

<https://doi.org/10.1038/s43247-024-01237-6>

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

Check for updates

Trystan Sanders <sup>1,2</sup>✉, Martin Solan <sup>1</sup> & Jasmin A. Godbold <sup>1</sup>

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 dependent 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.

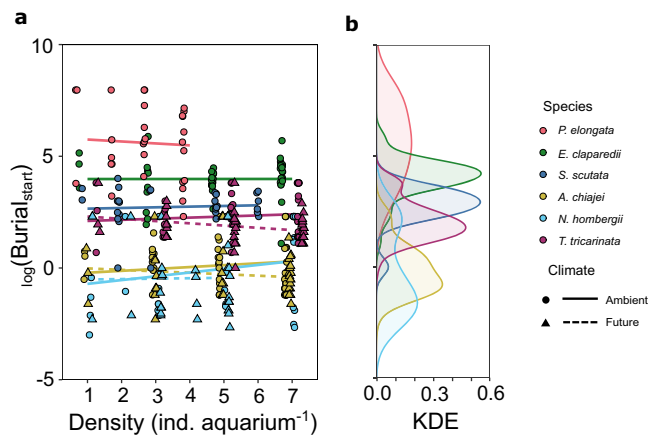
Grouping species by their functional traits - morphological, biochemical, physiological, structural, phenological or behavioural<sup>1,2</sup> - to infer or explain their influence on ecosystem functioning has a well-established history<sup>3,4</sup>, but trait-ecosystem function relationships are often built from fragmented information and seldom consider intraspecific variation in trait expression. Species that share traits do not necessarily form universally applicable functional effect groups<sup>5</sup>, as trait expression can depend on environmental and biotic setting<sup>6,7</sup>. Consequently, trait designations can lack relevance to, and be distinct from, what is observed in natural systems<sup>8–10</sup>. This oversight is surprising, as intraspecific trait variation is not only an important source of variation for species coexistence<sup>11</sup>, environmental filtering<sup>12</sup> and community assembly<sup>13</sup>, but some continuous traits, such as body size<sup>14</sup>, can determine an individual's contribution to ecosystem functioning<sup>15</sup> and extinction risk<sup>16</sup>. In addition, variation within a species can be as important as variation between species<sup>12,17–20</sup> and populations with greater genotypic variability can outperform those with fewer genotypes<sup>21</sup>, and enhance both ecosystem functioning and biodiversity of other trophic levels<sup>22</sup>. It is known that species' can modify their traits in response to environmental context (e.g. current velocity<sup>23</sup>, habitat configuration<sup>24–26</sup>, climate<sup>27,28</sup>) and/or biotic interactions (e.g. predation<sup>29,30</sup>, density<sup>19,31</sup>) which can disproportionately

influence how a community moderates ecosystem properties<sup>19,32–34</sup>. However, considerable gaps in understanding remain of how, when, and under what circumstances, differences in trait expression occur and lead to alternative functional outcomes<sup>35</sup>.

In response to changing abiotic and/or biotic conditions, species are also known to switch behaviour<sup>36</sup>, make physiological adjustments<sup>37</sup>, or undergo compensatory responses<sup>38</sup> as a precursor to<sup>39</sup>, and following, local alterations in species richness. Whilst the ecological consequences of altered diversity remains a strong focus in ecology<sup>40</sup>, including how the presence or absence of interspecific interactions promotes niche differentiation and ecosystem functioning<sup>41</sup>, 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 functions<sup>35,42–45</sup>. Temporal shifts in species abundance<sup>46,47</sup> can modify effect trait expression through altered synergistic or antagonistic conspecific interactions and consequential shifts in body mass and size<sup>48</sup>. While progress has been made in recent years on characterising the relevance of intraspecific trait variability to ecosystem functioning<sup>49,50</sup>, the extent to which abiotic (climate) and biotic (conspecific interactions) factors contribute to intraspecific effect trait variability and

<sup>1</sup>School of Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, European Way, Southampton SO14 3ZH, UK.

<sup>2</sup>Present address: Biosciences, University of Exeter, Exeter UK EX4 4QD, UK. ✉e-mail: [t.sanders3@exeter.ac.uk](mailto:t.sanders3@exeter.ac.uk)



**Fig. 1 | Individual burial times vary with conspecific density under future climate conditions.** **a** Time taken to start burial ( $\log(\text{Burial}_{\text{start}})$ , 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<sup>-1</sup>, 11–486 ind. m<sup>-2</sup>,  $n = 363$ ). A subset of three species (*A. chiajei*, *N. hombergii* and *T. tricarinata*) were also exposed to two climate treatments (ambient 12 °C/410 ppm pCO<sub>2</sub>; future 14 °C/550 ppm pCO<sub>2</sub>). **b** Kernel Density Estimation (KDE) for  $\log(\text{Burial}_{\text{start}})$  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.

related ecosystem processes is still poorly constrained, frustrating the inclusion of trait-variation in biodiversity-function research<sup>11</sup>.

Here, we determine the effect of conspecific density (11–486 ind. m<sup>-2</sup>) and near-term climate change (550 ppm pCO<sub>2</sub>, + 2 °C warming) on trait expression and trait-driven processes assumed to be important in the mediation of nutrient cycling<sup>51</sup> 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 (density<sup>7</sup>) and environmental conditions (climate<sup>27</sup>), but that the effect of individuals within a species would not be consistent as individual sensitivities to novel conditions vary<sup>19</sup>. 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<sup>-2</sup>) and future climate conditions (ambient: 12 °C, 410 ppm pCO<sub>2</sub> vs future: 14 °C, 550 ppm pCO<sub>2</sub>) 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, an 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  $\log(\text{Burial}_{\text{start}})$  ranged from three seconds (*Turritellinella tricarinata*, ambient, 208 ind. m<sup>-2</sup>, 3 ind. aquarium<sup>-1</sup>) to ~2 days (*Paraleptopentacta elongata*, ambient, 11 ind. m<sup>-2</sup>, 1 ind. aquarium<sup>-1</sup>), but depended on the interaction between species density and climate treatment (ANCOVA,  $F_{1,354} = 4.32$ ,  $p = 0.038$ ; Fig. 1a). Closer inspection of model coefficients indicated that, irrespective of species identity,  $\log(\text{Burial}_{\text{start}})$  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  $\log(\text{Burial}_{\text{start}})$  (coef. = 0.04,  $t = 0.79$ ,  $p = 0.149$ ; Supplementary Fig. 1). Kernel smoothing to derive probability density estimations (KDE), to visualise the distribution of intraspecific trait values, revealed species differences in  $\log(\text{Burial}_{\text{start}})$  variability (interquartile range, from 2.73 in *P. elongata* to 1.12 in *Sternaspis scutata*, Fig. 1b).

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

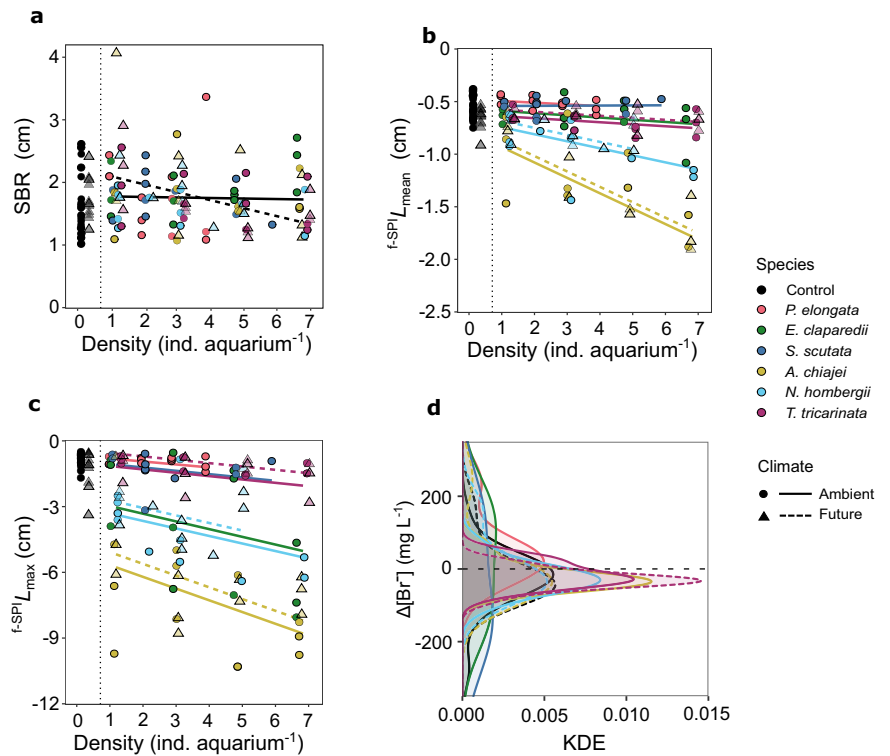
In general, faunally driven particle reworking activity was dependent on both conspecific density and climate treatment, but the magnitude of these effects varied between different aspects of species activities and depended on complex interactions between our explanatory variables. Surface boundary roughness (SBR) was dependent on an interaction between density and climate treatment (ANCOVA:  $F_{1,95} = 6.18$ ,  $p = 0.015$ ) with SBR decreasing with increasing density under future climate conditions (Fig. 2a). When species identity is treated as a random factor, the mean mixed depth of particle redistribution ( ${}^{\text{f-SPI}}L_{\text{mean}}$ ) increases with conspecific density (ANCOVA:  $F_{1,95} = 3.98$ ,  $p = 0.049$ ), but we identified species-specific responses of  ${}^{\text{f-SPI}}L_{\text{mean}}$  to density (L-ratio: 36.92, d.f. = 2,  $p < 0.001$ ).  ${}^{\text{f-SPI}}L_{\text{mean}}$  was deeper with increasing *Amphiura chiajei* (slope = -0.110) and *Nephtys 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  ${}^{\text{f-SPI}}L_{\text{mean}}$  values in future climate treatments relative to those in ambient treatments (ANCOVA:  $F_{1,95} = 3.68$ ,  $p = 0.058$ ; Fig. 2b). The maximum mixed depth of particle redistribution ( ${}^{\text{f-SPI}}L_{\text{max}}$ ) increased linearly with species density (ANCOVA:  $F_{1,96} = 7.93$ ,  $p = 0.010$ ; Fig. 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  ${}^{\text{f-SPI}}L_{\text{max}}$  was ~0.6 cm shallower in future climate treatments compared to ambient conditions (ANCOVA:  $F_{1,96} = 2.92$ ,  $p = 0.091$ ; Supplementary Fig. 2). KDE for ventilatory activity ( $\Delta[\text{Br}^-]$ ) provide evidence, in absolute terms, for active ventilatory activity (negative values, Fig. 2d), although this behaviour was not affected by conspecific density (ANCOVA:  $F_{1,91} = 0.58$ ;  $p = 0.447$ ) or climate treatment (ANCOVA:  $F_{1,91} = 0.73$ ,  $p = 0.397$ ).

### 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  $[\text{NH}_4\text{-N}]$  was dependent on climate treatment (ANCOVA:  $F_{1,95} = 50.82$ ,  $p < 0.001$ ), but not conspecific density (ANCOVA:  $F_{1,95} = 1.09$ ,  $p = 0.298$ ; Fig. 3a). Overall, mean ( $\pm$ SE)  $[\text{NH}_4\text{-N}]$  was lower under future climate conditions ( $10.80 \pm 0.26 \mu\text{mol L}^{-1}$ ) relative to ambient conditions ( $12.67 \pm 0.31 \mu\text{mol L}^{-1}$ ). Similarly, there was no effect of conspecific density on  $[\text{NO}_x\text{-N}]$  (ANCOVA:  $F_{1,96} = 2.27$ ,  $p = 0.135$ ) but, irrespective of species identity,  $[\text{NO}_x\text{-N}]$  was lower under future climate conditions (ANCOVA:  $F_{1,96} = 9.65$ ,  $p = 0.003$ ; Fig. 3b). Comparing model slopes using an L-ratio test revealed, for some species, weak effects of density on  $[\text{NO}_x\text{-N}]$  (L-ratio: 7.97, d.f. = 2,  $p = 0.019$ ; Fig. 3b). In contrast,  $[\text{PO}_4\text{-P}]$  was not dependent on species density (ANCOVA:  $F_{1,96} = 0.31$ ,  $p = 0.577$ ) or climate treatment (ANCOVA:  $F_{1,96} = 0.18$ ,  $p = 0.672$ ; Fig. 3c).

We used AIC to assess the suitability of trait-mediated particle reworking depth metrics (SBR,  ${}^{\text{f-SPI}}L_{\text{mean}}$  and  ${}^{\text{f-SPI}}L_{\text{max}}$ ) as predictors for

**Fig. 2 | The effect of climate treatment and conspecific density on particle reworking activity and bioirrigation.** Impact of conspecific densities (1–7 ind. aquarium<sup>-1</sup>, 11–486 ind. m<sup>-2</sup>,  $n = 114$ ) in sediment dwelling invertebrates (*Paraleptopentacta elongata*, *Edwardsia claparedii*, *Sternaspis scutata*, *Amphiura chiajei*, *Nephtys hombergii* and *Turritellina tricarinata*) and climate conditions (in a subset of species: *A. chiajei*, *N. hombergii* and *T. tricarinata*) on trait-mediated bioturbation processes: (a) surface boundary roughness, SBR, (b) mean particle reworking depth ( $f^{SPI}L_{mean}$ ), (c) maximum particle reworking depth ( $f^{SPI}L_{max}$ ) and (d) bioirrigation activity ( $\Delta[Br]$ ). Symbols denote ambient (circles, 12 °C/410 ppm pCO<sub>2</sub>) and future (triangles, 14 °C/550 ppm pCO<sub>2</sub>) 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  $\Delta[Br]$  in panel (d). Vertical dotted lines separate controls (no macrofauna, black symbols) from species (coloured symbols) treatments.



aRPD depth and results revealed that  $f^{SPI}L_{mean}$  explained the greatest amount of variability in aRPD depth (slope: ambient,  $1.31 \pm 0.22$  cm; future,  $1.23 \pm 0.25$  cm), but was dependent on the interaction between  $f^{SPI}L_{mean}$  and climate (ANCOVA interaction:  $F_{1,95} = 5.37$ ,  $p = 0.027$ ; Fig. 4a).  $f^{SPI}L_{max}$  displayed a weaker relationship with aRPD (slope: ambient,  $0.04 \pm 0.03$  cm; future,  $-0.04 \pm 0.25$  cm) but also depended on the interaction between  $f^{SPI}L_{max}$  and climate (ANCOVA interaction:  $F_{1,94} = 20.0$ ,  $p < 0.001$ ; Fig. 4b), while SBR was poor at explaining variability in aRPD (ANCOVA:  $F_{1,94} = 0.011$ ,  $p = 0.918$ ; Fig. 4c). Considering  $f^{SPI}L_{mean}$  as a predictor, aRPD was deeper and the gradient steeper under future conditions (intercept: ambient,  $0.627 \pm 0.25$  cm, future,  $0.709 \pm 0.26$  cm; slope: ambient,  $1.314 \pm 0.22$ , future,  $2.029 \pm 0.31$ ;  $t = 2.32$ ,  $p = 0.023$ ). 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* (Fig. 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 (Burial<sub>start</sub>, 29%; SBR, 89%;  $f^{SPI}L_{mean}$ , 41%;  $f^{SPI}L_{max}$ , 31%;  $\Delta[Br]$ , 88%; Fig. 5). For metrics associated with faunal mediated particle redistribution (SBR,  $f^{SPI}L_{mean}$ ,  $f^{SPI}L_{max}$ ), marginal  $R^2$  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 (Fig. 5).

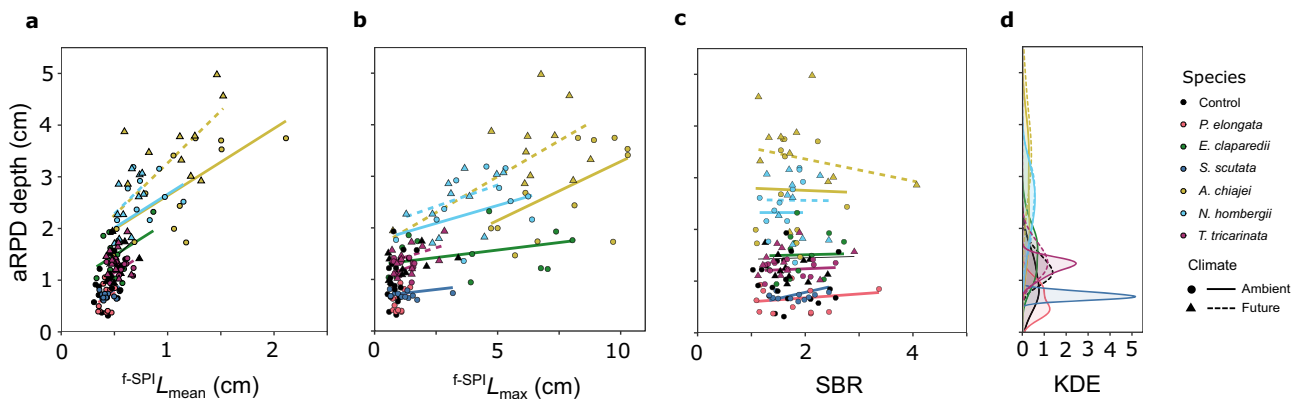
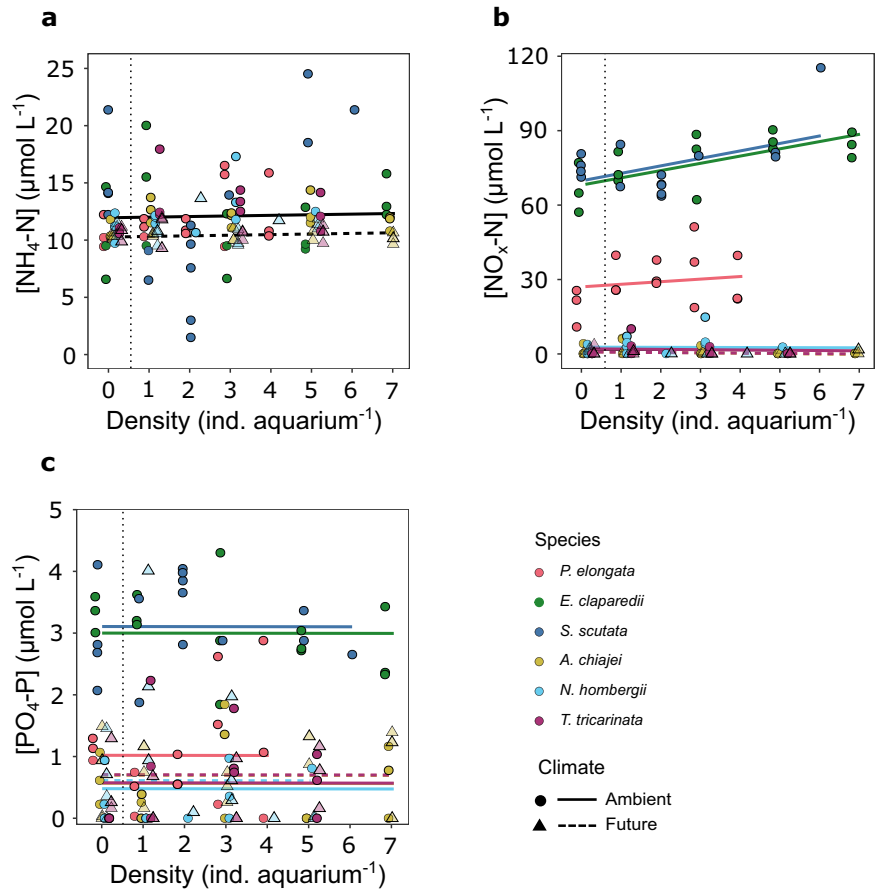
### Discussion

The measurable functional characteristics (traits) of organisms are not only used to make assessments of ecological conditions<sup>52,53</sup> but, increasingly, also to forecast future levels of ecological functioning<sup>54</sup>, particularly by those

interested in restoring or managing ecosystems for specific functions<sup>55–57</sup>. Whilst trait-based approaches that can quantify and predict ecological processes are both promising and needed<sup>10,58,59</sup>, it is often common practice to adopt categorical descriptors based on mean trait values (but see notable exceptions<sup>49,50,60</sup>). Here, however, we demonstrate that species-level functional characterisations fail to capture species-specific variation in response to changing abiotic and biotic circumstances<sup>61</sup>. 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 density<sup>62</sup>. 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 exceptions<sup>63</sup>, 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 community<sup>64–66</sup>. Indeed, there is evidence across a range of species and contexts that particle reworking activity and/or burrowing depth increases with density<sup>19,67–69</sup>. 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 functioning<sup>24,25,44,70–72</sup>. These changes are not necessarily aligned, even with assumed closely associated trait-function pairings<sup>73</sup>. 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 functioning<sup>74,75</sup>. This could be explained by changes in organism-environment interactions such as altered microbial diversity<sup>76</sup>, synergistic and/or antagonistic intraspecific interactions<sup>77</sup>, or the complexity of sediment biogeochemical processes that influence nutrient release which may

**Fig. 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<sup>-1</sup>, 11–486 ind. m<sup>-2</sup>, *n* = 135) on seawater (a) [NH<sub>4</sub>-N], (b) [NO<sub>x</sub>-N] and (c) [PO<sub>4</sub>-P] concentrations under ambient (circles, 12 °C/410 ppm pCO<sub>2</sub>) versus future (triangles, 14 °C/550 ppm pCO<sub>2</sub>) 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.

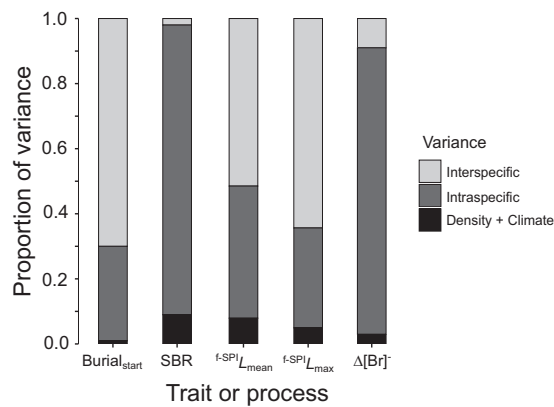


**Fig. 4 | Deeper mean particle reworking correlates with a deeper redox potential discontinuity depth.** Relationship between mean aRPD depth and (a) mean particle reworking depth ( $f\text{-SPI}L_{\text{mean}}$ ), (b) maximum particle reworking depth ( $f\text{-SPI}L_{\text{max}}$ ) and (c) surface boundary roughness (SBR) under ambient (circles, 12 °C/410 ppm pCO<sub>2</sub>, *n* = 35) and future (triangles, 14 °C/550 ppm pCO<sub>2</sub>, *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).

not correlate with simpler faunally driven processes<sup>78</sup>. 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 interactions<sup>79</sup> and suggest that density-dependent estimates of functioning are likely to considerably differ from equivalent estimates based on density-independent rates, as is commonly practiced<sup>80,81</sup>. Moreover, by ignoring density and other context-specific influences on functional trait expression and trait-mediated



**Fig. 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  $R^2$  values, a measure of model fixed effects.

processes, insignificant or weak trait-function relationships based on mean trait values run the risk of being misinterpreted as being unimportant<sup>82</sup>.

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 functions<sup>4,12,83</sup>. 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 tested<sup>8,10</sup>, and many functional group designations are not able to predict ecosystem functioning any better than a random allocation of categorical descriptors<sup>84</sup>, which may stem from inherent subjectivity in functional group categorisation<sup>85</sup>. 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 groups<sup>5</sup>. 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 elsewhere<sup>86,87</sup>. 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 change<sup>12</sup>.

Despite the well-established importance of intraspecific trait variability in functional diversity<sup>12,88</sup>, ecosystem functioning<sup>19</sup> and ecosystem services<sup>89</sup>, 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 ecosystems<sup>90,91</sup>. 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 stage<sup>92,93</sup>. These inherent sources of individual variability have long been excluded from trait-based approaches to ecosystem functioning research<sup>94,95</sup>, despite the well-established influence of both phenotypic plasticity and genotypic variation on individual trait expression<sup>96,97</sup>. We reveal substantial plasticity in functionally important trait-mediated processes suggesting that expression of effect traits can be mediated by biotic interactions between conspecifics<sup>19,81</sup> and/or between species<sup>77,98</sup>. 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 means<sup>94</sup>, or employing variance partitioning equations<sup>99</sup> using similar methodologies to this study<sup>100</sup>. 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 importance<sup>101,102</sup>. If we are to predict the consequences of changing environmental conditions, more emphasis is needed on empirically deriving the mechanistic basis of trait-function relationships<sup>103,104</sup> and in recognising that species functional activities are not set at discrete levels but vary along a continuum<sup>105</sup> and over time<sup>106</sup> 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* from Loch Linnhe, Oban (56°29'33"N 5°30'19"W, depth: 35 m) using a 0.1 m<sup>2</sup> van Veen grab. Individuals were transported to the University of Southampton's *Biodiversity and Ecosystem Futures Facility* at low density in continually aerated 20 L 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<sup>-1</sup> with a mixed algal diet consisting of *Tetraselmis suecica* and *Phaeodactylum tricorutum*. As species behaviour can depend on site-specific sediment properties<sup>7</sup>, 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<sup>-1</sup>, equivalent to 11–694 ind. m<sup>-2</sup>; Supplementary Fig. 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<sup>-1</sup>, or 11–486 ind. m<sup>-2</sup>. Water changes (50% volume aquarium<sup>-1</sup>) were made

weekly, and animals were fed three times week<sup>-1</sup> with 5 ml aquarium<sup>-1</sup> of microalgal mix consisting of *Tetraselmis suecica* and *Phaedactylum tricorutum* (~15 mg organic matter aquarium<sup>-1</sup> week<sup>-1</sup>), equating to ~1.1% of ash-free dry mass daily<sup>69,107</sup>. 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 pCO<sub>2</sub>) or future climate (+ 2 °C warming, 550 ppm pCO<sub>2</sub>; Supplementary Fig. 3) treatment based on IPCC model projections for 2100<sup>108</sup>. 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 pCO<sub>2</sub> was controlled and monitored every three mins using a LI-840 CO<sub>2</sub> analyser (LI-COR). In situ pH<sub>NBS</sub> 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<sub>T</sub>) 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 Fig. 4).

### Response trait expression

**Burial behaviour.** Individual burial behaviour, a proxy for an individual's response to their environment<sup>19,109</sup>, was recorded using a benchtop mounted USB camera (µEYE 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 cm<sup>2</sup>) and equilibrated for 24 h before measurements to the relevant climate conditions in a temperature-controlled water bath, aerated with either ambient or CO<sub>2</sub> 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 (Burial<sub>start</sub>).

### Ecosystem processes

**Particle redistribution.** Sediment particle reworking depth was quantified using fluorescent-Sediment Profile Imaging (f-SPI)<sup>110</sup>. Fluorescent green particles (luminophores;  $\theta < 200 \mu\text{m}$ , density 2.35 kg dm<sup>-3</sup>, Glass Pebbles Ltd., UK) were evenly spread across the sediment surface at a concentration of 0.417 g cm<sup>-2</sup> (= 60 g aquarium<sup>-1</sup>). 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<sup>-1</sup>) housed in a UV illuminated box<sup>111</sup>. Images were stitched together from composite images (RGB colour, JPEG compression; Supplementary Fig. 5–10) for each aquarium, and luminophore depth profiles were generated (Supplementary Fig. 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 ( $f\text{-SPI}L_{\text{mean}}$ , time dependent indication of mixing) and maximum ( $f\text{-SPI}L_{\text{max}}$ , 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 activity<sup>112</sup>.

**Bioirrigation.** Aggregate burrow ventilation activity was quantified by determining changes in seawater concentration of the inert tracer sodium bromide<sup>113</sup> over an 8-hour period (8 h–0 h) from an initial concentration of 10 mM (1.0289 g NaBr L<sup>-1</sup>). [Br<sup>-</sup>] was determined using a Tecator flow injection auto-analyser (FIA Star 5010). Negative  $\Delta[\text{Br}^-]$  values indicate an increase in net faunal ventilatory activity.

### Ecosystem functions

**Nutrient release.** Water column nutrient concentrations (NH<sub>4</sub>-N, NO<sub>x</sub>-N and PO<sub>4</sub>-P; µmol L<sup>-1</sup>) 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 colour<sup>114,115</sup> as an indicator of net oxidative state, assumed to be a good approximation of overall ecosystem condition<sup>116</sup>. Stitched images taken under white light (Canon 400D: 2017, 1 s exposure, f5.6, ISO 100, 81 µm pixel<sup>-1</sup>) were analysed using a standard grey scale analysis procedure to delimit the aRPD<sup>117</sup>.

### 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 designs<sup>118</sup>. 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)<sup>118</sup>. 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 procedure<sup>119</sup> 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) estimation<sup>118</sup>. As Burial<sub>start</sub> extended over five orders of magnitude, data were log-transformed prior to analysis so that Burial<sub>start</sub> 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 Burial<sub>start</sub>,  $\Delta[\text{Br}^-]$  and mean aRPD depth to visualise intraspecific variability using Kernel Density Estimation (KDE) procedures with biased cross-validation to select bandwidth<sup>120</sup>. To assess the impacts of trait-mediated processes on sediment physicochemical properties, the relationship between  $f\text{-SPI}L_{\text{mean}}$  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 squares<sup>100</sup>. 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<sup>2</sup>, which describes the proportion of variance explained by the fixed factor(s) alone. All data analyses were conducted within the R-programming environment<sup>121</sup> using the R packages; 'nlme' and 'ggplot2'<sup>119,122</sup>.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

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

Received: 11 October 2023; Accepted: 23 January 2024;

Published online: 12 February 2024

## References

- Nock, C. A., Vogt, R. J. & Beisner, B. E. *Functional traits*, Vol. 1, eLS. John Wiley & Sons (2016).
- Kelly, M. Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Philos. Trans. R. Soc. B* **374**, 20180176 (2019).
- Enquist, B. J. et al. A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* **449**, 218–222 (2007).
- McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185 (2006).
- Murray, F., Douglas, A. & Solan, M. Species that share traits do not necessarily form distinct and universally applicable functional effect groups. *Mar. Ecol. Prog. Ser.* **516**, 23–34 (2014).
- Helsen, K. et al. Biotic and abiotic drivers of intraspecific trait variation within plant populations of three herbaceous plant species along a latitudinal gradient. *BMC Ecology* **17**, 38 (2017).
- Wohlgemuth, D., Solan, M. & Godbold, J. A. Species contributions to ecosystem process and function can be population dependent and modified by biotic and abiotic setting. *Proc. R. Soc. B.* **284**, 20162805 (2017).
- Hale, R., Mavrogordato, M. N., Tolhurst, T. J. & Solan, M. Characterizations of how species mediate ecosystem properties require more comprehensive functional effect descriptors. *Sci. Rep.* **4**, 6463 (2014).
- de Juan, S. et al. Biological traits approaches in benthic marine ecology: dead ends and new paths. *Ecol. Evol.* **12**, e9001 (2022).
- Streit, R. P. & Bellwood, D. R. To harness traits for ecology, let's abandon 'functionality'. *Trends Ecol. Evol.* **38**, 402–411 (2023).
- Bolnick, D. I. et al. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* **26**, 183–192 (2011).
- Violle, C. et al. The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* **27**, 244–252 (2012).
- Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. Intraspecific variability and trait-based community assembly. *J. Ecol.* **98**, 1134–1140 (2010).
- Hébert, M. P., Beisner, B. E. & Maranger, R. A meta-analysis of zooplankton functional traits influencing ecosystem function. *Ecology* **97**, 1069–1080 (2016).
- Seguin, A., Harvey, E., Archambault, P., Nozais, C. & Gravel, D. Body size as a predictor of species loss effect on ecosystem functioning. *Sci. Rep.* **4**, 4616 (2014).
- Solan, M. et al. Extinction and ecosystem function in the marine benthos. *Science* **306**, 1177–1180 (2004).
- Albert, C. H. et al. Intraspecific functional variability: extent, structure and sources of variation. *J. Ecol.* **98**, 604–613 (2010).
- Dong, Y.-W. et al. Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. *Proc. R. Soc. B.* **284**, 20162367 (2017).
- Cassidy, C., Grange, L. J., Garcia, C., Bolam, S. G. & Godbold, J. A. Species interactions and environmental context affect intraspecific behavioural trait variation and ecosystem function. *Proc. R. Soc. B.* **287**, 20192143 (2020).
- Des Roches, S. et al. The ecological importance of intraspecific variation. *Nat. Ecol. Evol.* **2**, 57–64 (2018).
- Wilkinson, A., Solan, M., Taylor, A. F. S., Alexander, I. J. & Johnson, D. Intraspecific diversity regulates fungal productivity and respiration. *PLoS ONE* **5**, e12604 (2010).
- Crutsinger, G. M. et al. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313**, 966–968 (2006).
- Orejas, C. et al. The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia Pertusa*. *J. Exp. Mar. Biol. Ecol.* **481**, 34–40 (2016).
- Bulling, M. T. et al. Species effects on ecosystem processes are modified by faunal responses to habitat composition. *Oecologia* **158**, 511–520 (2008).
- Godbold, J. A., Bulling, M. T. & Solan, M. Habitat structure mediates biodiversity effects on ecosystem properties. *Proc. R. Soc. B.* **278**, 2510–2518 (2011).
- Caliman, A., Carneiro, L. S., Bozelli, R. L., Farjalla, V. F. & Esteves, F. A. Bioturbating space enhances the effects of non-additive interactions among benthic ecosystem engineers on cross-habitat nutrient regeneration. *OIKOS* **120**, 1639–1648 (2011).
- Godbold, J. A. & Solan, M. Long-term effects of warming and ocean acidification are modified by seasonal variation in species responses and environmental conditions. *Philos. Trans. R. Soc. B* **368**, 20130186 (2013).
- Godbold, J. A., Hale, R., Wood, C. L. & Solan, M. Vulnerability of macronutrients to the concurrent effects of enhanced temperature and atmospheric pCO<sub>2</sub> in representative shelf sea sediment habitats. *Biogeochemistry* **135**, 89–102 (2017).
- Maire, O. et al. Indirect effects of non-lethal predation on bivalve activity and sediment reworking. *J. Exp. Mar. Biol. Ecol.* **395**, 30–36 (2010).
- Stief, P. & Hoelker, F. Trait-mediated indirect effects of predatory fish on microbial mineralization in aquatic sediments. *Ecology* **87**, 3152–3159 (2006).
- Caliman, A. et al. Community biomass and bottom up multivariate nutrient complementarity mediate the effects of bioturbator diversity on pelagic production. *PLOS ONE* **7**, e44925 (2012).
- Langenheder, S., Bulling, M. T., Solan, M. & Prosser, J. I. Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. *PLoS ONE* **5**, e10834 (2010).
- Hull, P. M., Darroch, S. A. & Erwin, D. H. Rarity in mass extinctions and the future of ecosystems. *Nature* **528**, 345–351 (2015).
- McConkey, K. R. & O'Farrill, G. Cryptic function loss in animal populations. *Trends Ecol. Evol.* **30**, 182–189 (2015).
- Suding, K. N. et al. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.* **14**, 1125–1140 (2008).
- Wong, B. B. & Candolin, U. Behavioral responses to changing environments. *Behav. Ecol.* **26**, 665–673 (2015).
- Van Dievel, M., Janssens, L. & Stoks, R. Short- and long-term behavioural, physiological and stoichiometric responses to predation risk indicate chronic stress and compensatory mechanisms. *Oecologia* **181**, 347–357 (2016).
- Thomsen, M. S. et al. Consequences of biodiversity loss diverge from expectation due to post-extinction compensatory responses. *Sci. Rep.* **7**, 43695 (2017).
- Gonzalez, A. & Loreau, M. The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Evol. Syst.* **40**, 393–414 (2009).
- Cardinale, B. J. et al. Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
- Zuppinge-Dingley, D. et al. Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* **515**, 108–111 (2014).
- Walther, G.-R. Community and ecosystem responses to recent climate change. *Philos. Trans. R. Soc. B* **365**, 2019–2024 (2010).
- Langenheder, S., Bulling, M. T., Prosser, J. I. & Solan, M. Role of functionally dominant species in varying environmental regimes: evidence for the performance-enhancing effect of biodiversity. *BMC Ecol.* **12**, 14 (2012).
- Wohlgemuth, D., Solan, M. & Godbold, J. A. Specific arrangements of species dominance can be more influential than evenness in

- maintaining ecosystem process and function. *Sci. Rep.* **6**, 39325 (2016).
45. Polley, H. W., Wilsey, B. J. & Derner, J. D. Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecol. Lett.* **6**, 248–256 (2003).
  46. Harley, C. D. et al. S. L. The impacts of climate change in coastal marine systems. *Ecol. Lett.* **9**, 228–241 (2006).
  47. Bowler, D. E. et al. Cross-realm assessment of climate change impacts on species' abundance trends. *Nat. Ecol. Evol.* **1**, 0067 (2017).
  48. Woodward, G. et al. Body size in ecological networks. *Trends Ecol. Evol.* **20**, 402–409 (2005).
  49. Raffard, A., Santoul, F., Cucherousset, J. & Blanchet, S. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biol. Rev.* **94**, 648–661 (2019).
  50. Govaert, L., Hendry, A. P., Fattahi, F. & Möst, M. Quantifying interspecific and intraspecific diversity effects on ecosystem functioning. *Ecology* **105**, e4199 (2023).
  51. Snelgrove, P. V. R. et al. Global carbon cycling on a heterogeneous seafloor. *Trends Ecol. Evol.* **33**, 96–105 (2018).
  52. Bremner, J. Species' traits and ecological functioning in marine conservation and management. *J. Exp. Mar. Biol. Ecol.* **366**, 37–47 (2008).
  53. Gogina, M. et al. Towards benthic ecosystem functioning maps: quantifying bioturbation potential in the German part of the Baltic Sea. *Ecol. Indic.* **73**, 574–588 (2017).
  54. Elsen, P. R. et al. Accelerated shifts in terrestrial life zones under rapid climate change. *Glob. Change Biol.* **28**, 918–935 (2022).
  55. Temmink, R. J. M. et al. Mimicry of emergent traits amplifies coastal restoration success. *Nat. Comm.* **11**, 3668 (2020).
  56. Leuzinger, S. & Rewald, B. The who or the how? Species vs. ecosystem function priorities in conservation ecology. *Front. Plant Sci.* **12**, 758413 (2021).
  57. Kelley, J. L., Grierson, P. F., Collin, S. P. & Davies, P. M. Habitat disruption and the identification and management of functional trait changes. *Fish Fish.* **19**, 716–728 (2018).
  58. Miatta, M., Bates, A. E. & Snelgrove, P. V. R. Incorporating biological traits into conservation strategies. *Annu. Rev. Mar. Sci.* **13**, 421–443 (2021).
  59. Beauchard, O., Verissimo, H., Queirós, A. M. & Herman, P. M. J. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecol. Indic.* **76**, 81–96 (2017).
  60. Siefert, A. et al. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.* **18**, 1406–1419 (2015).
  61. Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I. & LeRoy Poff, N. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.* **13**, 267–283 (2010).
  62. Frances, D. N., Barber, A. J. & Tucker, C. M. Trait–density relationships explain performance in cladoceran zooplankton. *Ecology* **102**, e03294 (2021).
  63. Ryznar, E. R., Smith, L. L., Hà, B. A., Grier, S. R. & Fong, P. Functional trait variability supports the use of mean trait values and identifies resistance trade-offs for marine macroalgae. *J. Ecol.* **111**, 2049–2063 (2023).
  64. O'Connor, N. E. & Crowe, T. P. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology* **86**, 1783–1796 (2005).
  65. Winfree, R. et al. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* **18**, 626–635 (2015).
  66. Naeem, S. & Wright, J. P. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.* **6**, 567–579 (2003).
  67. Braeckman, U. et al. Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. *Mar. Ecol. Prog. Ser.* **399**, 173–186 (2010).
  68. De Backer, A. et al. Bioturbation effects of *Corophium volutator*: Importance of density and behavioural activity. *Estuar. Coast. Shelf Sci.* **91**, 306–313 (2011).
  69. Calder-Potts, R. N. et al. Density-dependent responses of the brittlestar *Amphiura filiformis* to moderate hypoxia and consequences for nutrient fluxes. *Mar. Ecol. Prog. Ser.* **594**, 175–191 (2018).
  70. Cardinale, B. J., Ives, A. R. & Inchausti, P. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos* **104**, 437–450 (2004).
  71. Weis, J. J., Cardinale, B. J., Forshay, K. J. & Ives, A. R. Effects of species diversity on community biomass production change over the course of succession. *Ecology* **88**, 929–939 (2007).
  72. Murray, F., Widdicombe, S., McNeill, C. L. & Douglas, A. Assessing the consequences of environmental impacts: variation in species responses has unpredictable functional effects. *Mar. Ecol. Prog. Ser.* **583**, 35–47 (2017).
  73. Solan, M., Batty, P., Bulling, M. & Godbold, J. A. How biodiversity affects ecosystem processes: implications for ecological revolutions and benthic ecosystem function. *Aquat. Biol.* **2**, 289–301 (2008).
  74. Teal, L. R., Parker, E. R. & Solan, M. Sediment mixed layer as a proxy for benthic ecosystem process and function. *Mar. Ecol. Prog. Ser.* **414**, 27–40 (2010).
  75. Teal, L. R., Parker, E. R. & Solan, M. Coupling bioturbation activity to metal (Fe and Mn) profiles in situ. *Biogeosciences* **10**, 2365–2378 (2013).
  76. Pérez-Izquierdo, L. et al. Plant intraspecific variation modulates nutrient cycling through its below ground rhizospheric microbiome. *J. Ecol.* **107**, 1594–1605 (2019).
  77. Clare, D. S., Spencer, M., Robinson, L. A. & Frid, C. L. J. Species densities, biological interactions and benthic ecosystem functioning: an in situ experiment. *Mar. Ecol. Prog. Ser.* **547**, 149–161 (2016).
  78. Caliman, A. et al. Biodiversity effects of ecosystem engineers are stronger on more complex ecosystem processes. *Ecology* **94**, 1977–1985 (2013).
  79. Little, C. J., Fronhofer, E. A. & Altermatt, F. Nonlinear effects of intraspecific competition alter landscape-wide scaling up of ecosystem function. *Am. Nat.* **195**, 432–444 (2020).
  80. Duport, E., Stora, G., Tremblay, P. & Gilbert, F. Effects of population density on the sediment mixing induced by the gallery-diffuser *Hediste (Nereis) diversicolor* O.F. Müller, 1776. *J. Exp. Mar. Biol. Ecol.* **336**, 33–41 (2006).
  81. Needham, H. R., Pilditch, C. A., Lohrer, A. M. & Thrush, S. F. Context-specific bioturbation mediates changes to ecosystem functioning. *Ecosystems* **14**, 1096–1109 (2011).
  82. Yang, J., Cao, M. & Swenson, N. G. Why functional traits do not predict tree demographic rates. *Trends Ecol. Evol.* **33**, 326–336 (2018).
  83. Gagic, V. et al. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B.* **282**, 20142620 (2015).
  84. Wright, J. P. et al. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecol. Lett.* **9**, 111–120 (2006).
  85. Ladds, M. A., Sibanda, N., Arnold, R. & Dunn, M. R. Creating functional groups of marine fish from categorical traits. *PeerJ* **6**, e5795–e5795 (2018).
  86. Kamimura, S. & Tsuchiya, M. The effect of feeding behavior of the gastropods *Batillaria zonalis* and *Cerithideopsisilla cingulata* on their ambient environment. *Mar. Biol.* **144**, 705–712 (2004).
  87. Rigolet, C., Thiébaud, E. & Dubois, S. F. Food web structures of subtidal benthic muddy habitats: evidence of microphytobenthos contribution supported by an engineer species. *Mar. Ecol. Prog. Ser.* **500**, 25–41 (2014).



88. Pichon, N. A., Cappelli, S. L. & Allan, E. Intraspecific trait changes have large impacts on community functional composition but do not affect ecosystem function. *J. Ecol.* **110**, 644–658 (2022).
89. Des Roches, S., Pendleton, L. H., Shapiro, B. & Palkovacs, E. P. Conserving intraspecific variation for nature's contributions to people. *Nat. Ecol. Evol.* **5**, 574–582 (2021).
90. Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G. & Violle, C. When and how should intraspecific variability be considered in trait-based plant ecology? *PPEES* **13**, 217–225 (2011).
91. Wong, M. K. L. & Carmona, C. P. Including intraspecific trait variability to avoid distortion of functional diversity and ecological inference: lessons from natural assemblages. *Methods. Ecol. Evol.* **12**, 946–957 (2021).
92. Rudolf, V. H. & Rasmussen, N. L. Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* **94**, 1046–1056 (2013).
93. Fritschie, K. J. & Olden, J. D. Disentangling the influences of mean body size and size structure on ecosystem functioning: an example of nutrient recycling by a non-native crayfish. *Ecol. Evol.* **6**, 159–169 (2016).
94. Moran, E. V., Hartig, F. & Bell, D. M. Intraspecific trait variation across scales: implications for understanding global change responses. *Glob. Chang Biol.* **22**, 137–150 (2016).
95. Chacón-Labela, J. et al. How to improve scaling from traits to ecosystem processes. *Trends Ecol. Evol.* **38**, 228–237 (2023).
96. Reusch, T. B. H. Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evol. Appl.* **7**, 104–122 (2014).
97. Foster, S. A. & Baker, J. A. Loss and re-emergence of plastic ancestral behavioural traits: influences on phenotypic and evolutionary pattern. *Anim. Behav.* **155**, 271–277 (2019).
98. Schenone, S., O'Meara, T. A. & Thrush, S. F. Non-linear effects of macrofauna functional trait interactions on biogeochemical fluxes in marine sediments change with environmental stress. *Mar. Ecol. Prog. Ser.* **624**, 13–21 (2019).
99. Read, Q. D., Henning, J. A. & Sanders, N. J. Intraspecific variation in traits reduces ability of trait-based models to predict community structure. *J. Veg. Sci.* **28**, 1070–1081 (2017).
100. de Bello, F. et al. Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods Ecol. Evol.* **2**, 163–174 (2011).
101. Mlambo, M. C. Not all traits are 'functional': insights from taxonomy and biodiversity-ecosystem functioning research. *Biodivers. Conserv.* **23**, 781–790 (2014).
102. Mouillot, D. et al. The dimensionality and structure of species trait spaces. *Ecol. Lett.* **24**, 1988–2009 (2021).
103. Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* **16**, 545–556 (2002).
104. Urban, M. C. et al. Improving the forecast for biodiversity under climate change. *Science* **353**, aad8466 (2016).
105. Picard, N., Köhler, P., Mortier, F. & Gourlet-Fleury, S. A comparison of five classifications of species into functional groups in tropical forests of French Guiana. *Ecol. Complex.* **11**, 75–83 (2012).
106. Dupont, L., Thierry, M., Zinger, L., Legrand, D. & Jacob, S. Beyond reaction norms: the temporal dynamics of phenotypic plasticity. *Trends Ecol. Evol.* **39**, 41–51 (2023).
107. Reed, A. J., Godbold, J. A., Solan, M. & Grange, L. J. Invariant gametogenic response of dominant infaunal bivalves from the Arctic under ambient and near-future climate change conditions. *Front. Mar. Sci.* **8**, 576746 (2021).
108. Bindoff, N. L., et al. Changing Ocean, Marine Ecosystems, and Dependent Communities. in IPCC Special Report on the Ocean and Cryosphere in a Changing Climate (ed Roberts D. C. Pörtner H.-O., Masson-Delmotte V., Zhai P., Tignor M., Poloczanska E., Mintenbeck K., Alegría A., Nicolai M., Okem A., Petzold J., Rama B., Weyer N.M.) Ch. 5, (IPCC, 2019).
109. Padilla, D. K. & Svedo, M. M. Chapter two - a systematic review of phenotypic plasticity in marine invertebrate and plant systems. *Adv. Mar. Biol.* **65**, 67–94 (2013).
110. Solan, M. et al. R. In situ quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. *Mar. Ecol. Prog. Ser.* **271**, 1–12 (2004).
111. Schiffrers, K., Teal, L. R., Travis, J. M. J. & Solan, M. An open source simulation model for soil and sediment bioturbation. *PLoS ONE* **6**, e28028 (2011).
112. Diaz, R. J. & Schaffner, L. C. Comparison of sediment landscapes in Chesapeake Bay as seen by surface and profile imaging, Vol. 163, *Virginia Institute of Marine Science Books and Book Chapters*, (1988).
113. Forster, S., Glud, R. N., Gundersen, J. K. & Huettel, M. In situ study of bromide tracer and oxygen flux in coastal sediments. *Estuar. Coast. Shelf Sci.* **49**, 813–827 (1999).
114. Lyle, M. The brown-green color transition in marine sediments: a marker of the Fe (III)-Fe (II) redox boundary 1. *Limnol. Oceanogr.* **28**, 1026–1033 (1983).
115. Gerwing, T. G. et al. Depth to the apparent redox potential discontinuity (aRPD) as a parameter of interest in marine benthic habitat quality models. *Int. J. Sediment Res.* **33**, 149–156 (2018).
116. Rhoads, D. C. & Germano, J. D. Characterization of organism-sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (REMOTS(TM) System). *Mar. Ecol. Prog. Ser.* **8**, 115–128 (1982).
117. Solan, M. & Kennedy, R. Observation and quantification of in situ animal-sediment relations using time-lapse sediment profile imagery (t-SPI). *Mar. Ecol. Prog. Ser.* **228**, 179–191 (2002).
118. Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed effects models and extensions in ecology with R*, Vol. 574, Springer, (2009).
119. Pinheiro, J. C., Bates, D. M. & R Core Team. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-162. <https://CRAN.R-project.org/package=nlme> (2023).
120. Guidoum, A. C. kedd: kernel estimator and bandwidth selection for density and its derivatives. R package version 1.0.3. <https://CRAN.R-project.org/package=kedd> (2015).
121. R Core Team R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, (2021).
122. Wickham, H. ggplot2: Elegant Graphics for Data Analysis. R package version 3.4.4. <https://CRAN.R-project.org/package=ggplot2> (2016).

## Acknowledgements

We are grateful to Michael McGibbon (University of Aberdeen) for nutrient and bromide analysis, Chris Rolfe (University of Cambridge) for sediment analysis and the crew of r.v. *MBA Sepia* for assisting field sampling. We also thank Chloe Smithers and Amy Swift (University of Southampton) for supporting laboratory work. This work was funded by the 'Implications of intraspecific trait variability across different environmental conditions for projections of marine ecosystem futures' project (NE/T001577/1), Natural Environment Research Council (NERC), UK. For the purpose of open access, the authors have applied a CC BY public copyright licence to any Author Accepted Manuscript version arising from this submission.

## 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).

### Additional information

**Supplementary information** The online version contains supplementary material available at

<https://doi.org/10.1038/s43247-024-01237-6>.

**Correspondence** and requests for materials should be addressed to Trystan Sanders.

**Peer review information** *Communications Earth & Environment* thanks Stefano Schenone and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Primary Handling Editors: Olivier Sulpis, Joe Aslin and Clare Davis. A peer review file is available.

**Reprints and permissions information** is available at <http://www.nature.com/reprints>

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2024