

1 **Ocean warming and acidification adjust inter- and intra-specific variability in the functional trait**
2 **expression of polar invertebrates**

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26 Climate change is known to affect the distribution and composition of species, but concomitant
27 alterations to functionally important aspects of behaviour and species-environment relations are
28 poorly constrained. Here, we examine the ecosystem ramifications of changes in sediment-dwelling
29 invertebrate bioturbation behaviour - a key process mediating nutrient cycling – associated with
30 near-future environmental conditions (+1.5 °C, 550 ppm [pCO₂]) for species from polar regions
31 experiencing rapid rates of climate change. We find that responses to warming and acidification vary
32 between species and lead to a reduction in intra-specific variability in behavioural trait expression
33 that adjusts the magnitude and direction of nutrient concentrations. Our analyses also indicate that
34 species behaviour is not predetermined, but can be dependent on local variations in environmental
35 history that set population capacities for phenotypic plasticity. We provide evidence that certain, but
36 subtle, aspects of inter- and intra-specific variations in behavioural trait expression, rather than the
37 presence or proportional representation of species *per se*, is an important and under-appreciated
38 determinant of benthic biogeochemical responses to climate change. Such changes in species
39 behaviour may act as an early warning for impending ecological transitions associated with
40 progressive climate forcing.

41

42 **1 | Introduction**

43 Narratives of the ecological consequences of climate change often centre on biodiversity, food-web
44 structure and productivity [1-3], rather than the ecological consequences of alternative outcomes
45 that typically form the prelude to compositional restructuring and/or altered levels of biodiversity [4-
46 5]. Species responses to a changing climate can include avoidance through dispersal [6], acclimation
47 through phenotypic plasticity [7-8], including adjustments to physiological regulation [9], and
48 adaptation through genetic modification [10]. However, these alternative strategies are not always
49 viable or, when available, are not necessarily equally weighted as an effective means of response
50 [11]. Indeed, in areas of greater risk from environmental change, such as those at higher latitudes,
51 opportunities for dispersal (including instances of > 40 days, [12]) and adaptation are often limited

52 due to local evolutionary history and ecology [13], meaning that phenotypic plasticity becomes the
53 *de facto* mechanism of response [14]. For organisms with very long generation times, as is common
54 in polar regions [15-16], behavioural acclimatisation can maximise an individual's chance of survival
55 [17-18] in advance of genetic adaptation [19], unless fecundity is sufficient to increase the likelihood
56 that gene adaptations arise in the population [20]. Previous work mainly focuses on invertebrate
57 physiological plasticity in relation to ocean warming [21-22] and acidification [23-25], with less
58 emphasis on behavioural plasticity [26], even though changes in behaviour often form the first
59 practical response to altered environmental context [27-28] and can have consequences for other
60 ecosystem attributes [29]. Consequently, the specifics of how and when climate related change
61 affects the way in which species behaviour modifies ecosystem functioning is under-appreciated [30-
62 31].

63

64 The activities of sediment-dwelling invertebrates redistribute pore water fluids and sediment
65 particles, ultimately affecting carbon and nutrient cycles [32-33]. It follows, therefore, that any
66 directional change in species behaviour or trait expression will have important consequences for
67 ecosystem process and function [34]. Such changes, although species and context dependent [35-
68 37], reflect individual responses to changing circumstances that may maintain [38], reduce [35] or
69 enhance [39-41] functioning, making it difficult to characterise species contributions to alterations in
70 ecosystem properties. Disentangling these effects is frustrated by the fact that changes in behaviour
71 are also accompanied by compensatory responses [42-43] that affect dominance patterns [44-45],
72 and other factors, which can partially, or wholly, offset functional responses to forcing [46].

73 Nevertheless, field observations show that a shift in the type and amount of faunal activity can lead
74 to environmental transitions [3] that exert a disproportionate influence on ecosystem properties and
75 functioning over and above the effects caused by changes in species diversity [47-48] and
76 composition [49,45]. It is important to note, however, that although flexible behavioural strategies
77 can improve short-term fitness [50-51], any associated functional consequences [52-53] may not

78 materialise until much later and can be hard to distinguish from other temporal changes in the
79 system [54].

80

81 We anticipated that changes in species behaviour will be more pronounced in regions of fast paced
82 climate change [3, 55], as genetic and other coping mechanisms are less likely to be enacted in time.

83 We speculated, given the closure of dispersal and adaptation as viable options, that adjustments to
84 individual behaviour would dominate species responses to change [56] at higher latitudes. Here,

85 using sediment-dwelling invertebrate species obtained from the Arctic Barents Sea (the bivalve

86 *Astarte crenata*, sea star *Ctenodiscus crispatus* and polychaete *Cistenides hyperborea*) and Antarctic

87 Peninsula (the protobranch *Aequiyoldia eightsi* and bivalve *Laternula elliptica*), two areas currently

88 experiencing amplified climate change [57-58], we explore the combined effects of near-term ocean

89 warming (+1.5 °C) and elevated levels of atmospheric carbon dioxide (550 ppm [CO₂]) on aspects of

90 species behaviour known to influence biogeochemical cycling. As we anticipate that the direction and

91 magnitude of change in behaviour will diverge between species [4, 59-60], we also include individuals

92 of *Astarte crenata* and *Ctenodiscus crispatus* from two locations within the Barents Sea that contrast

93 in temperature and sea ice dynamics; here, our expectation is that individual species responses will

94 be in line with previous observations [3], but will be more pronounced when species are from

95 locations experiencing narrower environmental variation. We use these data to demonstrate the

96 importance of behavioural change and compensatory mechanisms, including numeric and/or

97 biomass increases and performance enhancement [42-43], in moderating how benthic environments

98 respond to external forcing. We show, for five species of polar benthic invertebrates, that the ability

99 to modify behaviour in the face of climatic forcing does not guarantee that species contributions will

100 remain unchanged. Our findings emphasise the importance of context-dependency and have

101 implications for the functional contributions of populations facing climate change, their capacity to

102 adapt in the face of further environmental transitions, and suggest that the onset of phenotypic

103 expression may serve as an early warning for impending ecological change.

104

105 **2 | Results**

106 We find evidence that individual movement and burial behaviour, sediment particle reworking
107 activity, burrow ventilatory activity, and associated nutrient concentrations at the sediment-water
108 interface, can be dependent on environmental condition (ambient climate treatment vs future
109 climate treatment of +1.5 °C and 550 ppm [CO₂]), location, and species identity (Supplementary
110 Models S1 to S29). However, observed effects seldom formed full factorial interactions between the
111 three dependent variables (8 of 29 models). Despite observing mortalities in the bivalve *Astarte*
112 *crenata* (2 individuals, 1 from each climate), *Ctenodiscus crispatus* (4 individuals, 3 ambient and 1
113 future climate), and *Cistenides hyperborea* (1 ambient climate), it was possible to relate our
114 response variables in ecosystem process (sediment particle reworking: surface boundary roughness,
115 median mixed depth of particle reworking and maximum mixed depth of particle reworking; burrow
116 ventilation activity) and functioning (nutrient concentrations: ammonium, nitrite, nitrate and
117 phosphate) to species behaviour (individual movement: response time; burial behaviour: burial
118 time) in all aquaria. We found no evidence that differences in mortality (assessed using total
119 biomass as a random effect) affected response.

120

121 **2.1 | Effects on individual behaviour**

122 All individuals of *C. crispatus* ($n_T = 18$) initiated movement within 60 minutes, with 16 individuals
123 completing reburial, but we found no evidence that response time was affected by environmental
124 condition, location or their interaction (intercept only model: L-ratio = 1.420, d.f. = 1, $p = 0.234$; Fig.
125 1a). However, response times were less variable between individuals from station B13 (coefficient of
126 variation, CV = 34.5%) relative to individuals from station B16 (CV = 62.9%). Regardless of location,
127 mean burial time of *C. crispatus* was influenced by environmental condition ($F_{[1,12]} = 5.285$, $p < 0.05$),
128 with reburial time halving under future conditions (Fig. 1b). For *C. hyperborea*, 9 individuals ($n_T = 11$)
129 responded within 60 minutes, with comparable response rates across both environmental conditions

130 ($F_{[1,7]} < 0.001$, $p = 0.992$; Fig. 1a). However, no individuals reburied under ambient conditions and an
131 insufficient number of individuals ($n = 3$) reburied within 60 minutes under future conditions for
132 reliable statistical analysis. For *A. eightsi*, response time was not dependent on environmental
133 condition (intercept only model, L-ratio = 2.277, d.f. = 1, $p = 0.131$; Fig. 1c), despite a substantial
134 reduction in intra-specific variability under future conditions (CV: ambient, 95.7 %; future, 51.5%).
135 Burial time for *A. eightsi* was weakly dependent on environmental condition (L-ratio = 3.5943, d.f. =
136 1, $p = 0.0580$), despite a reduction in intra-specific variability (CV: ambient = 42.3%, future = 28.4%)
137 and burial time (Fig. 1d). We found no effect of biomass as a random factor in any of these models.
138

139 **2.2 | Effects on ecosystem process**

140 Surface boundary roughness (SBR) in the presence of *A. crenata* and *C. crispatus* (Fig. 2a–b) was
141 dependent on the independent effects of species (L-ratio = 10.056, d.f.= 1, $p < 0.01$) and location (L-
142 ratio = 4.010, d.f. = 1, $p < 0.05$), but not environmental condition (L-ratio = 3.238, d.f. = 1, $p = 0.072$).
143 For *C. hyperborea*, we also found no evidence that SBR was affected by changes in environmental
144 condition (L-ratio = 0.025, d.f. = 1, $p = 0.8740$) despite an increase in intra-specific variability under
145 future conditions (CV: ambient, 2.5%; future, 31.4%; Fig. 2c). For *A. eightsi* and *L. elliptica*, we found
146 no effect of environmental condition, species identity, or their interactions, on SBR ($F_{[1,8]} = 3.005$, $p =$
147 0.121; Fig. 2d).

148
149 The median mixed depth of particle reworking ($f\text{-SPL}_{\text{med}}$) for *A. crenata* and *C. crispatus* was
150 dependent on the independent effect of environmental condition ($F_{[1,18]} = 5.2018$, $p < 0.05$; Fig. 2e).
151 However, there was no effect of environmental condition on $f\text{-SPL}_{\text{med}}$ for *C. hyperborea* (L-ratio =
152 0.338, d.f. = 1, $p = 0.126$; Fig. 2f) or for *A. eightsi* and *L. elliptica* ($F_{[1,8]} = 2.955$, $p = 0.124$; Fig. 2g). In
153 contrast, maximum mixed depth ($f\text{-SPL}_{\text{max}}$) was dependent on a species identity \times location interaction
154 for *A. crenata* and *C. crispatus* ($F_{[1,20]} = 7.8123$, $p < 0.05$), with species identity ($\omega^2 = 0.537$) more
155 influential than location ($\omega^2 = 0.316$). Specifically, $f\text{-SPL}_{\text{max}}$ was deeper in aquaria containing *C.*

156 *crispatus* from station B16 than it was in aquaria containing *A. crenata* from station B16 and, to a
157 lesser extent, station B13 (Fig. 2h). For *C. hyperborea*, $f^{SPL_{max}}$ was not dependent on environmental
158 condition (intercept only model: $f^{SPL_{max}}$, L-ratio = 0.695, d.f. = 1, $p = 0.405$), but there was some
159 evidence for a reduction in intra-specific variability between treatments (CV: ambient, 22.8 %; future,
160 11.5 %; Fig. 2i). In contrast, we found that $f^{SPL_{max}}$ for *A. eightsi* and *L. elliptica* was dependent on an
161 environmental condition \times species identity interaction ($F_{[1,8]} = 7.962$, $p < 0.05$), with species identity
162 ($\omega^2 = 1.103$) more influential than environmental condition ($\omega^2 = 0.907$). Specifically, $f^{SPL_{max}}$ was
163 deeper for *A. eightsi* relative to *L. elliptica*, with a larger difference observed under future conditions
164 (Fig. 2j).

165

166 The burrow ventilation activity ($[\Delta Br^-]$) of *A. crenata* and *C. crispatus* was dependent on an
167 environmental condition \times location \times species identity interaction ($F_{[1,16]} = 7.910$, $p < 0.05$), with
168 species identity the most influential independent variable ($\omega^2 = 0.678$), followed by location ($\omega^2 =$
169 0.481) and environmental condition ($\omega^2 = 0.376$). In individuals from station B13, irrespective of
170 species identity, $[\Delta Br^-]$ was unchanged by environmental condition (Fig. 2k). However, whilst $[\Delta Br^-]$ of
171 *A. crenata* from station B16 was negligible ($[\Delta Br^-]$ values were positive) in both ambient and future
172 environmental conditions, $[\Delta Br^-]$ for *C. crispatus* increased 7-fold (values more negative) under the
173 future environmental condition (Fig. 2l). $[\Delta Br^-]$ of *C. hyperborea* was also affected by environmental
174 condition (L-ratio = 5.879, d.f. = 1, $p < 0.05$) with an increase in burrow ventilation activity under
175 future environmental conditions (Fig. 2m). In contrast, there was no effect of environmental
176 condition or species identity on $[\Delta Br^-]$ for *A. eightsi* and *L. elliptica* (intercept only; L-ratio = 0.764, d.f.
177 = 1, $p = 0.382$; Fig. 2n), but we did observe a reduction in intra-specific variability between
178 treatments (CV: ambient, 713 %; future, 293 %).

179

180 **2.3 | Effects on ecosystem functioning**

181 Our analyses reveal that, for *A. crenata* and *C. crispatus*, ammonium ([NH₄-N]) was influenced by the
182 independent effect of species identity ($F_{[1,22]} = 14.951$, $p < 0.0001$), with positive lnRRs in aquaria
183 containing *C. crispatus* and negative lnRRs in aquaria containing *A. crenata* (Fig. 3a). We find that the
184 effect size for [NH₄-N] is not dependent on environmental condition in the presence of *C. hyperborea*
185 (intercept only models: [NH₄-N], $F_{[1,4]} = 1.047$, $p = 0.364$; Fig. 3b), *A. eightsi* or *L. elliptica* (intercept
186 only model, L-ratio = 0.009, d.f. = 1, $p = 0.925$; Fig. 3c). For nitrite ([NO₂-N]), whilst there is evidence
187 of a weak dependence on environmental condition in the presence of *L. elliptica* and *A. eightsi* (L-
188 ratio = 3.532, d.f. = 1, $p = 0.060$; Fig. 3g), the effect size of [NO₂-N] in the presence of *A. crenata* and
189 *C. crispatus* was dependent on an environmental condition \times location \times species identity interaction
190 (L-ratio = 4.629, d.f. = 1, $p < 0.05$). For the latter, model coefficients revealed that location was most
191 influential (L-ratio = 7.714, d.f. = 4, $p = 0.103$), followed by species identity (L-ratio = 6.955, d.f. = 4, p
192 = 0.138) and environmental condition (L-ratio = 5.952, d.f. = 4, $p = 0.203$). In aquaria containing
193 infauna from station B13 (*A. crenata* and *C. crispatus*), irrespective of species identity, and for *A.*
194 *crenata* in station B16, the effect size of [NO₂-N] was not affected by environmental condition (Fig.
195 3d–e). For station B16, however, the effect size of [NO₂-N] in aquaria containing *C. crispatus*
196 decreased under future environmental conditions. Similarly, the effect size for nitrate ([NO₃-N]) in
197 the presence of *A. crenata* or *C. crispatus* was dependent on an environmental condition \times location \times
198 species identity interaction ($F_{[1,16]} = 3.057$, $p = 0.09$), with species identity the most influential
199 independent variable ($\omega^2 = 0.281$), followed by location ($\omega^2 = 0.207$) and environmental condition (ω^2
200 = 0.136). Notably, environmental condition had no effect on the activities of *A. crenata* and *C.*
201 *crispatus* at station B13 but did influence the behaviour of *C. crispatus* at station B16 (Fig. 3h–i). In
202 contrast, for aquaria with *C. hyperborea*, we find no influence of environmental condition on the
203 effect size of [NO₂-N] ($F_{[1,4]} = 1.324$, $p = 0.314$; Fig. 3f), but the effect size of [NO₃-N] increased under
204 future conditions ($F_{1,4} = 60.821$, $p < 0.01$; Fig. 3j). For *L. elliptica* and *A. eightsi*, the effect size of [NO₃-
205 N] was dependent on the independent effect of environmental condition (L-ratio = 9.720, d.f. = 1, $p <$
206 0.01; Fig. 3k), with an increased effect size under future conditions for both species.

207

208 The effect size for phosphate ($[PO_4-P]$) was not dependent on any of our explanatory variables
209 (intercept only model; Fig. 3l) for *A. crenata* and *C. crispatus*. However, we found independent
210 effects of environmental condition on $[PO_4-P]$ for *C. hyperborea* (L-ratio = 3.123, d.f. = 1, $p = 0.078$;
211 Fig. 3m) and independent effects of environmental condition (L-ratio = 7.865, d.f. = 1, $p < 0.01$) and
212 species identity (L-ratio = 4.662, d.f. = 1, $p < 0.05$) on $[PO_4-P]$ for *A. eightsi* and *L. elliptica* (Fig. 3n).
213 Intra-specific variability (CV) in the effect size for $[PO_4-P]$ decreased under future conditions for *A.*
214 *eightsi* (ambient, 69.7%; future, 50.6%) and *C. hyperborea* (ambient, 68.6%; future, 49.7%), but
215 increased for *L. elliptica* (ambient, 11.7%; future, 47.6%).

216

217 **3 | Discussion**

218 Our findings demonstrate that conditions representative of anticipated near-future climate change
219 can lead to fundamental shifts in functionally important aspects of sediment-dwelling invertebrate
220 behaviour. These effects can be substantive; here we observed a doubling of burial rate, deepening
221 of particle mixing and a change in the magnitude and direction of biogeochemical dynamics that are
222 sufficient to change the functional role of a species (*A. eightsi* [36]). This observation is important,
223 because alterations in individual functional capacity that are distinct from functional shifts caused by
224 changes in community composition and/or novel environmental conditions are common [61,3], and
225 likely result from changes in the strength and nature of a portfolio of sublethal responses, including
226 species interactions [62-63], compensatory mechanisms [41-42] and/or other subtle phenotypic
227 responses [54,64]. Changes in macronutrient cycling under climate forcing is not trivial to detect [65],
228 however, and may be masked by the pH buffering effects of $[CO_2]$ driven alkalinity changes [66] on
229 microbial mediated pathways of nutrient recycling.

230

231 The behavioural changes with warming and acidification observed here may be even more important
232 ecologically in polar regions than they would be at lower latitudes. Seasonality results in many

233 species entering low energy and activity states similar to aestivation in winter that can last several
234 months [67-68]; in this study, as in *L. elliptica* [69], although juvenile *A. eightsi* growth is known to be
235 similar across summer and winter [70]. Therefore, in the presence of species that respond to
236 seasonal cues, greater levels of species activity, leading to greater microbial and nutrient
237 remobilisation from sediments [32-33], may occur for longer in polar regions as the summer season
238 extends under climate change [71]. If widespread, it follows that there will be positive ramifications
239 for phytoplankton productivity over the long term [1, 3]. Although this is not the only mechanism
240 underpinning nutrient provision for productivity, we speculate that outcomes associated with
241 benthic responses to climate change could include changes in the phenology of the initiation of
242 productivity and early intensity of phytoplankton growth [72], with downstream impacts for primary
243 and secondary consumers.

244

245 Whilst the effects of a near-future climate in our experiments were comparatively weaker than the
246 effects of species identity and location, consistent with theoretical expectations [73-74], we did note
247 a reduction in intra-specific variation that reflected changes in environmental context and location
248 [37]. This can be very important for maintaining populations [75], enabling adaptation to changing
249 environmental conditions [76] and stability in ecosystem functioning [77]. However, whilst sublethal
250 responses may enable species to persist in, or for longer, under novel circumstances, other
251 phenotypic costs may constrain or inhibit an individual's ability to adjust further [78-79]. Hence,
252 reductions in intra-specific variation may serve as an early warning for impending ecological
253 transitions associated with progressive forcing and potentially inform more timely management
254 actions, reinforcing the need for continual monitoring of faunal activity and the ecological constraints
255 that modify functionally important aspects of species behaviour [80].

256

257 The variation in intra-specific behaviour observed here under enhanced warming and [CO₂] is
258 consistent with other behavioural studies [81], physiological responses in polar benthic species [21]

259 and incorporates regional contextualisation [13]. Whilst our study was not explicitly designed to
260 examine species range shifts or gradients of environmental change, an important feature was that
261 our locations were positioned to the north and south of the oceanographic polar front, contrasting in
262 benthic biogeography [82], bioturbation activity and functioning [3]. Hence, we were able to show
263 that individuals predisposed to a wider inter-annual thermal range exhibit a more reserved
264 behavioural response to change than those inhabiting a narrower thermal range [83]. Thus, plasticity
265 in response mirrors the level of local environmental fluctuation [84]. Whilst spatial associations
266 between environmental temperature range and physiological thermal tolerances are not atypical in
267 ectothermic species [13, 85, 86], this does mean that high latitude populations may be at greater risk
268 of local extinction over the long term. As thermal tolerance narrows with decreasing seasonality in
269 temperature towards the poles [16, 87], and will likely be further constrained with ocean warming
270 [88], populations already at the edge of their thermal limits will most likely have less scope to
271 compensate and adapt to change [89]. Indeed, changes in species composition and abundance are
272 well documented across areas of environmental transition [3] and show similar patterns of functional
273 change, as observed here. Temperature-driven responses are, however, typically complicated by
274 interactions with other abiotic drivers [74] and are likely to lead to both amplified and dampened
275 effects in spatially stochastic ecosystems [90]. Yet, previous investigations have predominantly
276 focused on spatial distributions of species turnover [64], functional diversity [91-92] and redundancy
277 [93], rather than characterising intraspecific variability of species-environment interactions. The
278 latter can be a more important driver of the short-term functional response of communities than
279 changes in species composition, dominance, or richness [94-95]. For example, the shallower
280 burrowing activity of invertebrates held under more acidified conditions [96] allows species to evade
281 the physiological effects of decreasing pH, but simultaneous burrowing and ventilatory [40]
282 responses to warming to maintain environmental continuity may negate the need for such avoidance
283 behaviour [97]. We observed similar changes across multiple aspects of functionally important
284 behaviour that may have led to non-additive effects on net functioning that were not possible to

285 distinguish. Nevertheless, the cumulative effect of such short-term behavioural responses is likely to
286 be decisive for the composition [28], population dynamics [98], connectivity [99] and functioning
287 [100] of benthic communities that will be moderated by seasonal timing [54] and local circumstance
288 [13, 36], including interannual variability [3].

289

290 Quantitative information on the functional role of individual species is rare for both polar regions
291 [101], yet understanding, and accounting for, species responses to climate change is fundamental to
292 improving the likelihood of determining the most realistic ecosystem future [102]. We contend that
293 this task will be frustrated by context-dependent variation in both intra- and inter-specific responses
294 to forcing that are not readily captured using fixed trait modalities [35, 103]. Where the overall
295 outcome of species responses remains largely unresolved, reductions in the variation of conspecific
296 responses [95, 104] may form a viable alternative for some predictive models. Furthermore, our
297 findings lend support to the view that location-dependent variation in behavioural responses can be
298 attributed to localised thermal plasticity driven by exposure to divergent temperature seasonality
299 trends [8, 84, 105]. Inter- and intra-specific variations in vulnerability, effect-and-response traits [79]
300 and interactions between species [106-107] can facilitate functional redundancy and/or post-change
301 compensations [42-43]. A mechanistic approach that explicitly tests suspected abiotic and biotic
302 signals is necessary for establishing patterns of response [108] across multiple levels of biological
303 organisation [109-110], enabling more likely projections of the functional consequences of change.

304

305 **4 | Material and methods**

306 **4.1 | Fauna and sediment collection**

307 We obtained individuals of the bivalve *Astarte crenata*, asteroid *Ctenodiscus crispatus* and
308 polychaete *Cistenides hyperborea* from replicate SMBA (Scottish Marine Biological Association, 50 ×
309 50 cm) box cores, and 15 minute Agassiz trawls in the Barents Sea (stations B13, 74.3 °N, 30.0 °E;
310 B16, 80.3 °N, 30.0 °E, 263-375m depth; JCR18006, *RSS James Clark Ross*, Supplementary Fig. S1a,

311 Table S1) in July 2019. Individuals of the protobranch *Aequiyoldia eightsi* and bivalve *Laternula*
312 *elliptica* were collected by SCUBA divers at Rothera Point, Adelaide Island, West Antarctic Peninsula
313 (67.3 °S, 68.1 °W, 10-20 m depth, Supplementary Fig. S1b) in March-April 2019. We obtained surficial
314 sediment (< 5 cm depth) from SMBA box cores at the Barents Sea stations B13, B14 and B16
315 (Supplementary Table S1) for the Arctic species, and from the intertidal mud flats of the Hamble, UK
316 (50.9 °N, 1.3 °W) for the Antarctic species. Each sediment was sieved (500 µm) within a seawater
317 bath to retain the fine fraction and to remove macrofauna and debris. Sediment particle size
318 (Supplementary Fig. S2) was determined using a Malvern Mastersizer 2000 He-Ne LASER diffraction
319 sizer. Mean particle size, sorting, skewness and kurtosis were quantified using GRADISTAT [111]. Loss
320 on ignition was used to determine sediment organic matter content (%).

321

322 **4.2 | Experimental design and set-up**

323 Sediment (mean ± s.e., n = 38: particle size = $60.30 \pm 3.91\mu\text{m}$, organic matter content = 5.502 ± 0.212 ;
324 Supplementary Table S2) and species were distributed across 42 clear acrylic aquaria (internal LWH:
325 12 x 12 x 33 cm, 3 replicates treatment⁻¹: species × location × climate scenario; Supplementary Table
326 S3), designed to accommodate representative field densities (Arctic species, 2 ind. aquarium⁻¹;
327 Antarctic species, 1 ind. Aquarium⁻¹; ([112]; Supplementary Table S4) and the size and burrowing
328 requirements of each species (sediment depth: *A. crenata*, *C. crispatus* & *C. hyperborea*, 16 cm; *A.*
329 *eightsi*, 12 cm; *L. elliptica*, 19 cm; [113-114]). Aquaria were randomly placed within one of two
330 insulated seawater reservoirs ([3], Supplementary Fig. S3) in the Biodiversity and Ecosystem Futures
331 Facility, University of Southampton (UK). All aquaria were filled with seawater (salinity 33, 10 µm
332 sand filtered, UV sterilized) to ~12 cm above the sediment-water interface and maintained in the
333 dark. After transitional period to aquarium conditions (21 days, 09-29/09/2019), fauna was exposed
334 to ambient ($1 \pm 0.5^\circ\text{C}$, ~400 ppm atmospheric [CO₂]) or indicative near-future ($2.5 \pm 0.5^\circ\text{C}$, ~550 ppm
335 atmospheric [CO₂]) environmental conditions. Water temperature and atmospheric [CO₂] were
336 increased from ambient to treatment levels in 0.5°C and 50 ppm increments every 7 days (21 days,

337 29/09/2019-20/10/2019) to minimise adverse physiological responses [115]. During both the
338 transitionary and experimental period (92 days, 21/10/2019 – 21/01/2020), species were fed *ad*
339 *libitum*; *C. crispatus* and *C. hyperborea* with commercially available fish food (Aquarian Tropical
340 Flake; 0.03 g week⁻¹), and *A. crenata*, *A. eightsi* and *L. elliptica* with precultured phytoplankton (15 ml
341 3× week⁻¹, 33:33:33 mix: *Isochrysis* sp., *Tetraselmis* sp., and *Phaeodactylum* sp.). This period of time
342 was sufficient for the establishment of microniche formation [116] and vertical biogeochemical
343 gradients indicated by colour change [117]) to form in the sediment. Partial seawater exchanges
344 (weekly, 50% volume) prevented accumulation of excess food and nutrients. Measurements in
345 behaviour, ecosystem process and functioning were taken at the end of the experimental period.

346

347 **4.3 | Seawater carbonate chemistry, temperature, and salinity**

348 Atmospheric [CO₂] (Supplementary Fig. S4) was controlled using a custom-made CO₂-air mixing
349 system which continually maintained and monitored [CO₂] in the air mixture supplied to each
350 individual experimental core using infrared analysers (LI-COR LI-840A) [54]. This approach facilitates
351 natural variability within the carbonate system [118]. Temperature, pH (NBS scale, Mettler-Toledo
352 InLab Expert Pro temperature-pH combination electrode; weekly three-point calibration using
353 technical buffer solutions pH 4.01, 7.00, 9.21, Mettler-Toldedo), and salinity (WTW™ TetraCon™ 325
354 Standard conductivity electrode; weekly calibration using conductivity standard solution 12.88mS,
355 Mettler-Toldedo) were measured weekly and total alkalinity (A_T, Apollo SciTech Titrator AS-ALK2)
356 was measured in weeks 2, 6 and 11 in each experimental core. A_T analysis followed standard HCl
357 titration protocols of the Carbonate Facility, University of Southampton. DIC, [pCO₂], [Ω_{calcite}],
358 [Ω_{aragonite}], [NCO₃] and [CO₃] were calculated (*CO2calc* carbon calculator, v 4.0.9) ([119];
359 Supplementary Figures S5, S6).

360

361 **4.4 | Behavioural response of individuals**

362 Behaviour of *C. crispatus*, *C. hyperborea* and *A. eightsi* were quantified using measurements of
363 movement and burial behaviour at the sediment surface. Individuals (morphology, ± 0.01 mm;
364 blotted wet weight, ± 0.001 g, Supplementary Table S5) were placed in separate treatment-
365 acclimatised viewing trays containing sediment (depth 5 cm) overlain with sea water (depth 3 cm)
366 and viewed (≤ 60 minutes) with a benchtop video camera (Logitech C920 HD Pro, 1080p;
367 Supplementary Fig. S7). The time taken to initiate movement (response time, s) and to complete
368 burial (burial time, s) was recorded (3 frame s^{-1} , SkyStudioPro) and analysed frame-by-frame (VLC
369 Media Player). We incorporated biomass as a random factor in the statistical analysis to account for
370 any intra-specific variation in size.

371

372 **4.5 | Effects on ecosystem process and functioning**

373 Sediment particle reworking activity of all five species was determined from the redistribution of
374 fluorescent particulate luminophore tracers (30 g aquarium $^{-1}$, 125 – 250 μm diameter, 12 days
375 09/01/2020-21/01/2020; [120]). All four aquarium sides were imaged under UV light (Canon EOS
376 400D, 3888 x 2592 pixels, effective resolution 74 x 74 μm pixel $^{-1}$), stitched together (Adobe
377 Photoshop CC 2019; Supplementary Figures S8 to S12), and the distribution of luminophores was
378 analysed using ImageJ (version 1.46r; [120]). From these profile data (Supplementary Fig. S13), we
379 calculated the mean ($f\text{-SPL}_{\text{mean}}$, time dependent indication of mixing), median ($f\text{-SPL}_{\text{med}}$, typical short-
380 term depth of mixing) and maximum ($f\text{-SPL}_{\text{max}}$, maximum extent of mixing) mixed depth of particle
381 redistribution. Given the shape of the vertical distribution of luminophores (non-continuous), $f\text{-SPL}_{\text{mean}}$
382 was an unsuitable descriptor of the distribution profile and not considered for statistical analysis. The
383 rugosity of the sediment-water interface (upper – lower limit = surface boundary roughness, SBR)
384 provides an indication of surficial activity.

385

386 Ventilatory behaviour [101] of all five species was estimated from absolute changes in the
387 concentration of sodium bromide [NaBr] [54]. Dissolved [NaBr] was standardised across all aquaria

388 (mean starting concentration = $1353.816 \pm 317.264 \text{ mg L}^{-1}$) and [NaBr] was determined using a
389 Tecator flow injection auto-analyser (FIA Star 5010 series). Negative values of [NaBr] ($\Delta[\text{Br}^-] \text{ mg L}^{-1}$)
390 over an 8-hour period indicate increased infaunal ventilatory activity.

391

392 As faunal activity mediates nutrient concentrations, we determined water column $[\text{NH}_4\text{-N}]$, $[\text{NO}_3\text{-N}]$,
393 $[\text{NO}_2\text{-N}]$ and $[\text{PO}_4\text{-P}]$ ($\mu\text{mol L}^{-1}$, $\sim 10\text{ml}$, filtered $0.45 \mu\text{m}$ NALGENE nylon matrix) for all five species
394 once a month (Supplementary Fig. S14) using a QuAatro 39 auto-analyser (SEAL Analytical) as a
395 measure of ecosystem functioning. As nutrient concentrations will also reflect differences in the
396 volume of sediment between species treatments, we calculated the log response ratio ($\ln\text{RR} =$
397 $\ln[\text{conc}_{\text{before}}/\text{conc}_{\text{after}}]$; [121]), an effect size that quantifies proportionate change. As patterns of $[\text{NO}_x\text{-}$
398 $\text{N}]$ are reciprocal to those of $[\text{NH}_4\text{-N}]$ but indicate beneficial biogeochemical processes (e.g.
399 denitrification), $\ln\text{RR}$ values for $[\text{NO}_2\text{-N}]$ and $[\text{NO}_3\text{-N}]$ were multiplied by -1 to align the direction of
400 ecosystem functioning.

401

402 **4.6 | Statistical analysis**

403 Analysis of Variance (ANOVA) models were developed for each dependent variable (movement and
404 burial behaviour: response time, burial time; ecosystem process: SBR , $f\text{-SPI}_{\text{Lmedian}}$, $f\text{-SPI}_{\text{Lmax}}$, $\Delta[\text{Br}^-]$;
405 ecosystem functioning: $[\text{NH}_4\text{-N}]$, $[\text{NO}_3\text{-N}]$, $[\text{NO}_2\text{-N}]$, $[\text{PO}_4\text{-P}]$). For *A. crenata* and *C. crispatus*, we
406 determined the effects of the independent variables; environmental condition (2 levels: ambient,
407 future), location (2 levels: stations B13 and B16; Supplementary Fig. S1a), species identity (2 levels),
408 and their interactions, whilst for *A. eightsi* and *L. elliptica*, we determined the effects, alone and in
409 combination, of the independent variables environmental condition (2 levels) and species identity (2
410 levels). As *C. hyperborea* was found at a single station, we determined only the effects of
411 environmental condition (2 levels). Intra-specific variability within treatment levels was determined
412 using the coefficient of variation.

413

414 Model assumptions were visually assessed using standardised residuals vs fitted values plots, Q-Q
415 plots, and Cook's distance [122]. Where there was a violation of homogeneity of variance, we used a
416 *varIdent* variance-covariance structure and generalised least-squares (GLS) estimation [123-124] to
417 allow residual spread to vary amongst groups. We determined the optimal fixed-effects structure
418 using backward selection informed by Akaike Information Criteria (AIC) and inspection of model
419 residual patterns. For the GLS analysis, we determined the optimal variance-covariance structure
420 using restricted maximum-likelihood (REML) estimation by comparing the initial ANOVA model
421 without variance structure to equivalent GLS models incorporating specific variance terms. These
422 models were compared against the initial ANOVA model using AIC informed by visualisation of model
423 residuals. We determined the optimal fixed structure of the most suitable model by applying
424 backward selection using the likelihood ratio test with maximum-likelihood (ML) estimation
425 [122,124]. For ANOVA models with interactions, we calculated the effect size (ω^2 , [125]) of each
426 independent variable in R [126] using the *effectsize* package [127]. For GLS models with interactions,
427 we determined the relative importance of each independent variable by comparing the minimal
428 adequate model with a model with the independent variable of interest, and all its interactions,
429 removed using likelihood ratio (L-ratio) in the *nlme* package [123]. Details of initial and minimal
430 adequate models (Model S1 to S29) are provided in electronic supplementary material.

431

432 **5 | Author contributions**

433 TJW, MS and JAG conceived and designed the study. TJW, AJR and JAG collected the Arctic fauna and
434 LP collected the Antarctic fauna. TJW conducted the experiments and drafted the manuscript. TJW,
435 MS and JAG completed the statistical analysis. All authors read, contributed to, and approved the
436 manuscript.

437

438 **6 | Competing interests**

439 The authors declare that they have no competing interests.

440

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444 public copyright licence to any Author Accepted Manuscript version arising from this submission.

445

446 **8 | Data Availability**

447 All data associated with this analysis are scheduled to be made publicly available from the Polar Data
448 Centre at the point of acceptance (<https://www.bas.ac.uk/data/uk-pdc/>; doi:10.5285/7adc7b14-
449 *abae-4ab9-b60b-b9b6e0e9f320*; Data records S1). Extended data items, including the “minimum
450 datasets” that are necessary to interpret, verify and extend the research in the article, can be found
451 in the electronic supplementary material.

452

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462

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811 **11 | Figure legends**

812 **Figure 1.** The effects of species identity, location and environmental condition (ambient, open
813 symbols; future, closed symbols) on (a,c) mean (\pm s.e.) response time and (b,d) mean (\pm s.e.) burial
814 time for *Ctenodiscus crispatus* (\square) and *Cistenides hyperborea* (\triangle) obtained from station B13 (red)
815 and B16 (blue) in the Barents Sea and *Aequiyoldia eightsi* (\diamond) obtained from Rothera Point (black).
816 Individuals of *C. hyperborea* did not rebury under ambient conditions.

817

818 **Figure 2.** The effects of species identity, location and environmental condition (ambient, open
819 symbols; future, closed symbols) on (mean \pm s.e.) (a,b,c,d) SBR (mm), (e,f,g) $f\text{-SPL}_{\text{median}}$ (mm), (h,i,j) $f\text{-}$
820 SPL_{max} (mm) and (k,l,m,n) $[\Delta\text{Br}^-]$ ($\text{mg}\cdot\text{L}^{-1}$) in mesocosms containing (a,b,d,h,k,l) *Astarte crenata* (\circ) or
821 *Ctenodiscus crispatus* (\square) from station B13 (red), B16 (blue) or both locations combined (gold),
822 (c,f,i,m) mesocosms containing *Cistenides hyperborea* (\triangle) obtained from station B13 and (d,g,j,n)
823 mesocosms containing *Aequiyoldia eightsi* (\diamond) or *Laternula elliptica* (∇) obtained from Rothera Point.
824 For $\Delta[\text{Br}^-]$, negative values indicate increased bioirrigation. Sediment profile images and associated
825 luminophore distribution profiles are presented in Supplementary Figures S8-S11

826

827 **Figure 3.** The effects of species identity, location and environmental condition (ambient, open
828 symbols; future, closed symbols) on (mean \pm s.e.) effect size of nutrient concentrations (lnRR) over
829 the experimental period as indicated by (a,b,c) $[\text{NH}_4\text{-N}]$, (d,e,f,g) $[\text{NO}_2\text{-N}]$, (h,i,j,k) $[\text{NO}_3\text{-N}]$ and (l,m,n)
830 $[\text{PO}_4\text{-P}]$ in mesocosms containing (a,d,e,h,i,l) *Astarte crenata* (\circ) or *Ctenodiscus crispatus* (\square) from
831 station B13 (red), B16 (blue) or both (gold), (b,f,j,m) mesocosms containing *Cistenides hyperborea*
832 (\triangle) obtained from station B13 and (c,g,k,n) mesocosms containing *Aequiyoldia eightsi* (\diamond) or
833 *Laternula elliptica* (∇) obtained from Rothera Point. A positive effect size indicates an increase in
834 nutrient release from the sediment into the water column over the experimental period, while a

835 negative effect size signifies an increase in the uptake of nutrients from the water column into the
836 sediment.