: F1,96 = 0.18, p = 0.672; Figure 3c).

We used AIC to assess the suitability of trait-mediated particle reworking depth metrics (SBR, f-SPI*L*mean and f-SPI*L*max) as predictors for aRPD depth and results revealed that f-SPI*L*mean explained the greatest amount of variability in aRPD depth (slope: ambient, 1.31 ± 0.22 cm; future, 1.23 ± 0.25 cm), but was dependent on the interaction between f-SPI*L*mean and climate (ANCOVA interaction: F1,95 = 5.37, p = 0.027; Figure 4a). f-SPI*L*max displayed a weaker relationship with aRPD (slope: ambient, 0.04 ± 0.03 cm; future, -0.04 ± 0.25 cm) but also depended on the interaction between f-SPI*L*max and climate (ANCOVA interaction: F1,94 = 20.0, p < 0.001; Figure 4b), while SBR was poor at explaining variability in aRPD (ANCOVA: F1,94 = 0.011, p = 0.918; Figure 4c). Considering f-SPI*L*mean as a predictor, aRPD was deeper and the gradient steeper under future conditions (intercept: ambient, 0.627 ± 0.25 cm, future, 0.709 ± 0.26 cm; slope: ambient, 1.314 ± 0.22, future, 2.029 ± 0.31; t = 2.32, p = 0.023). The extent to which climate and density treatments influenced overall intraspecific variability in aRPD depth (defined as the interquartile range derived from KDE) differed between species, ranging from 0.24 cm in *T. tricarinata* to 1.53 cm in *A. chiajei* (Figure 4d), with *S. scutata* having a very limited effect on aRPD across all individual densities.

**Relative importance of intraspecific variation**

A large proportion of overall variability in trait-mediated processes, as determined from the decomposition of model sums of squares, was explained by intraspecific variation, but the magnitude of explained intraspecific variability was dependent on the trait or process (Burialstart, 29 %; SBR, 89 %; f-SPI*L*mean, 41 %; f-SPI*L*max, 31 %; ∆[Br-], 88 %; Figure 5). For metrics associated with faunal mediated particle redistribution (SBR, f-SPI*L*mean, f-SPI*L*max), marginal R2 values derived from Linear mixed effects models indicate that climate conditions, conspecific density, and their interactions with one another, explain 5 - 9 % of all observed (intraspecific + interspecific) variability. This equates to 16 - 20 % of the estimated levels of intraspecific variability (Figure 5).

**Discussion**

The measurable functional characteristics (traits) of organisms are not only used to make assessments of ecological conditions52,53 but, increasingly, also to forecast future ecological functioning54, particularly by those interested in restoring or managing ecosystems for specific functions55-57. Whilst trait-based approaches that can quantify and predict ecological processes are both promising and needed10,58,59, it is often common practice to adopt categorical descriptors based on mean trait values (but see notable exceptions49,50,60). Here, however, we demonstrate that species-level functional characterisations fail to capture species-specific variation in response to changing abiotic and biotic circumstances61. Specifically, we find that functionally important processes which result from multiple aspects of species behavioural traits and trait-environment interactions can vary depending on the density of conspecifics and/or climate conditions and that this can be sufficient in magnitude to alter a species relative functional role. Such departures from mean functional roles result from changes in *per capita* contributions, rather than density effects, as the summed contribution of individuals is not a linear additive function of density62. As species behaviour is known to change across emerging or novel contexts, our findings indicate that functional effect group structures and compositions that are grounded in mean trait values can, with some exceptions63, form a poor representation of population trait expression and, therefore, are difficult to justify and apply more widely.

It is generally assumed that a species’ overall contribution to ecosystem functioning positively correlates with its abundance in a community64-66. Indeed, there is evidence across a range of species and contexts that particle reworking activity and/or burrowing depth increases with density19,67-69. However, the density of conspecifics within a community also alters the nature of intraspecific and interspecific interactions, which, in turn, can change individual contributions to ecosystem processes and functioning24,25,44,70-72. These changes are not necessarily aligned, even with assumed closely associated trait-function pairings73. For some of our species, sediment mixing depth increased with density, while associated levels of nutrient concentration remained the same, indicating that some measures of process-driven behaviour are not completely synonymous with functioning74,75. This could be explained by changes in organism-environment interactions such as altered microbial diversity76, synergistic and/or antagonistic intraspecific interactions77, or the complexity of sediment biogeochemical processes that influence nutrient release and may not correlate with simpler faunally driven processes78. A notable outcome of our study is that functionally relevant behavioural changes in response to altered abiotic and biotic contexts add an additional layer of complexity to trait-mediated processes. It is evident from our effect trait density distributions that species functional contributions are best represented by a range, rather than a single value, and that effect trait spaces defined in this way may overlap or flex with context. For example, the range of effect trait values across different levels of conspecific density was minimal in the gastropod *Turritellinella tricarinata,* but much more extensive for the ophiuroid *Amphiura chiajei* which, in turn, had greater influence on sediment physio-chemical properties (aRPD). These asymmetries in *per capita* effects are likely to emerge from competitive interactions79 and suggest that density-dependent estimates of functioning are likely to considerably differ from equivalent estimates based on density-independent rates, as is commonly practiced80,81. Moreover, by ignoring density and other context-specific influences on functional trait expression and trait-mediated processes, insignificant or weak trait-function relationships based on mean trait values run the risk of being misinterpreted as being unimportant82.

The value of utilising species functional traits over their taxonomic identity is based on the critical assumption that a functional trait has a measurable impact on one or more ecosystem processes and functions4,12,83. Indeed, while we demonstrate a trait-function relationship between particle reworking depth and aRPD depth, the strength of this relationship is inconsistent between species and is not reciprocated in other closely associated ecosystem functions, such as water column nutrient concentrations. More widely, many trait-function relationships are assumed, seldom empirically tested8,10, and many functional group designations are not able to predict ecosystem functioning any better than a random allocation of categorical descriptors84, which may stem from inherent subjectivity in functional group categorisation85. Even basic information linking traits to functioning is poorly documented, such that species are often categorised based on close affinities, yet species that share traits, or are close taxonomically, do not necessarily cluster in distinct functional groups5. Here, for example, we find that particle reworking depth in *T. tricarinata* is a poor predictor of sediment physicochemical properties and associated nutrient concentrations, yet the reverse also holds true for functionally and taxonomically similar gastropods elsewhere86,87. Integration of trait variation, using continuous rather than fixed trait values, whilst avoiding the use of assumed trait affinities, offers opportunity to dynamically distinguish the functional role of species under specific circumstances when evaluating species responses to environmental anthropogenic change12.

Despite the well-established importance of intraspecific trait variability in functional diversity12,88, ecosystem functioning19 and ecosystem services89, the nature of context dependent trait expression is rarely incorporated into measures of biodiversity, or efforts to determine the impacts of environmental conditions on the properties and functioning of ecosystems90,91. Our empirical estimates put observed intraspecific variability across our pool of species at 29 - 89 % of all variability, indicating that classical discrete classification of species into functional groups based on mean trait expression does not account for a substantial proportion of natural trait variability. Importantly we find that climate conditions and conspecific density explain up to 1/5th of this intraspecific variability; however, this is not true for all traits or processes measured, with some (e.g., SBR and bioirrigation) exhibiting minimal variation within and between species. Indeed, it is likely that intraspecific variation is even higher in natural systems, since our study design necessitated sampling individuals of similar biomass and condition for comparative purposes, which minimises variability related to body size, season and life stage92,93. These inherent sources of individual variability have long been excluded from trait-based approaches to ecosystem functioning research94,95, despite the well-established influence of both phenotypic plasticity and genotypic variation on individual trait expression96,97. We reveal substantial plasticity in functionally important trait-mediated processes suggesting that expression of effect traits can be mediated by biotic interactions between conspecifics19,81 and/or between species77,98. Adopting an approach that is more focussed on individuals rather than species, and which recognises and embraces the context dependency of responses, will facilitate the integration of genotypic (permanent) and plastic (transient) variation necessary to understand and predict how the response of communities to change may modify ecosystem properties. Such approaches may include incorporating trait values into predictive models as distributions rather than means94, or employing variance partitioning equations99 using a similar methodologies to this study100. However, we show here that not all traits are valid indicators for distinguishing species’ functional roles, nor are they equally ranked in terms of functional importance101,102. If we are to predict the consequences of changing environmental conditions, more emphasis is needed on empirically deriving the mechanistic basis of trait-function relationships103,104 and in recognising that species functional activities are not set at discrete levels but vary along a continuum105 and over time106 that reflects individual responses to changing circumstances.

**Methods**

**Faunal collection and experimental set-up.** This study included six functionally contrasting sediment-dwelling invertebrate species spanning four phyla, including rare, common and an invasive species to comprehensively assess the effects of individual density on trait expression, trait-mediated processes and ecosystem functioning.Individuals of the holothurian *Paraleptopentacta elongata*, actinarian anemone *Edwardsia claparedii*, gastropod *Turritellinella tricarinata*, and polychaete *Nephtys hombergii* were collected from Rame mud, Plymouth (50°18'01"N 4°16'03"W, depth: 42 m), the invasive polychaete *Sternaspis scutata* from Plymouth Breakwater (50°20'15"N 4°09'23"W, depth: 12 m) and the ophiuroid *Amphiura chiajei* fromLoch Linnhe, Oban (56°29'33"N 5°30'19"W, depth: 35 m) using a 0.1 m2 van Veen grab. Individuals were transported to the University Southampton's Biodiversity and Ecosystem Futures Facility at low density in continually aerated 20L buckets within 5 h (Plymouth) or 12 h (Oban) and acclimated to aquarium conditions (12.0 ± 0.5 ˚C, 12:12 light-dark cycle, Aquabar T-series blue LED, 450 nm) for two weeks. During the acclimation period, all species were fed to excess three times week-1 with a mixed algal diet consisting of *Tetraselmis suecica* and *Phaeodactylum tricornutum*. As species behaviour can depend on site-specific sediment properties7, all mesocosms contained a homogenised 50:50 mixture of sediment (mean particle size, 185 ± 60 µm; organic matter content, 5.4 ± 0.2 %) from Oban and Plymouth. Sediment was sieved (1000 μm mesh) in a seawater bath to remove macrofauna, allowed to settle for 24 h to retain the fine fraction (less than 63 μm) and homogenized. All species treatments were assembled in 12×12×35 cm (l×w×h) transparent acrylic aquaria, except for *P. elongata* which were assembled in 30×30×30 cm acrylic aquaria. All aquaria contained sediment to ~10 cm depth overlain with 22 cm of seawater (salinity 32 +/- 0.1, 10 µm filtered and UV sterilised). After 24 h and before addition of the fauna, 70 % of the overlying water was replaced to remove excess nutrients associated with assembly.

**Individual density and climate treatments.** To test the effect of individual density on trait-mediated processes, we assembled six monoculture species treatments across four representative natural densities (n = 3; 1 - 10 ind. aquarium-1, equivalent to 11 - 694 ind. m-2; Supplementary Figure 3, Supplementary Table 1). After accounting for mortality throughout the 62-day experiment, (mean: 11.6 ± 5.7 %; Supplementary Table 2), final individual densities were 1 - 7 ind. aquarium-1, or 11 - 486 ind. m-2. Water changes (50 % volume aquarium-1) were made weekly, and animals were fed three x week-1 with 5 ml aquarium-1 of microalgal mix consisting of *Tetraselmis* *suecica* and *Phaedactylum tricornutum* (~ 15 mg organic matter aquarium-1 week-1), equating to ~1.1 % of ash-free dry mass daily69,107. To test the combined effects of individual density and climate change, a subset of species (*N. hombergii*, *T. tricarinata* and *A. chiajei*; representing the three most abundant species at the sampling location) were maintained in either an ambient (12 °C, 410 ppm pCO2) or future climate (+ 2 °C warming, 550 ppm pCO2; Supplementary Figure 3) treatment based on IPCC model projections for 2100108. A subset of species were exposed to future climate conditions due to low numbers of individuals of some species imposing limitations on sufficient experimental replication. Atmospheric pCO2 was controlled and monitored every three mins using a LI-840 CO2 analyser (LI-COR). *In situ* pHNBS and salinity were measured every two weeks using a Seven2go S8 pH meter (Mettler Toledo) and a Cond 3310 conductivity and temperature meter (WTW), respectively. Total alkalinity (*A*T) was measured in 26 cores every three weeks throughout the 62-day experiment by autotitration (Apollo SciTech Alkalinity Titrator AS-ALK2) following standard protocols at the Carbonate Facility at the National Oceanography Centre, Southampton, UK. Carbonate chemistry parameters and methodologies for calculations are given in the supplementary information (Supplementary Table 3, Supplementary Figure 4).

**Response trait expression**

**Burial behaviour.** Individual burial behaviour, a proxy for an individual’s response to their environment19,109, was recorded using a benchtop mounted USB camera (uEYE USB camera, 1.3 MP, 25 FPS; IDS Imaging Development Systems, Obersulm, Germany) at the end of the experiment. Sediment and 5 cm of overlying water (both of the same origin as in experimental aquaria) were prepared in trays of the same surface area as the experimental aquaria (144 cm2) and equilibrated for 24 h before measurements to the relevant climate conditions in a temperature-controlled water bath, aerated with either ambient or CO2 enriched air. Burial behaviour was assessed by gently removing individuals from each aquarium through a 500 µm sieve before placing them at their experimental densities on the surface of pre-prepared, settled sediment and quantifying the time taken to start burying into the sediment (Burialstart).

**Ecosystem processes**

**Particle redistribution.** Sediment particle reworking depth was quantified using fluorescent-Sediment Profile Imaging (f-SPI)110. Fluorescent green particles (luminophores; θ < 200 µm, density 2.35 kg dm-3, Glass Pebbles Ltd., UK) were evenly spread across the sediment surface at a concentration of 0.417 g cm-2 (= 60 g aquarium-1). After 10 days, luminophore depth distributions were quantified for all four sides of each aquarium using a dSLR camera (Canon 400D: 2017, 15 s exposure, f5.6, ISO 400, 81 µm pixel-1) housed in a UV illuminated box111. Images were stitched together from composite images (RGB colour, JPEG compression; Supplementary Figures 5-10) for each aquarium, and luminophore depth profiles were generated (Supplementary Figure 11) using a customized script in ImageJ (v. 1.47 s), a java-based public domain program developed at the US National Institutes of Health (http://rsb.info.nih.gov/ij/index.html). From these data, the mean (f-SPI*L*mean, time dependent indication of mixing) and maximum (f-SPI*L*max, maximum extent of mixing over the long-term) mixed depth of particle redistribution was calculated. In addition, the maximum vertical deviation of the sediment-water interface (upper – lower limit, surface boundary roughness, SBR) provides an indication of surficial activity112.

**Bioirrigation.** Aggregate burrow ventilation activity was quantified by determining changes in seawater concentration of the inert tracer sodium bromide113 over an 8-hour period (8 h - 0 h) from an initial concentration of 10 mM (1.0289 g NaBr L-1). [Br-] was determined using a Tecator flow injection auto-analyser (FIA Star 5010). Negative ∆[Br-] values indicate an increase in net faunal ventilatory activity.

**Ecosystem functions**

**Nutrient release.** Water column nutrient concentrations (NH4-N, NOx-N and PO4-P; µmol L-1) were quantified over a 10-day period and determined in standardized water samples (10 cm water depth, 0.45 µm filtered) following standard procedures using a Lachat Quikchem 8500 flow-injection auto-analyser. In addition, we measured the mean depth of the apparent redox potential discontinuity (aRPD) based on the discrimination of sediment colour114,115 as an indicator of net oxidative state, assumed to be a good approximation of overall ecosystem condition116. Stitched images taken under white light (Canon 400D: 2017, 1s exposure, f5.6, ISO 100, 81 µm pixel-1) were analysed using a standard grey scale analysis procedure to delimit the aRPD117.

**Data analysis**

To investigate the effect of individual density and climate on functionally relevant behavioural trait expression and nutrient concentrations, we used linear mixed effects (LME) models which are robust to unbalanced experimental designs118. To account for mortality within treatments (Table S2), individual density was modelled as a continuous variable (co-factor) and statistical inference was determined using ANCOVA on data from distinct samples with the following structure: density (continuous) × climate (factor; two levels), random = species. Species identity was included as a random factor since we were not explicitly testing for differences between individual species, nor striving to characterize or speculate on the underlying causes of variation in traits between species. Prior to analyses, data were visually assessed for homogeneity of variance (residuals vs. fitted values) and normality (QQ plots)118. Where there was evidence of violation of homogeneity of variance, data were analysed using a VarIdent variance–covariate structure and a generalized least-squares (GLS) estimation procedure119 to allow the residual spread to vary with individual explanatory variables. The optimal variance-covariate structure was determined using restricted maximum likelihood (REML) estimation. Model improvement through incorporation of the variance structure was assessed using Akaike Information Criteria (AIC). Optimal model fixed and random structure was determined by backward selection using the L-ratio test with maximum likelihood (ML) estimation118. As Burialstart extended over five orders of magnitude, data were log-transformed prior to analysis so that Burialstart conformed to an appropriate scale. Control aquaria containing no fauna were excluded from statistical analyses of traits and processes (but not ecosystem functions) and are presented graphically for comparative purposes. Gaussian density plots were generated for Burialstart, ∆[Br-] and mean aRPD depth to visualise intraspecific variability using Kernel Density Estimation (KDE) procedures with biased cross-validation to select bandwidth120. To assess the impacts of trait-mediated processes on sediment physicochemical properties, the relationship between f-SPI*L*mean and aRPD depth was modelled using LME with species as a random factor and climate as a fixed factor. Intraspecific trait variability (ITV) across all six species was estimated by decomposition of sum of squares100. Briefly, this is obtained by comparing the sum of squares output from ANOVA (trait ~ species identity) associated with the model factor (inter-species) with the residual sum of squares (intra-species). The proportion of ITV attributed to conspecific density and climate treatment combined, was further estimated from LME models by calculation of marginal R*2,* which describes the proportion of variance explained by the fixed factor(s) alone. All data analyses were conducted within the R-programming environment121 using the R packages; ‘nlme’ and ‘ggplot2’119,122.

**Data availability**

All datasets generated and analysed in the current study are publicly available from the British Oceanographic Data Centre repository (doi: 10.5285/efa039d8-e411-724c-e053-6c86abc0317e).

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**Author contributions**

T.S. conceived and designed the study, conducted the experiments, data collection and analysis and drafted the manuscript. M.S and J.A.G. conceived and designed the study, and contributed to drafting the manuscript.

**Competing interests**

The authors declare no competing interests.

**Ethical compliance**

Ethical approval for this study was given internally by the University of Southampton’s ERGO 2 ethical approval system (#64297.A1).

**Figure captions**

**Figure 1. Individual burial times vary with conspecific density under future climate conditions.** (**a**) Time taken to start burial (log(Burialstart), seconds) in benthic marine invertebrates (*Paraleptopentacta elongata, Edwardsia claparedii, Sternaspis scutata, Amphiura chiajei, Nephtys hombergii* and *Turritellinella tricarinata*) maintained at different densities (1 - 7 ind. aquarium-1, 11 - 486 ind. m-2, n = 363). A subset of three species (*A. chiajei*, *N. hombergii* and *T. tricarinata*) were also exposed to two climate treatments (ambient 12 °C/410 ppm pCO2; future 14 °C/550 ppm pCO2). (**b**) Kernel Density Estimation (KDE) for log(Burialstart) of each species. Colours represent individual species and symbols depict ambient (circles) and future (triangles) climate conditions. In (**a**) Linear mixed effects model predictions are shown by solid lines for ambient and dashed lines for future climate treatments.

**Figure 2. The effect of climate treatment and conspecific density on particle reworking activity and bioirrigation.** Impact of conspecific densities (1 - 7 ind. aquarium-1, 11 - 486 ind. m-2, n = 114) in sediment dwelling invertebrates (*Paraleptopentacta elongata, Edwardsia claparedii, Sternaspis scutata, Amphiura chiajei, Nephtys hombergii* and *Turritellinella tricarinata*) and climate conditions (in a subset of species: *A. chiajei*, *N. hombergii* and *T. tricarinata*) ontrait-mediated bioturbation processes: (**a**) surface boundary roughness, SBR, (**b**) mean particle reworking depth (f-SPILmean), (**c**) maximum particle reworking depth (f-SPILmax) and (**d**) bioirrigation activity (∆[Br-]). Symbols denote ambient (circles, 12 °C/410 ppm pCO2) and future (triangles, 14 °C/550 ppm pCO2) climate conditions. Species-specific linear model predictions are shown in panels **a-c** with solid regression lines representing ambient climate and dashed lines representing future climate treatments. Distribution plots of Kernel Density Estimations (KDE) are shown for ∆[Br-] in panel (**d**). Vertical dotted lines separate controls (no macrofauna, black symbols) from species (coloured symbols) treatments.

**Figure 3**. **Sediment nutrient release is not impacted by increasing conspecific density or climate conditions.** Impact of macrofaunal species density (*Paraleptopentacta elongata, Edwardsia claparedii, Sternaspis scutata, Amphiura chiajei, Nephtys hombergii* and *Turritellinella tricarinata*; 1 - 7 ind. aquarium-1, 11 - 486 ind. m-2, n = 135) on seawater (**a**) [NH4-N], (**b**) [NOx-N] and (**c**) [PO4-P] concentrations under ambient (circles, 12 °C/410 ppm pCO2) versus future (triangles, 14 °C/550 ppm pCO2; in a subset of three species: *A. chiajei*, *N. hombergii* and *T. tricarinata*) climate conditions. Vertical dotted lines separate control cores containing no macrofauna from those containing macrofauna. Species are represented by colour, as indicated in the key. Linear mixed effects model predictions for ambient (solid lines) versus future (dashed lines) conditions are shown. Vertical dotted lines separate controls (no macrofauna) from species treatments.

**Figure 4. Deeper mean particle reworking correlates with a deeper redox potential discontinuity depth.** Relationship between mean aRPD depth and (**a**) mean particle reworking depth (f-SPILmean), (**b**) maximum particle reworking depth (f-SPILmax) and (**c**) surface boundary roughness (SBR) under ambient (circles, 12 °C/410 ppm pCO2, n = 35) and future (triangles, 14 °C/550 ppm pCO2, n = 69;in a subset of three species: *Amphiura chiajei*, *Nephtys hombergii* and *Turritellinella tricarinata*) climate conditions in the presence of different sediment invertebrate species (*Paraleptopentacta elongata, Edwardsia claparedii, Sternaspis scutata, A. chiajei, N. hombergii* and *T. tricarinata*). Black symbols represent control aquaria without macrofauna. In (**a**-**c**) Linear mixed effects model predictions are depicted for ambient (solid lines) versus future (dashed lines) climate conditions. Density distributions for mean aRPD depth based on Kernel Density Estimation (KDE) are shown in panel **d** for ambient (solid lines) and future conditions (dashed lines).

**Figure 5. Conspecific density and climate conditions drive 10 - 19 % of overall intraspecific variability.** Proportion of overall effect trait and ecological process variability attributed to between (interspecific, light grey) and within (intraspecific, dark grey) species variation estimated by decomposition of the Sum of Squares for the five measured traits (left to right: time to start burial, surface boundary roughness, mean particle reworking depth, maximum particle reworking depth, and ventilation activity). The proportion of variance explained by experimental treatments (density + climate, black) was estimated from marginal R2 values, a measure of model fixed effects.

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