**Species interactions and environmental context affect intraspecific behavioural trait variation and ecosystem function**

Cassidy, Camilla; Grange, Laura; Garcia, Clement ; Bolam, Stefan; Godbold, Jasmin

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2    **variation and ecosystem function**

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4    Camilla Cassidy[1], Laura J. Grange[2], Clement Garcia[3], Stefan G. Bolam[3], Jasmin A. Godbold[1]

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6    [1] School of Ocean and Earth Science, National Oceanography Centre Southampton,

7    University of Southampton, European Way, Southampton, SO14 3ZH, United Kingdom

8    [2] School of Ocean Sciences, Bangor University, Bangor, United Kingdom, LL57 2DG

9    [3] Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory,

10    Pakefield Road, Lowestoft, Suffolk, NR33 0HT, United Kingdom

11    Corresponding author: Camilla Cassidy, camillacassidy@soton.ac.uk

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13    Camilla Cassidy ORCID ID: 0000-0001-7947-7458

14    Laura J. Grange ORCID ID: 0000-0001-9222-6848

15    Clement Garcia ORCID ID: 0000-0001-5916-8914

16    Stefan Bolam ORCID ID: 0000-0001-6604-4741

17    Jasmin A. Godbold ORCID ID: 0000-0001-5558-8188

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**Abstract**

Functional trait-based approaches are increasingly adopted to understand and project ecological responses to environmental change, however most assume trait expression is constant between conspecifics irrespective of context. Using two species of benthic invertebrate (brittlestars *Amphiura filiformis* and *A. chiajei*) we demonstrate that trait expression at individual and community levels differs with biotic and abiotic context. We use PERMANOVA to test the effect of species identity, density and local environmental history on individual (righting and burrowing) and community (particle reworking and burrow ventilation) trait expression, as well as associated effects on ecosystem functioning (sediment nutrient release). Trait expression differs with context, with repercussions for the faunal mediation of ecosystem processes; we find increased rates of righting and burial behaviour and greater particle reworking with increasing density that are reflected in nutrient generation. However, the magnitude of effects differed within and between species, arising from site-specific environmental and morphological differences. Our results indicate that traits and processes influencing change in ecosystem functioning are products of both prevailing and historic conditions that cannot be constrained within typologies. Trait-based study must incorporate context-dependent variation, including intraspecific differences from individual to ecosystem scales, to avoid jeopardising projections of ecosystem functioning and service delivery.

## 1 Introduction

Decades of empirical study, motivated by unprecedented species loss and environmental change, have provided unequivocal evidence that altering biodiversity affects ecosystem functioning (e.g. primary production, nutrient cycling, sediment stability) and, ultimately, the provision of ecosystem services (Adair et al., 2018). Current research emphasizes that rather than the number of species, ecosystem functioning is instead mediated by the functional traits (e.g. behavioural, morphological or life history characteristics) expressed within a community (Gagic et al., 2015; Read et al., 2017). As a result, functional trait-based approaches are increasingly adopted as predictive tools by ecosystem managers (Rijnsdorp et al., 2015; Bolam et al., 2017) as they incorporate species performance into projections of environmental change. In doing so, they confer understanding of the biological mechanisms underpinning faunal mediation of ecosystem functioning (Laughlin, 2014; Funk et al., 2017; Thomsen et al., 2019).

Conventional trait-based approaches and proposed frameworks implicitly assume that the expression of traits remains constant between conspecifics, irrespective of biotic or environmental context (Albert et al., 2010; Hevia et al., 2017). Studies may neglect intraspecific variability out of economic or logistical necessity, as measuring individual trait values *in situ* is not always possible. For management purposes, therefore, authors may rely on trait values from literature or databases to characterise the functional importance of species (Gogina et al., 2016; Bolam et al., 2017; Solan et al., 2019). In these approaches the quantification of trait values and allocation of species to functional groups is frequently based on single mean trait values per species, and does not account for the scope and importance of intraspecific trait variability (Finerty et al., 2016; Des Roches et al., 2018). If

73 the type or value of traits expressed are understood to determine a species' role in the

74 ecosystem (Wohlgemuth et al., 2017), any intraspecific variation potentially alters its

75 contributions to ecosystem functioning and renders conventional typologies unsuitable.

76

77 Individual organisms are non-identical, with differing forms of trait expression distributed

78 unevenly throughout communities (Carmona et al., 2016; Roscher et al., 2018). It has long

79 been appreciated that age classes, ontogenetic stages or sexes make differing contributions

80 to ecosystem functioning. For example, individuals within a population are often grouped as

81 being agender, despite knowledge that differing sexes can exhibit strongly distinct life

82 strategies and energetic or resource demands (Rudolf & Rasmussen, 2013). Such

83 physiological differences, including associated morphological differences in the mean and

84 variance of body size, determine the scale of an individual's contribution to ecosystem

85 functioning (Norkko et al., 2013; Fritschie & Olden, 2016). However, intraspecific variation

86 occurs beyond demographic influences (Mitchell & Bakker, 2014a). Some site-specific

87 differences originate as a genetic component, stemming from long-term adaptation to

88 historic conditions that creates distinct genetic ecotypes through multi-generational

89 selection processes (Calosi et al., 2013; Robins et al., 2013). In addition, variation also arises

90 over shorter temporal scales in the form of acclimation responses to prevailing biotic and

91 abiotic conditions (Wohlgemuth et al., 2017).

92 Mechanisms of phenotypic plasticity result in widespread and often substantial trait

93 variability over time and space (Roscher et al., 2018). Transient trait expression in

94 individuals alters their activities and potential contributions to ecosystem processes in

95 response to habitat features (Törnroos et al. 2015; Read et al., 2017), climatic drivers

96    (Baranov et al., 2016; Nagelkerken & Munday, 2016; Landeira-Dabarca et al., 2018; Peterson

97    et al., 2019), and resource availability (Hawlena et al., 2011; Murray et al., 2017).

98    Incorporating the context-dependency of trait expression is vital for accuracy in the

99    increasingly urgent quantification of ecosystem functioning under changing abiotic

100   conditions (Landeira-Dabarca et al., 2018). Trait expression, furthermore, also shifts

101   dramatically in response to biotic influences, primarily from neighbouring individuals and/or

102   species (Hawlena et al., 2011; Wohlgemuth et al., 2017; Calder-Potts et al., 2018; Thomsen

103   et al., 2019). Competitive or complementary interactions determine species coexistence and

104   exclusion (Turcotte & Levine, 2016; Pérez-Ramos et al., 2019), and so potentially facilitate

105   enhanced productivity, ecosystem functioning and service delivery (Finerty et al., 2016).

106   Within species, local density-dependent effects can influence the expression of movement

107   and life history traits, influencing habitat use as conspecifics specialise behaviourally or

108   physiologically to exploit available space and resources (Kraft et al., 2015) or escape

109   predation (Rosenberg & Selander, 2000). It is increasingly recognised that intraspecific

110   differences in trait expression are not only widespread but also form an important

111   component of biodiversity (Des Roches et al., 2018). The representation of species using

112   single or average trait values may fail to quantify responses to numerous aspects of

113   ecological and environmental context (Read et al., 2017), jeopardising the reliability of

114   approaches to ecosystem study and management (Reich et al., 2014; Bennett et al., 2016).

115   In this study, we investigate the importance of incorporating intraspecific and individual-

116   level trait variation into trait-based study, illustrating that faunally-mediated community

117   processes and ecosystem functioning with which these traits are associated are subject to

118   context-dependent change. To achieve these aims, we interrogate the effect of biotic

119   context and differing abiotic history on communities of two co-occurring species of infaunal

120   marine invertebrate (brittlestars *Amphiura filiformis* and *A. chiajei*). We hypothesise that i)

121   biotic and site-specific environmental context influence the expression of individual traits

122   and community-level behaviour, and that ii) this variability would aid in understanding

123   concurrent differences in biogeochemical proxies (nutrient concentration) for ecosystem

124   function. To this effect, our results show that, contrary to the assumptions of prevailing

125   trait-based modelling approaches, the trait expression and subsequent functional

126   contributions of conspecific individuals cannot be assumed to be constant.

127   **2 Materials and methods**

128   **2.1 Species collection and experimental design**

129   Two species of ophiuroid brittlestars (*A. filiformis* and *A. chiajei*) were collected from two

130   proximate sea lochs; Kilmaronag Shoal, Loch Etive (56°27'34.20"N, 5°20'29.28"W) and the

131   Lynn of Lorne, Loch Linnhe (56°29'49.6"N, 5°29'56.2"W), Scotland, UK (Supporting

132   information, Fig. S1). Taxa with pelagic larvae, such as these species, have substantial

133   distribution potential and are exchanged across landscape-scale distances and

134   hydrographical barriers only in these early ontogenetic stages (Robins et al., 2013; Ershova

135   et al., 2019). Given the proximate distance (~12 km) and presence of substantial changes in

136   seabed terrain and flow conditions between sites (Gage, 1972; Friedrich et al., 2014), we

137   infer that individuals from each site are likely not genetically distinct but will have been

138   exposed throughout their post-larval lifetimes to differing ecological and environmental

139   conditions (Alp et al., 2012). Loch Etive is subject to greater stratification and more frequent

140   episodic flushing relative to Loch Linnhe that affects nutrient and organic material dynamics

141   (Friedrich et al., 2014). Sediment at Loch Etive is finer and contains a significantly higher

142    total organic carbon (TOC) content in comparison to the Loch Linnhe site (ANOVA: $F_{2,10}$=

143    30.78, $P < 0.001$, Supporting information, Table S1 and Fig. S2 & S3).

144

145    Individuals were returned to the University of Southampton in aerated water baths and

146    acclimated to aquarium conditions (~ 12.6 ° C, 12 h light: 12 h dark cycle, continually

147    aerated) for a 30-day period. Estuarine mud from Hamble-le-Rice, Hampshire (50°52'23.1"N

148    1°18'49.3"W), was sieved (500 μm mesh) in a seawater bath to retain the fine fraction and

149    remove macrofauna and allowed to settle for 48 h before being homogenised and

150    distributed to Perspex aquaria (internal dimensions, LWH 12 x 12 x 35 cm; settled depth ~

151    10 cm overlaid with ~ 20 cm depth seawater, salinity 33). After 24 h and prior to the

152    addition of the organisms, the seawater was replaced to remove excess dissolved nutrients

153    associated with mesocosm assembly.

154

155    Our experiment required 102 aquaria arranged in a full factorial design (Supporting

156    information, Table S2 & S3). Replicate faunal assemblages (hereafter referred to as

157    'communities') from each sampling site (2 levels; Loch Etive and Loch Linnhe, which

158    represent historic exposures to discrete abiotic conditions hereafter referred to as

159    'populations') contained *A. filiformis* and *A. chiajei* in one of three species treatments (3

160    levels; monoculture of *A. filiformis*, monoculture of *A. chiajei*, or both species in mixture),

161    across three naturally observed densities (3 levels; low, medium and high, between 250 -

162    1000 ind. m$^{-2}$, Supporting information, Table S3). These species were selected for use given

163    their close taxonomic relation, their shared tolerance for variable biotic and abiotic contexts

164    (Calder-Potts et al., 2018), and their widespread co-occurrence throughout European shelf

165    waters (Gage, 1972) where they exert a dominant influence on local biochemical cycling

166    (Murray et al., 2013). The three density levels manipulated span the range reported from

167    across their European distribution *(*O'Connor et al., 1983; Duineveld et al., 1987; Munday &

168    Keegan, 1992) and therefore are not location specific. For this study, we adjusted the

169    densities of both species to reflect the approximate 3 *A. filiformis* : *2 A. chiajei* ratio

170    observed at the sample sites only as to avoid introducing novel aspects of biotic context.

171    Each combination of factors was replicated six times, with the exception of two treatments

172    (n = 4 and n = 5) (total n = 102, Supporting information, Table S3).

173

174    **2.2 Measures of individual trait expression**

175    Individual-level behavioural trait expression was represented through movement and burial

176    behaviours measured at the sediment surface following incubation and the quantification of

177    community- and ecosystem- properties. Individuals were inverted and placed on the

178    sediment surface in a temperature-controlled tray of sediment (3 cm depth overlaid with 5

179    cm depth seawater) under the same density and species treatment (monoculture or mixed)

180    conditions in which they had been previously maintained. A bench top video camera (uEYE

181    USB camera, 1.3 MP, 25 FPS; IDS Imaging Development Systems, Obersulm, Germany) was

182    used to record two righting and burial behaviours: i) the time taken for each individual to

183    begin movement activity, a response trait, and ii) the time taken for each individual to right

184    itself and bury fully into the sediment, an effect trait. Behaviour at the sediment surface

185    reflects the strength and nature of organismal responses to their biological and physical

186    surroundings (Rosenberg & Selander, 2000), and burial rate is indicative of functionally-

187    relevant movement behaviours at the individual level (Nagelkerken & Munday, 2016).

188

189 As morphological traits can significantly influence an individual's functional contribution

190 (Norkko et al., 2013), we determined arm length (cm) and disc diameter (cm) using image

191 analysis (ImageJ, version 1.46r; Schneider et al., 2012; Supporting information, Fig. S4), and

192 biomass (g), for each individual. Given the strong co-linearity between the metrics

193 (Supporting information, Fig. S5), the mean arm length (mean length of all five arms for

194 each individual, producing an individual-level morphological trait) was used to represent

195 morphological trait expression due to its greater relevance in brittlestar motility and feeding

196 behaviours (Rosenberg & Selander, 2000; Astley et al., 2012).

197

198 **2.3 Measures of community behaviour**

199 Burrow ventilation behaviour (bioirrigation) was estimated from the relative change in

200 water column concentrations of the inert tracer sodium bromide (NaBr, dissolved in 20 mL =

201 ~ 5 mM aquaria$^{-1}$), over an 8 h period (NaBr, dissolved in 20 mL = ~ 5 mM aquaria-1; Δ[Br−],

202 mg L$^{-1}$; negative values indicate increased activity; Forster et al., 1999). Filtered water

203 samples (5 mL, 0.45 μm cellulose acetate membrane filter) were taken on Day 29 of the

204 experimental period and stored at 6 °C prior to colorimetric analysis (FIAstar 5000 flow

205 injection analyser, FOSS Tecator).

206

207 Faunally mediated particle reworking (bioturbation) was estimated non-invasively using

208 sediment profile imaging (f-SPI) (Solan et al., 2004). To visualize particle movement 24 g dry

209 weight aquaria$^{-1}$ of dyed sediment that fluoresces in UV light (green colour; < 125 μm;

210 Brianclegg Ltd., UK) was introduced to the sediment surface on Day 23 and imaged 8 days

211 later (Day 31). This length of time is sufficient to allow visualisation of particle movement

212 whilst avoiding vertical homogenization of the tracers. Images of all four sides of each

213  mesocosm were taken within a UV illuminated imaging box. Following Solan et al. (2004),

214  images were saved in RGB colour mode with JPEG compression and analysed using a

215  custom-made semi-automated macro that runs within ImageJ (version 1.46r), a Java-based

216  public domain program (Schneider et al., 2012). From these data, the maximum depth of

217  particle reworking ($^{f\text{-}SPI}L_{max}$) was calculated and surficial activity was estimated by

218  quantifying surface boundary roughness (SBR), which is the maximum vertical deviation of

219  the sediment-water interface (upper – lower limit; Hale et al., 2014).

220

221  **2.4 Measures of ecosystem functioning**

222  Ecosystem functioning was represented through the proxy of sediment nutrient release,

223  which is mediated by the sediment movement behaviours of benthic fauna (Kristensen et

224  al., 2014; Wohlgemuth et al., 2017). Nutrient concentrations (ammonium, $NH_4$- N; nitrate,

225  $NO_3$-N; nitrite, $NO_2$-N; and phosphate, $PO_4$-P; µmol $L^1$) were determined from filtered water

226  samples (20 mL, Fisherbrand, nylon 0.45 µm, ⌀ 25 mm) taken on the final day of the

227  experiment (Day 30). Samples were frozen (−18 °C) and analysed using a segmented flow

228  autoanalyser (QuAAtro39 AutoAnalyzer).

229

230  **2.5 Statistical analysis**

231  Permutational multivariate analysis of variance (PERMANOVA) and ANOVA were used to

232  determine the independent and interacting effects of population (2 levels; Loch Etive, Loch

233  Linnhe), density (3 levels; low, medium, high) and species identity (for intraspecific trait

234  expression, 4 levels; *A. filiformis* in monoculture, *A. filiformis* in mixture, *A. chiajei* in

235  monoculture, *A. chiajei* in mixture) or species mixtures treatment (for community and

236  ecosystem measures, 3 levels; *A. filiformis* monoculture, *A. chiajei* in monoculture, *A.*

237  *filiformis - A. chiajei*  mixed treatment) on individual and community behavioural trait

238  expression, and associated ecosystem function. All statistical analyses were performed using

239  the *R* statistical and programming environment (R Core Team, 2017) and the vegan package

240  (Oksanen et al., 2017).

241

242  **2.5.1 Individual trait expression**

243  Multivariate analyses were used to represent overall differences in the behavioural

244  'personalities' of individuals between species identities and contexts (Moran et al., 2017),

245  integrating response (time to begin movement) and effect (time to complete burial) traits.

246  PERMANOVA (iterations = 999) was used, as it is robust to non-normality and differing

247  correlation structures and so is particularly suited for the detection of differences in

248  intraspecific trait expression (Mitchell & Bakker, 2014b). Patterns of intraspecific trait

249  expression differ between the behavioural traits, and between context treatments

250  (Supporting information, Fig. S6). Permutational analysis of multivariate dispersion

251  (PERMDISP) was used to test for homogeneity of variance between populations ($F_{1,190}$ =

252  0.57, $P$ = 0.45), species identities ($F_{1,188}$ = 1.20, $P$ = 0.31) and densities ($F_{1,189}$ = 1.22, $P$ = 0.30).

253  These results support that any significant differences in PERMANOVA between treatments

254  are due to changes in the values of trait expression, not shifts in the overall extent of

255  variation itself. Nevertheless, to negate any dispersion effects caused by unequal numbers

256  of individuals between groups, we standardised abundance between species treatments

257  and density levels (n = 192) (Supporting Information, Table S3).

258

259  PERMANOVA models were developed test the independent and interacting effects of; i)

260  community-level effects (population, species identity, density), and ii) individual-level

261    differences in morphological trait expression (mean arm length) between communities

262    (population, species identity), on multivariate intraspecific behavioural trait expression.

263    Data exploration showed there were differences in morphological trait expression between

264    populations (ANOVA: $F_{1,188}$ = 4.03, $P$ = 0.046) and species (ANOVA: $F_{1,188}$ = 14.99, $P$ < 0.001)

265    which may contribute to observed site-specific and interspecific effects.

266

267    To quantify the extent of intraspecific trait variation, the coefficient of variation (CV; the

268    ratio of standard deviation to the mean) was determined for the expression of each

269    individual-level trait (time to begin movement, time to complete burial, and mean arm

270    length).

271

272    **2.5.2 Community behaviour and ecosystem functioning**

273    4-way ANOVA was used to test the independent and interactive effects of context

274    (population, species treatment, density) and intraspecific variation in morphological trait

275    expression (CV of mean arm length) on each community-level behaviour ($\Delta[Br^-]$, $^{f\text{-}SPI}L_{max}$,

276    SBR), and a 3-way ANOVA was used to test the independent and interactive effects of

277    context (population, species treatment, density) on nutrient concentration ($[NH_4\text{-}N]$, $[NO_3\text{-}$

278    $N]$, $[NO_2\text{-}N]$, $[PO_4\text{-}P]$). Model assumptions were assessed visually for normality (Q-Q plot),

279    heterogeneity of variance (plotted residuals vs. fitted values), and the presence of outliers

280    or overly influential data points (Cook's Distance) and the minimal adequate effects

281    structure was determined using backward selection informed by Akaike Information Criteria

282    (AIC) (Zuur et al., 2009).

283

284    **3 Results**

**3.1 Individual trait expression**

With respect to all aspects of context (population, species identity, density), PERMANOVA revealed that behavioural trait expression was dependent on the independent effects of species identity ($F_{3,168}$ = 6.08 $P$ < 0.01), density ($F_{2,168}$ = 3.82, $P$ < 0.01), and population ($F_{1,168}$ = 4.24, $P$ = 0.025) (Fig. 1a – 1f).

When considered alongside only those aspects of context which define the identity (population, species identity) and morphological trait expression (mean arm length) of individuals, behavioural trait expression was dependent on the interactive effects of mean arm length x population of origin (PERMANOVA: $F_{1,176}$ = 3.71, $P$ = 0.036) (Fig. 1e – 1h), in addition to the independent effect of species identity (PERMANOVA: $F_{3,176}$ = 5.72, $P$ < 0.01) (Fig. 1a – 1b).

Though analysed together in a multivariate manner, both movement behaviours (time to begin activity, and time to complete burial) were visualised independently to highlight differences in expression between each trait. Overall, *A. chiajei* took significantly longer before beginning or completing burial than *A. filiformis*, however intraspecific differences are present in both species and between individuals maintained in monoculture or in a mixed community. The extent of these context-dependent differences varied depending on the trait, and patterns between treatment conditions were consistently less prominent for the time taken to begin movement. For both *A. chiajei* and *A. filiformis,* the time taken to fully complete burial was increased in mixed species treatments in comparison to monoculture, with a similar if weaker pattern suggested for *A. chiajei and* the time taken to begin movement (Fig. 1a – 1b). For both species, the time taken to complete burial

309      decreased with density (Fig. 1c – 1d). Individuals from Loch Linnhe had significantly (ANOVA:

310      $F_{1,188}$ = 4.033, $P$ = 0.046) larger mean arm lengths (*A. filiformis* mean ± SE (n = 55) 27.88 ±

311      11.17, *A. chiajei* mean ± SE (n = 51) 36.54 ± 12.85, Supporting information, Fig. S7) than

312      those originating from Loch Etive (*A. filiformis* mean ± SE (n = 40) 27.06 ± 7.57, *A. chiajei*

313      mean ± SE (n = 46) 30.30 ± 11.68), and completed movement behaviours more rapidly (Fig.

314      1e – 1h). The coefficient of variation of both behavioural traits (time to begin activity and

315      time to complete burial) within communities did not differ significantly between variables or

316      their interactions (ANOVA: $P$ > 0.05 for all, Supporting information, Table S4), though trends

317      suggest comparatively greater extents of variation may occur for both behavioural traits for

318      individuals maintained under elevated density or in a mixed species treatment, or those

319      originating from Loch Etive (Supporting information, Fig. S8).

320

321      **3.2 Community behaviour**

322      Community-level bioturbation and bioirrigation behaviours were differentially affected by

323      abiotic and biotic context (species mixture treatment, density, population) and

324      morphological trait variation. The maximum depth of particle redistribution, $^{f\text{-}SPI}L_{max}$, was

325      significantly affected by the independent effects of density (ANOVA: $F_{2,60}$ = 5.85, $P$ < 0.01)

326      and population (ANOVA: $F_{1,60}$ = 8.68, $P$ < 0.01). $^{f\text{-}SPI}L_{max}$ increased with density (Fig. 2a), while

327      remaining shallower in mesocosms with individuals from Loch Etive in comparison to Loch

328      Linnhe (coefficient ± SE = 0.40 ± 0.51, t = 0.78, $P$ = 0.44) (Fig. 2b). SBR differed significantly

329      with the interactive effects of density x species treatment (ANOVA: $F_{4,74}$ = 3.16, $P$ = 0.018),

330      and population of origin x morphological trait variation (ANOVA: $F_{1,74}$ = 4.81, $P$ = 0.031). The

331      magnitude of differences in SBR between species treatments were increased at greater

332      densities (Fig. 2c), with higher surface boundary roughness found in Loch Linnhe

333    communities with greater morphological trait variation (CV mean arm length) (Fig. 2d).

334    Though the extent of variation for average arm length did not differ significantly between

335    densities (ANOVA: $F_{2,78}$ = 1.76, $P$ = 0.18), species treatments (ANOVA: $F_{2,78}$ = 0.61, $P$ = 0.55)

336    or populations (ANOVA: $F_{1,78}$ = 0.02, $P$ = 0.88), variation in the morphology of individuals

337    was comparatively elevated for individuals originating from Loch Linnhe or maintained

338    under medium density (Supporting information, Fig. S9). Bioirrigation activity ($\Delta[Br^-]$) did

339    not vary with abiotic or biotic context as results showed that, although the density x

340    population interaction was included in the minimal adequate mode, its effects were non-

341    significant (ANOVA: $F_{2,90}$ = 1.11, $P$ = 0.34, Supporting information, Fig. S10).

342

343    **3.3 Ecosystem functioning**

344    The effect of biotic and abiotic context on sediment nutrient release differed between

345    nutrients (Fig. 3). [$NH_4$-N] was significantly influenced by the interactive effect of population

346    x density (ANOVA: $F_{2,85}$ = 3.15, $P$ = 0.048). Overall, [$NH_4$-N] was increased in communities

347    originating from Loch Linnhe in comparison to those from Loch Etive (coefficient ± SE = 2.31

348    ± 1.81, t = 1.27, $P$ = 0.21), with clearer differences in [$NH_4$-N] between populations at lower

349    densities (Fig. 3a). [$NH_4$-N] was also significantly affected by species treatment (ANOVA: $F_{2,85}$

350    = 3.22, $P$ = 0.045), being greatest in *A. chiajei* monoculture communities (Fig. 3b). [$NO_3$-N]

351    was significantly affected by density (ANOVA: $F_{2,89}$ = 16.38, $P$ < 0.01) and population

352    (ANOVA: $F_{1,89}$ = 6.95, $P$ < 0.01), decreasing with density, and with lower concentrations

353    found in Loch Linnhe communities (coefficient ± SE = -3.95 ± 1.5, t = -2.64, $P$ < 0.01) (Fig. 3c

354    & 3d). [$NO_2$-N] was significantly affected by population (ANOVA: $F_{1,83}$ = 5.94, $P$ = 0.017),

355    showing greater concentrations communities originating from Loch Linnhe (coefficient ± SE

356    = 17.83 ± 7.43, t = 2.4 $P$ = 0.019) (Fig. 3e). [$PO_4$-P] was significantly affected by the

357  interactive effect of species treatment x density (ANOVA: $F_{4,84}$ = 2.81, $P$ = 0.030), with

358  overall $PO_4$-P concentration, and the magnitude of difference between species treatments,

359  decreasing with density (Fig. 3f).

360

361  **4 Discussion**

362  Overall, our results demonstrate significant influence of context on the trait expression of

363  individuals. We show that this context-dependency then affects the functional roles and

364  contributions of species by mechanistically underpinning concurrent change in community

365  behaviour and ecosystem functioning.

366

367  We found site-specific and interspecific differences in morphological trait expression. By

368  consequence, it is difficult to interrogate the role of population or species *per se* in

369  determining behavioural trait expression. Body size determines the scaling relationship

370  between the traits expressed by a species and their ecosystem role, and larger individuals

371  are often liable to have stronger effects on ecosystem functioning (Larsen et al., 2005).

372  Given this relationship, intraspecific morphological variability has already been incorporated

373  into some functional trait approaches via a community average (Solan et al., 2004). Body

374  size traits are a complex and potentially transient response to genetic influences, age, food

375  and other resources (Liao et al., 2016). Even where two organisms are allegedly found

376  within the same functional group, larger individuals are expected to have proportionally

377  larger effects to ecosystem functioning (e.g. displace more sediment and pump more water

378  (Norkko et al., 2013), and intraspecific morphological expression may be a significant

379  influence on the functional roles of species. However, even beyond the contributions of

380  morphological differences, individuals with shared local histories are likely to consistently

381   express similar traits (Fisher et al., 2015; Moran et al., 2017; Peterson et al., 2019). Abiotic

382   context influences the presence, plasticity and strength of traits expressed within a

383   community (Calosi et al., 2013; Törnroos et al., 2015; Nagelkerken & Munday, 2016).

384   Organic matter content and sediment grain size, which differ between Loch Etive and Loch

385   Linnhe, notably affect organism behaviour in terms of sediment mixing and bioirrigation

386   (Bulling et al., 2008; Godbold & Solan, 2009). Origin in the distinct conditions of either loch

387   contributes to differences in trait expression at an individual-level, and in the community-

388   level net effects which these traits in part underpin (Wohlgemuth et al., 2017).

389

390   Further, density and species identity influence intraspecific behavioural trait expression as

391   community composition determines the neighbour-effects that dictate behaviours including

392   space and resource use (De Backer et al., 2011; Kraft et al., 2015; Calder-Potts et al., 2018).

393   These effects in turn underpin the role of shifting biodiversity in driving altered ecosystem

394   functioning (Thomsen et al., 2019). Changes in the extent and structure of biodiversity alter

395   not only functional diversity at the community-level, but form differing biotic contexts with

396   influence on the trait expression and functional roles of component individuals

397   (Wohlgemuth et al., 2017; Adair et al., 2018). Behavioural factors are among the more

398   flexible aspects of an animal's phenotype as they are less likely to be constrained by strict

399   physiological tolerances, and so their variation readily reflects short- and long-term

400   responses of each species to local conditions (Fisher et al., 2015). The competitive

401   advantage offered by this trait dissimilarity, and so its role in determining community

402   structure, depends on whether individuals are involved in intra- and interspecific

403   competition, as species may benefit from expressing novel (Finerty et al., 2016) or more

404   acquisitive phenotypes (Bennett et al., 2016). Our results show that, even where species are

405    distinguished by interspecific differences in behavioural or morphological traits (Buchanan,

406    1964), each taxa may also display distinct intraspecific responses between communities of

407    differing compositions (Zuo et al., 2017).

408

409    The potential for intraspecific variation should not be overlooked, given that it can strongly

410    determine the functional identity and context-dependent contributions of each species (Des

411    Roches et al., 2018). Context-dependent variation may have consequences for ecosystem

412    functioning as it can change, expand, or narrow the distribution of relevant traits expressed

413    and so alter the assumed functional contributions of organisms (Matesanz & Ramírez-

414    Valiente, 2019). Differences in sediment reworking between treatments mechanistically

415    underpin the differences in dissolved nutrient release observed between the same

416    conditions, demonstrating that change in behavioural trait expression influences

417    biogeochemical processes and so mediates the functioning of benthic habitats (Kristensen

418    et al., 2014; Wohlgemuth et al., 2017). However, establishing the relative importance of

419    intraspecific and interspecific variation has long been a focus of trait-based ecology (Albert

420    et al., 2010; Zuo et al., 2017). The necessity of considering intraspecific variation is likely to

421    be determined by the extent of variability within a trait (Henn et al., 2018), the strength of

422    its relationship with ecosystem function (Mensens et al., 2017), and indeed the research

423    question at hand. We suggest that quantifying the extent of intraspecific variation should be

424    a particular priority where environmental conditions are changing, or where taxa are

425    compared across gradients. Mesocosm experimental studies or sub-sampling of trait

426    expression *in situ* offers ability to establish the realised functional contributions or

427    variability of species in complement to conventional trait-based study (Henn et al., 2018). It

428    is probable that interspecific differences will exceed intraspecific differences in terms of

429    magnitude (Derroire et al., 2018), and that quantification of intraspecific variability will be

430    less likely to alter projections of functioning and service delivery at ecosystem-scales with

431    high species richness (Wright et al., 2016). Nonetheless, to do so characterises the sources,

432    pathways, and potential consequences of altered conditions (Albert et al., 2010; Fisher et

433    al., 2015). Intraspecific trait variation and its covariation with interspecific trait variation

434    together determine community responses to ecological change (Zuo et al., 2017).

435

436    Given that natural systems are increasingly subject to drivers of ecological change, we

437    highlight the need to determine the contexts in which intraspecific variability arises (Moran

438    et al., 2017; Matesanz & Ramírez-Valiente, 2019). Within this framework, we must isolate

439    the circumstances where it contributes to the functional integrity of ecosystems (Wright et

440    al., 2016; Zuo et al., 2017). Failure to do so jeopardises understanding and prediction of

441    ecosystem functioning due to inadequate characterisation of traits and, by result,

442    biodiversity (Wohlgemuth et al., 2017; Adair et al., 2018; Des Roches et al., 2018). Trait-

443    based models for predicting community structure across environmental gradients perform

444    poorly when they fail to integrate the effects of intraspecific variation in functional traits, as

445    existing typologies are insufficiently broad (Read et al., 2017). Our findings demonstrate

446    that trait-based approaches to ecosystem study require more detailed functional metrics

447    than has previously been assumed. Future efforts should seek to report responses under

448    multiple ecosystem conditions, to demonstrate the potential breadth of resulting

449    intraspecific diversity, and consider how these effects will propagate up biological scales

450    (Carmona et al., 2016; Finerty et al., 2016; Funk et al., 2017; Matesanz & Ramírez-Valiente,

451    2019).

452

**5 Conclusions**

Our findings show that the expression of traits by individuals and so the net behaviour of their communities differs with biotic and abiotic context. Such changes in individual functional contributions have important implications for mediation of ecosystem functioning. Our study highlights that trait-based approaches which do not consider the context-dependency of trait expression are at risk of misrepresenting the functional roles of taxa. Quantification of intraspecific variability will offer ecologists better insight into biological responses to environmental conditions, and aid ecosystem management approaches seeking to maintain good ecosystem function and service delivery in the face of environmental change.

**Data accessibility**

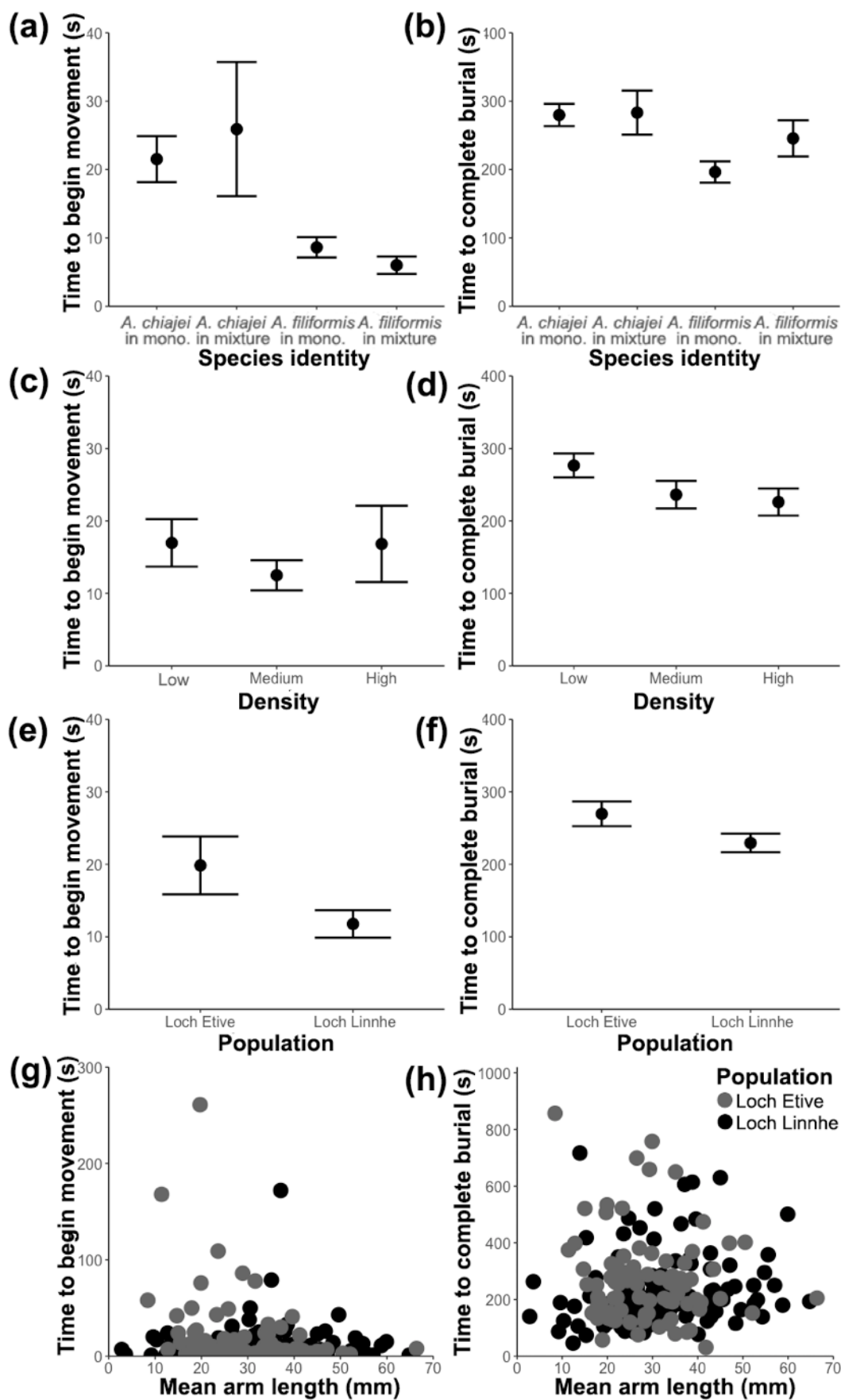Supporting information for this article have been uploaded as supplementary material. Raw data is archived at the Dryad Digital Repository (https://doi.org/10.5061/dryad.14t4h37).

**Figures**

479　**Fig. 1:** The effect of biotic and abiotic context on time elapsed (mean ± SE) (s) for *Amphiura*

480　*chiajei* and *Amphiura filiformis* to (**a, c, e, g**) begin movement and (**b, d, f, h**) complete burial

481　into the sediment, where (**a** - **b**) show the independent effects of species identity, (**c** - **d**)

482　show the independent effect of density, (**e** - **f**) show the independent effect of population of

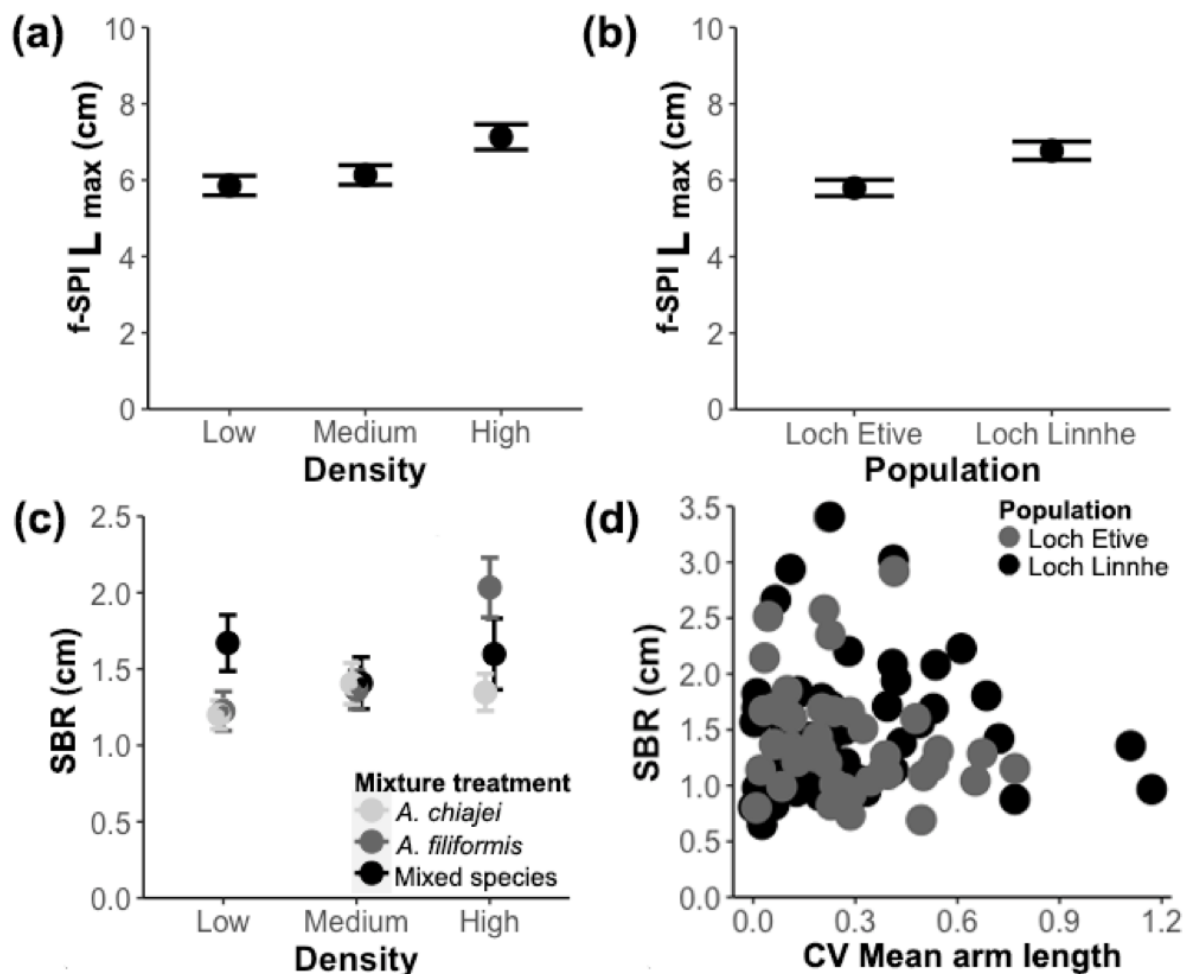483　origin, and (**g** - **h**) show the interactive effect of population x mean arm length (mm).

484



485

486　**Fig. 2:** The effects of biotic and abiotic context on (mean ± SE, n= 6) (**a**) and (**b**) $^{f-SPI}L_{max}$ (cm)

487　and (**c**) and (**d**) surface boundary roughness (SBR) (cm) in mesocosms containing *Amphiura*

488　*filiformis* and *Amphiura chiajei* in monoculture or mixture, showing the (**a**) independent

489　effect of density and (**b**) the independent effect of population, (**c**) the interactive effect of

490    density x species treatment, and (**d**) the interactive effect of morphological trait variation
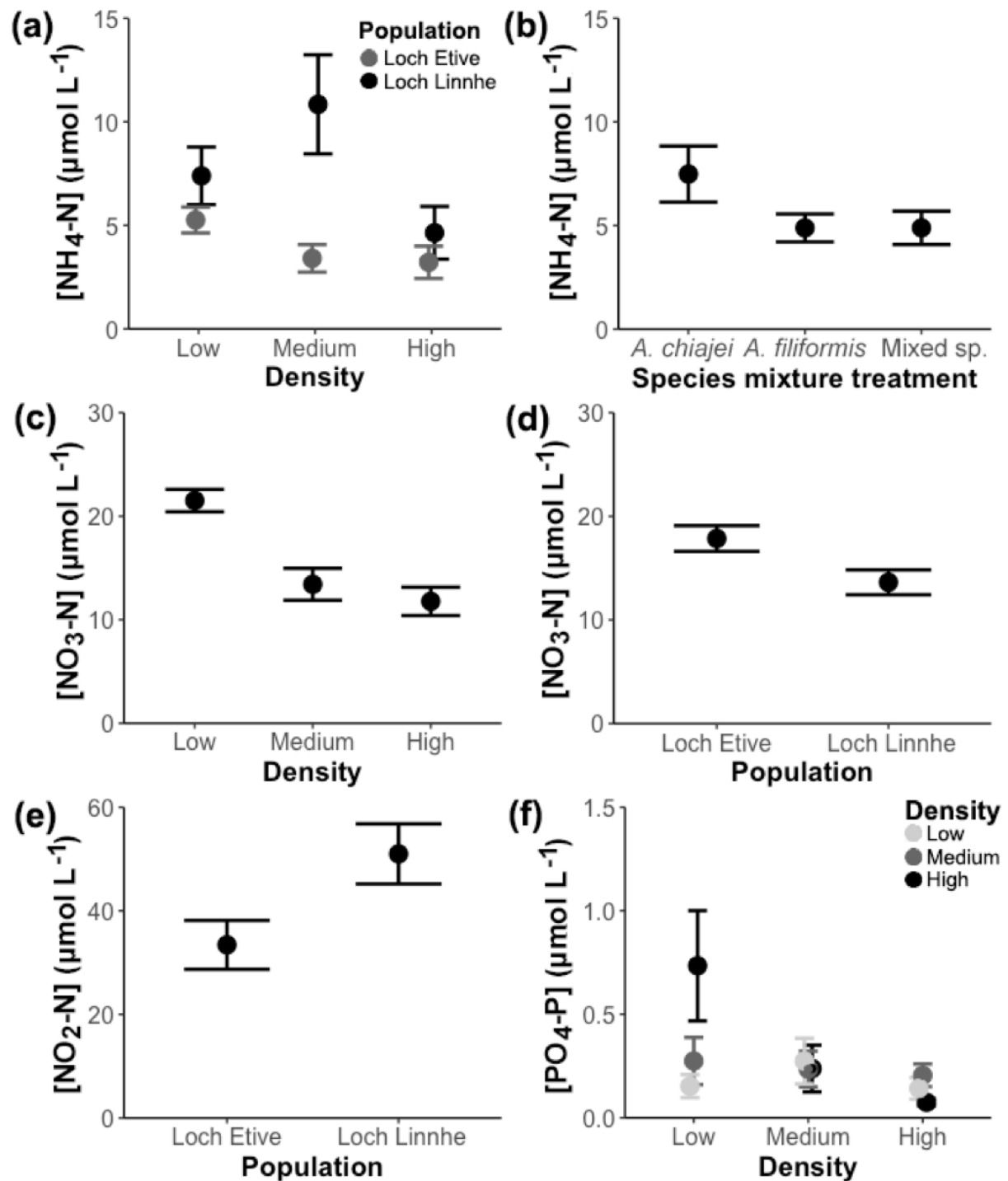
491    (CV of mean arm length) and population.

492



493

494    **Fig. 3:** The effects of differing biotic and abiotic context on (mean ± SE, n= 6) (µmol L$^{-1}$) (**a**)

495    and (**b**) [NH$_4$-N], (**c**) and (**d**) [NO$_3$-N], (**e**) [NO$_2$-N], and (**f**) [PO$_4$-P] where (**a**) shows the

496    interactive effects of density x population, (**b**) shows the independent effect of species

497    treatment, (**c**) and (**d**) show the independent effects of density and population, respectively,

498    (**e**) shows the independent effect of population, and (**f**) the interactive effect of density x

499    species treatment.

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