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Published in:

Annals of Botany

DOI:

[10.1093/aob/mcad183](https://doi.org/10.1093/aob/mcad183)

Publication date:

2024

Document version:

Peer reviewed version

Link:

[Link to publication in PEARL](#)

Citation for published version (APA):

Amstutz, A., Firth, L. B., Foggo, A., Spicer, J. I., & Hanley, M. E. (2024). The north–south divide? Macroalgal functional trait diversity and redundancy varies with intertidal aspect. *Annals of Botany*, 133(1), 145-152. <https://doi.org/10.1093/aob/mcad183>

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The north-south divide? Macroalgal functional trait diversity and redundancy varies with intertidal aspect

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Running Title: Aspect and Seaweed Functional Traits

1 **Abstract**

2 **Background and Aims:** Marine macroalgae ('seaweeds') are critical to coastal
3 ecosystem structure and function, but also vulnerable to the many environmental
4 changes associated with Anthropogenic Climate Change (ACC). The local habitat
5 conditions underpinning observed and predicted ACC-driven changes in intertidal
6 macroalgal communities are complex and likely site-specific, in addition to more
7 commonly reported regional factors like sea surface temperatures.

8 **Methods:** We examined how the composition and functional trait expression of
9 macroalgal communities in SW England varied with aspect (i.e., north-south
10 orientation) at four sites with opposing Equator- (EF) and Pole-facing (PF) surfaces.
11 Previous work at these sites had established that average annual (low tide) temperatures
12 vary by 1.6°C and that EF surfaces experience six-fold more frequent extremes (i.e., >
13 30°C).

14 **Key Results:** PF macroalgal communities were consistently more taxon rich; eleven
15 taxa were unique to PF habitats, with only one restricted to EF. Likewise, functional
16 richness and dispersion were greater on PF surfaces (dominated by algae with traits
17 linked to rapid resource capture and utilization, but low desiccation tolerance), although
18 differences in both taxon and functional richness were likely driven by the fact that less
19 diverse EF-surfaces were dominated by desiccation-tolerant fucoids.

20 **Conclusions:** Although we cannot disentangle the influence of temperature variation on
21 algal ecophysiology from the indirect effects of aspect on species interactions (niche
22 pre-emption, competition, grazing etc), our study system provides an excellent model
23 for understanding how environmental variation at local scales affects community

24 composition and functioning. By virtue of enhanced taxonomic diversity, PF-aspects
25 supported higher functional diversity, and consequently, greater effective functional
26 redundancy. These differences may imbue PF-aspects with resilience against
27 environmental perturbation, but if predicted increases in global temperatures are
28 realised, some PF-sites may shift to a depauperate, desiccation-tolerant seaweed
29 community with a concomitant loss of functional diversity and redundancy.

30

31 **Keywords:**

32 *Anthropogenic Climate Change; Aspect; Biodiversity-ecosystem functioning; Extreme*
33 *Temperatures; Functional Redundancy; Functional Traits; Rocky Shore; Seaweed*

34

35 **Introduction**

36 Globally, ecosystems face unprecedented pressures from a combination of habitat loss,
37 over exploitation, invasive species, and a rapidly changing climate (MEA, 2005; Venter
38 et al., 2016; Parmesan et al., 2022). The potential impact of these changes on
39 biodiversity and ecosystem service provision is well established (Isbell et al., 2017; Paul
40 et al., 2020). Central to the biodiversity-ecosystem functioning (BEF) relationship, is
41 the notion of ‘functional complementarity/redundancy’; i.e., how the impact of species
42 losses on ecosystem function and resilience may be compensated if functionally similar
43 organisms are present but increase drastically once all species within a functional group
44 are lost (Yachi & Loreau, 1999; Naeem, 2002; Seddon et al., 2016). Although several
45 studies have demonstrated the robustness of the functional redundancy concept, it is
46 apparent that assessment and prediction of the ecological consequences of
47 environmental change for the contribution of functional diversity to the BEF
48 relationship differs between ecosystems and environments (Cardinale, 2011; Fetzer et
49 al., 2015; Dolbeth et al., 2019).

50 Capturing the effects of environmental perturbation upon functional redundancy and the
51 BEF in field conditions is challenging. Manipulation of single and multiple key
52 environmental factors like temperature and precipitation is possible (Firth and Williams,
53 2009), but inevitably limited to imposing a short-duration ‘pulse’ or a limited range of
54 relatively fixed experimental treatments (compared to ambient), in a single habitat type
55 (Pfisterer & Schmid, 2002; Allison, 2004; Grime et al., 2008; Vetter et al., 2020).
56 Although microbial microcosms offer a tractable way to manipulate, replicate and
57 control species (functional) composition and multiple external environmental conditions

58 (Fetzer et al., 2015; Banitz et al., 2020), they are a poor surrogate for the very different
59 biological responses of plants and animals to fluctuating environments in natural field
60 conditions (Fetzer et al., 2015). Not least of these differences is the fact that the
61 regeneration biology of many eukaryotes is cued to variations and interactions of
62 climate extremes, rather than changes in average temperature or precipitation (Parmesan
63 & Hanley, 2015; Parmesan et al., 2022). In addition, shifts in species geographic
64 distributions of the kind associated with Anthropogenic Climate Change (ACC) and
65 particularly with extreme weather events (Crisp, 1964; Firth et al., 2015, 2021; Filbee-
66 Dexter et al., 2020) impose rapid changes in local community structure and ecosystem
67 functioning (Usinowicz and Levine, 2018; Aguilera et al., 2020; Vetter et al., 2020).

68 Taken together, these issues highlight the importance of comparative, field-based
69 studies to better understand and predict the consequences of environmental variation for
70 ecosystem functioning. The challenge is finding ecological communities in different
71 habitats where natural fluctuations and extremes in critical environmental factors like
72 (for example) temperature occur. Aspect (i.e., north-south orientation) may be one such
73 opportunity.

74 In terrestrial systems, variation in species distributions has long been associated with
75 habitat orientation towards the sun (Cantlon, 1953; Nevo, 2012). Recent studies in
76 marine intertidal systems also highlight considerable local differences in thermal
77 conditions and species assemblages on Pole-Facing (PF) versus Equator-Facing (EF)
78 surfaces (Seabra et al., 2011; Firth et al., 2016; Lima et al., 2016). Moreover, when
79 compared at relatively local scales (i.e., PF and EF slopes are metres apart), other
80 confounding factors (resource and propagule availability, precipitation, disturbance,

81 etc.) likely remain relatively constant, while natural average and extreme temperatures
82 vary significantly. For example, Amstutz et al (2021) reported average annual low tide
83 (i.e., ‘air’) temperatures 1.6°C higher on EF than PF rock surfaces, with high extremes
84 (i.e., > 30°C) six times more frequent on EF-surfaces. Unsurprisingly, community
85 composition also varied with aspect, but the effect was apparent both within (e.g., more
86 patellid and trochid grazing molluscs on PF-surfaces), as well as between (e.g., more
87 carnivorous dogwhelks on PF-surfaces, but fewer filter-feeding barnacles) trophic
88 levels. Moreover, Amstutz et al (2021) also observed aspect-related variation in
89 reproductive phenology and thermal stress responses in two patellid limpet species.

90 In demonstrating substantial variation in average and extreme temperature conditions
91 over just a few meters, Amstutz et al (2021) highlighted the excellent potential intertidal
92 gullies have for elucidating the effect of ACC-linked warming on community pattern
93 and process. Their study however, focussed on intertidal invertebrate abundance and did
94 not consider how functional traits within communities varied with aspect. Marine
95 macroalgae (‘seaweeds’) play a critical role in ecological structure and functioning in
96 the intertidal and coastal shelf environments (Ling et al., 2009; Johnson et al., 2011;
97 Pessarrodona et al., 2022), but are especially vulnerable to the physico-chemical
98 changes associated with ACC (Harley et al., 2012; Smale et al., 2013). As a result,
99 dramatic changes in macroalgal assemblages have been observed (Wernberg et al.,
100 2011; Vale et al., 2021; Smale et al 2022), although the majority of range shifts and
101 species turnover responses reported in the literature are attributed to regional increases
102 in sea surface temperatures (SSTs) and their effects upon subtidal algae. Given the
103 importance of local habitat (e.g., surface topography and aspect) for organism
104 behaviour, abundance and distribution, and provision of refugia from the environmental

105 stresses that characterise the intertidal (Helmuth et al., 2006; Johnson et al., 2008;
106 Bracewell et al., 2018; Jurgens et al., 2022), our ability to predict intertidal community
107 and species response to ACC must consider these factors (Barton et al., 2019; Amstutz
108 et al., 2021; Vale et al., 2021). Consequently, the aim of this study was to elucidate how
109 ACC-linked warming is likely to affect community assembly and process in intertidal
110 macroalgal assemblages and subsequent shifts in the trait characteristics possessed by
111 seaweeds on cooler PF- and warmer EF-aspects. To do this, we investigated how
112 intertidal aspect (and the temperature variation associated with PF- and EF-slope
113 orientation) influenced intertidal macroalgae communities, specifically testing the
114 predictions that (i) community composition and taxon richness vary between EF- and
115 PF-surfaces and that consequently, (ii) functional diversity, and thence redundancy, also
116 vary with aspect.

117

118 **Methods**

119 *Study sites and sampling*

120 Intertidal surveys were carried out on four natural rocky shores on the north and south
121 coasts of the southwest peninsula of England: Bude (50.836667, -4.556944) and Croyde
122 (51.133889, -4.243889) on the north coast and, Bantham (50.276944, -3.884722) and
123 South Milton Sands (50.253889, -3.861944) on the south coast. All sites share similar
124 geology (Upper Palaeozoic, inter-bedded shales and sandstones) with strata tilted at 80°-
125 90° (i.e., vertical dip) running perpendicular (i.e., east-west strike) to the shoreline and
126 where erosion of softer sediments had created a series of almost-vertical 1-5m high,

127 gullies with pole- (north-) or equator- (south-) facing rock surfaces (Amstutz et al.,
128 2021).

129 At each location, four gullies were haphazardly selected, but with the *proviso* that they
130 provided access to long sections of opposing PF and EF vertical rock surfaces at mid-
131 shore level. This spatial configuration reduced the possibility of variation in wave
132 exposure between EF and PF rock surfaces. In summer 2016 (June and July) and winter
133 (January/February) 2017, twelve 0.5 x 0.5 m (0.25m²) quadrats were haphazardly
134 positioned along each of four gullies at each site, such that PF- and EF-quadrats
135 opposed each other at the same relative shore height in each gully (a total 192 quadrats
136 per season). Quadrats were placed on vertical, flat surfaces, avoiding crevices, pools and
137 other microhabitats, and the overall percentage cover of all component macroalgae was
138 estimated.

139 *Analysis of Community Structure*

140 We identified seaweeds in the field as accurately as possible, lumping problem taxa to
141 genera where necessary (hereafter referred to as operational taxonomic units - OTUs –
142 rather than ‘species’). We estimated the number of OTUs in each gully by averaging
143 across quadrats, and tested for an effect of ‘Aspect’, ‘Season’ and ‘Site’ (fixed effects)
144 using a Poisson error generalized linear model in R ver 4.0 (R Core Team 2021). The
145 model was simplified using single term deletions based upon change in AIC >2;
146 estimated marginal means tests (R package *emmeans*, Lenth, 2020) were used to derive
147 pair-wise comparisons between aspects within sites where appropriate.

148 To test the hypothesis that macroalgal assemblages differed across aspects in the
149 different sites we used pairwise contrasts within a mixed model PERMANOVA

150 implemented in PRIMER v6, with ‘Aspect’ and ‘Season’ as fixed factors and ‘Site’ as a
151 random factor. To minimise effects of abundant taxa, data were 4th-root transformed
152 prior to calculation of a similarity matrix based upon Bray-Curtis distances. The
153 pairwise contrast compared aspects within sites across different seasons; data
154 imbalances in terms of numbers of quadrats (e.g., zero counts) led us to average
155 macroalgal data to the gully level, thus each ‘Aspect’ × ‘Site’ × ‘Season’ had $n = 4$, and
156 $N = 64$. Patterns of similarity and difference were visualized using the ‘ordiplot’
157 function in R package *vegan* (Oksanen et al., 2020).

158 *Analysis of Functional Traits*

159 Functional diversity was estimated in two complimentary ways to account for the
160 functional contributions of the considerable number of gullies supporting fewer than
161 three algal taxa (in which cases some functional diversity metrics cannot be calculated),
162 and to allow us to incorporate encrusting alga for which we lacked functional trait data
163 in the database we employed.

164 First we used the extensive database of functional trait scores provided by Mauffrey et
165 al., (2020a,b) to calculate values of Functional Richness (*FRic*) (Villéger et al., 2008)
166 and Functional Dispersion (*FDis*) (Laliberté & Legendre, 2010), as measures of
167 functional alpha and beta diversity respectively, using *dbFD* in the R package *FD*
168 (Laliberté & Legendre, 2010, Laliberté et al., 2014). *FRic* is a measure of the total
169 extent of niche space occupied by an assemblage and is distinct from the number of
170 functional groups present. *FDis* is a measure of the mean distance of all species to the
171 weighted centroid of the community in the trait space. Mauffrey et al’s., (2020b)
172 database includes traits linked to photosynthetic capacity, structure, and space use that

173 together provide information about resource acquisition, productivity and competitive
174 dominance, desiccation and herbivory tolerance, and resistance to water movement. We
175 selected 11 of the 12 traits employed by Mauffrey et al., (2020b) (we excluded the
176 presence of pneumatocysts, as when sampled, none of our taxa possessed them).
177 Functional diversity measures were calculated based upon Euclidean distances using
178 standardized, abundance-weighted trait scores (where relevant). Where OTUs at the
179 species level in our dataset had traits not present in the Mauffrey et al., (2020b)
180 database, we attributed trait scores either by averaging across congeners in the database
181 or by using multivariate imputation by chained equations (*MICE* package: van Buuren
182 & Groothuis-Oudshoorn, 2011) provided that >70% of species scores were present. We
183 tested these measures of functional diversity using the same linear modelling approach
184 applied to taxonomic species richness, transforming data to achieve homogeneity of
185 variances where necessary.

186 Second, we allocated the 24 macroalgal OTUs recorded to the ‘Emergent Functional
187 Groups’ described by Mauffrey et al., (2020a). We included additional functional
188 groups for encrusting red and brown algae respectively, in order to compare at the gully
189 level how the rate of accumulation of observed functional group richness responds to
190 increasing taxonomic species richness in the two different aspects (see SoI Table 1). We
191 also performed this comparison for *FRic* and *FDis*, testing heterogeneity of response in
192 diversity accumulation using type III SS linear models.

193 We hypothesized that rates of accumulation of functional groups/diversity per OTU
194 would not differ if the degree of relative functional richness per OTU is consistent

195 across aspects (see Micheli & Halpern 2005). The lower the rate of accumulation of
196 functional groups/diversity, the more likely the OTUs are to be functionally redundant.

197

198 Results

199 *Aspect and Community Structure*

200 Although total algal cover varied little on PF-slopes with season (circa 3%), on EF-
201 slopes cover more than doubled between summer (circa 8%) and winter (circa 17%).
202 These values are, fairly typical of the moderately exposed, barnacle and limpet
203 dominated shores of SW England. Twenty-four OTU's were recorded, and of these,
204 eleven were present only on PF-surfaces (SoI Table 1). Two taxa (*Lithophyllum*
205 *incrustans* and *Lomentaria articulata*) were also noticeably more common (i.e., more
206 than an average 5% difference) on PF-slopes in summer and/or winter surveys. Only
207 one species (*Blidingia minima*) was restricted to EF aspects, and this was a single
208 record, but *Fucus* sp. (hereafter 'fucoids' - combined because individuals were often too
209 small to be confidently identified to species), were especially noteworthy in being
210 consistently more abundant on EF- than PF-slopes (average 1.6% EF vs 0.5% PF in
211 summer and 1.7% EF vs 0.8% PF in winter). Three entire gulley sites were devoid of
212 macroalgae, these were excluded from further analyses due to their disproportionate
213 leverage values.

214 PF- were more species-rich than EF-surfaces in all sites (Fig 1), supporting an average
215 of 3.7 more OTUs ('Aspect' Wald $\chi^2 = 22.866$; $P < 0.001$), while summer samples
216 supported on average 1.1 more OTUs than winter samples ('Season' $\chi^2 = 1.972$; $P =$
217 0.160). Sites did not differ significantly ($\chi^2 = 3.422$; $P = 0.181$), and no significant
218 interactions involving 'Aspect' were found ('Aspect' \times 'Season' $\chi^2 = 0.325$; $P = 0.569$;
219 'Aspect' \times 'Site' $\chi^2 = 2.942$; $P = 0.230$).

220 Unsurprisingly, algal assemblages varied across all four sites (PERMANOVA $P_{su}F_{3,48} =$
221 4.0475; $P < 0.001$), but while there was a seasonal effect ($P_{su}F_{1,48} = 8.9749$; $P = 0.0385$),
222 we also found a consistent influence of aspect on community composition ($P_{su}F_{1,48} =$
223 16.211; $P = 0.0289$). Contrasts of aspects within sites reinforced this picture (Fig 2,
224 **Supplemental Figures 1a and b**), indicating highly significant differences in algal
225 assemblages between aspects in both seasons at Bude ($t = 3.8256$; $P < 0.001$), Croyde (t
226 $= 2.8244$; $P < 0.001$), and South Milton ($t = 3.0468$; $P < 0.001$). The pattern of
227 difference was less marked at Bantham ($t = 1.931$; $P = 0.0207$), largely as a result of
228 variability attributable to equator-facing gullies lacking macroalgal colonisation. We
229 detected no significant interactions between ‘Site’, ‘Season’ and ‘Aspect’. Collectively,
230 there was strong support for our hypothesis that macroalgal community composition
231 and species (OTU) richness vary between EF- and PF-surfaces.

232

233 *Functional Trait Variation and Redundancy*

234 Following a square-root transformation to homogenise variance prior to analysis by
235 linear model, we established that ‘Aspect’ was a significant predictor of number of
236 functional groups ($F_{1,40} = 20.113$, $P < 0.001$). There was, however, no influence of
237 ‘Season’ ($F_{1,40} = 0.0418$, $P = 0.8391$), or ‘Site’ ($F_{2,40} = 0.5479$, $P = 0.5824$) and no
238 significant interaction between ‘Aspect’ and ‘Season’ ($F_{1,40} = 0.2832$, $P = 0.5976$).
239 Consequently, the emergent pattern of more Functional Units on PF-slopes was
240 consistent across seasons and sites (Figure 3a).

241 By contrast, although there was a tendency towards higher Functional Richness ($FRic$)
242 on PF- slopes at three sites (Figure 3b), we established that $FRic$ did not vary with

243 ‘Aspect’ ($F_{1,26} = 0.6286$, $P = 0.435$) or ‘Site’ ($F_{3,26} = 2.0277$, $P = 0.1346$). There was a
244 seasonal effect ($F_{1,26} = 0.64361$, $P = 0.0175$), most likely attributed to the influence of
245 homogeneous data for two of the sites, South Milton Sands and Bude on EF- slopes.
246 There was no ‘Site’ × ‘Aspect’ interaction ($F_{3,26} = 2.2047$, $P = 0.1115$). For Functional
247 Dispersion (*FDis*), there were no significant effects of ‘Aspect’ ($F_{1,40} = 2.4159$, $P =$
248 0.1280), ‘Season’ (removed during model simplification) or ‘Site’ ($F_{2,40} = 0.7764$, $P =$
249 0.4669) and no ‘Site’ × ‘Aspect’ interaction ($F_{2,40} = 2.0204$, $P = 0.1454$).

250 A Poisson error GLM comparing how functional group richness responded to increasing
251 taxonomic (OTU) richness suggested that PF-slopes accumulated functional groups less
252 quickly than EF-aspects (Figure 4a), this effect was however, (marginally) non-
253 significant ($\chi^2 = 3.3893$; $P = 0.0656$). Following square-root transformation, analysis of
254 Functional Richness (*FRic*) data with a type III SS linear model also failed to show any
255 increase concomitant with the accumulation of OTUs ($F_{1,31} = 0.0519$; $P = 0.0821$),
256 despite a positive trend on PF-slopes (Figure 4b). Similar analysis of Functional
257 Dispersion (*FDis*) data however, revealed a significant difference ($F_{1,57} = 8.761$; $P =$
258 0.004) in the steeper rate of increase on EF- compared to PF-slopes (Figure 4c).

259 Consequently, we conclude that while functional group richness achieved higher
260 maxima on PF-aspects, the rate of per OTU accumulation of functional groups was
261 lower; i.e., OTUs (‘species’) were packed more tightly into trait space, on cooler, PF-
262 aspects and are accordingly, displaying greater functional redundancy than EF-aspects.
263 This in turn supports our second hypothesis that macroalgal functional diversity, and
264 thus functional redundancy, vary with intertidal aspect.

265

266 Discussion

267 Understanding variation in the functional diversity of primary producers across
268 environmental gradients can provide essential information about how community
269 structure and ecosystem functioning respond to anthropogenic stressors and
270 environmental change (Cappellatti et al., 2020; Kuhn et al., 2021; Westerband., et al
271 2021a, b). Our study revealed major differences, not only in overall macroalgal cover
272 and OTU ('species') composition, but also considerable variation in functional diversity
273 and redundancy between PF- and EF-slopes separated by just a few meters. Intuitively,
274 it seems likely that the difference in temperature regimes (i.e., 1.6°C annual average,
275 seasonal average, and six-fold variation in extremes) between EF and PF surfaces
276 (Amstutz et al 2021) is pivotal in explaining observed differences in the macroalgal
277 community. What we cannot disentangle is the relative importance of temperature on
278 algal ecophysiology weighed against the role played by the various other intertidal
279 organisms that influence algal settlement, establishment, and persistence. For example,
280 Amstutz et al., (2021) found a higher barnacle (*Chthamalus* sp.) abundance on EF-
281 aspects, corroborating a reported tolerance of heat and desiccation stress in the
282 Cirripedia (Southward, 1958; Wethey, 1983). It remains unclear however, whether
283 *Chthamalus* reduced the area available for macroalgal settlement because of an
284 ecophysiological tolerance of warmer slopes or was simply taking advantage of reduced
285 algal cover. Similarly, higher limpet and trochid abundance on PF slopes (Firth et al.,
286 2016; Amstutz et al., 2021) may signpost how ecophysiological responses in the grazer
287 community influence macroalgal species distributions and trait expression, or instead
288 reflect macroalgae abundance and food and shelter provision for the grazers.

289 While more research is needed to determine the ecological mechanisms explaining how
290 and why algal abundance and distribution varies between PF- and EF-surfaces, our
291 results underscore how macroalgal functional diversity and redundancy reflect
292 differences in environmental conditions. Not only did functional group richness achieve
293 higher diversity on PF-aspects, the rate of functional group accumulation per OTU was
294 slower, indicating that OTUs packed more tightly into PF-aspect trait space. Moreover,
295 the comparative accumulation rates of alpha (*FRic*) and beta (*FDis*) functional diversity,
296 signal that EF-aspects have greater change in beta diversity per unit change of alpha
297 diversity. Taken together these findings point to the conclusion that PF-aspects harbour
298 greater functional redundancy, i.e., ecosystem function in the more diverse PF-aspects is
299 more robust to species loss since functionally similar macroalgae are present to
300 compensate (Yachi & Loreau, 1999; Naeem, 2002; Safi et al., 2011; Seddon et al.,
301 2016).

302 Given the relative paucity of OTUs on EF-aspects (few plots supported more than one
303 or two species of thermo-tolerant macroalgae), it is unsurprising that we found greater
304 effective functional redundancy on the richer PF assemblages. Our understanding of
305 why these differences emerged can be informed by an examination of the OTU trait
306 expression on different aspects. Furoids (assigned by Mauffrey et al., (2020a) into
307 ‘Emergent Functional Group (EFG) 2’) dominated EF-plots. This group is characterised
308 by species with a longer and more branched thallus with high surface area to perimeter
309 (SA:P) and C:N ratios, traits indicative of high light capture potential, resistance to
310 desiccation/herbivory, capacity for resource retention, and allocation to structural rather
311 than photosynthetic tissues (Mauffrey et al., 2020a). Of these emergent trait
312 characteristics, resistance to desiccation and resource retention would seem to be the

313 most valuable for any alga experiencing comparatively high mean and extreme
314 temperatures on EF-aspects.

315 Although representation varied with season (see SoI Table 1), PF-aspects were
316 generally dominated by OTUs assigned by Mauffrey et al., (2020a) to ‘EFGs’ 7, 8 or 9.
317 Group 7 (comprising here *Blidingia minima*, *Porphyra* sp., and *Ulva* sp.) are
318 characterised by high Specific Thallus Area (STA), a trait linked to relatively high
319 investment in photosynthetic over structural tissue. ‘EFG 8’ (*Membranoptera alata* and
320 *Osmundea* sp.) similarly possess traits associated with relatively rapid resource
321 utilization (i.e., comparatively high STA, thallus Surface Area to Volume (SA:V) ratio
322 and N content). ‘EFG 9’ (*Cladophora* sp., *Lomentaria articulata* and *Rhodothamniella*
323 *floridula*), is also characterised by relatively high SA:V and N content. All three EFGs
324 therefore express traits linked to relatively high investment in rapid resource capture and
325 utilization, rather than structural resistance to environmental stressors like desiccation or
326 herbivory.

327 Given the comparative abundance of limpets and trochids on PF-aspects (Amstutz et al.,
328 2021), apparently low grazing resistance in these EFGs seems counter-intuitive.
329 Although limpets do consume macroalgae directly (Davies et al., 2007; Lorenzen, 2007;
330 Notman et al., 2016), like trochids, their main mode of feeding is a surface scraper of
331 microscopic biofilms (Crothers 2001; Jenkins et al., 2001). Consequently, the
332 comparatively higher grazer abundance on PF-aspects may not directly impact
333 established macroalgae (indeed, the most abundant species in our surveys, especially
334 PF-aspects, *Lithophyllum incrustans*, is a ‘crustose’ rhodophyte highly resistant to
335 surface grazing). This assertion does, however, raise an important point. If grazer

336 activity is principally focussed on rock-surface biofilms, then grazer selective pressure
337 could well be more pronounced at the algal establishment phase. Consequently, we may
338 need to focus on trait expression in gametophytes and newly settled sporophytes to fully
339 understand algal-grazer-environment interactions (Martins et al., 2023).

340 Although further research, perhaps including the potential interactive effects of tidal
341 height, exposure and surface heterogeneity (refugia) is needed to elucidate whether and
342 how observed temperature differences influence algal distributions and trait expression,
343 our study highlights the value that local variation in aspect can play in our
344 understanding of ACC-stressors on community assembly and function (see also
345 Amstutz et al., 2021). We also highlight the importance of ‘Free Air’ temperatures,
346 rather than the more commonly studied Sea Surface Temperatures (SSTs), on intertidal
347 species biology (see also Firth et al., 2011; Seabra et al., 2016). Only by considering the
348 more extreme temperature variation and stress experienced by intertidal organisms
349 when emersed, are we likely to understand how ACC affects shifts in species
350 distributions. Diaz-Acosta et al., (2021) for example noted that although warm-water
351 species had increased along the shores of the northwest Iberian Peninsula, physiological
352 responses (like photosynthesis) did not always match observed distributional shifts in
353 response to increasing SSTs. By revealing major variation in algae trait expression and
354 functional redundancy between warmer FF- and cooler PF-aspects, we signpost how
355 even an average air temperature difference of 1.6°C could affect intertidal community
356 assembly and functional resilience. Our results suggest that for cooler microsites (e.g.,
357 PF-aspects and higher latitude shores), a shift to a less species rich, desiccation-tolerant
358 (fucoid-dominated), seaweed community is likely even if at lower range of air
359 temperature increases predicted by contemporary models (e.g., the IPCC SSP 2.6

360 scenario) are realised this century. With this, a reduction in functional diversity and loss
361 of functional redundancy may make these simplified systems more susceptible to
362 additional environmental perturbation in a globally changing world.

363 **Acknowledgments**

364 The authors thank Professor Camille Parmesan for guidance with project development.
365 The project was funded by a School of Biological & Marine Science (University of
366 Plymouth) post-graduate studentship award to AA.

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573

574 **Figure Legends**

575

576 Figure 1: The influence of rock surface aspect on mean (\pm SE, averaged across two
577 seasons) species richness (determined using ‘Operational Taxonomic Units - OTUs) of
578 intertidal macroalgal communities sampled at four sites around the SW peninsula of
579 England (SMS = South Milton Sands).

580

581 Figure 2. The influence of surface aspect on intertidal macroalgal communities sampled
582 at four sites (symbols and line types) across the SW peninsula of England in 2016.
583 nMDS based upon Bray-Curtis dissimilarity matrix; ellipses indicate standard
584 deviations around group centroids, stress = 0.168.

585

586 Figure 3: The influence of rock surface aspect on mean (\pm SE) functional group number,
587 Functional Richness (FRic; Villéger et al., 2008), and Functional Dispersion (FDis;
588 Laliberté & Legendre, 2010), of intertidal macroalgae communities sampled at four
589 sites around the SW peninsula of England (SMS = South Milton Sands); **data from both**
590 **seasons aggregated.**

591

592 Figure 4: The influence of rock surface aspect on the accumulation of additional (a)
593 macroalgal functional groups (b) functional richness (*FRic*; Villéger et al., 2008), and
594 (c) functional dispersion (*FDis*; Laliberté & Legendre (2010)), associated with a
595 concomitant increase in the number of ‘Operational Taxonomic Units (OTUs) for
596 intertidal macroalgae communities at four sites in SW England; **data from both seasons**
597 **aggregated.**

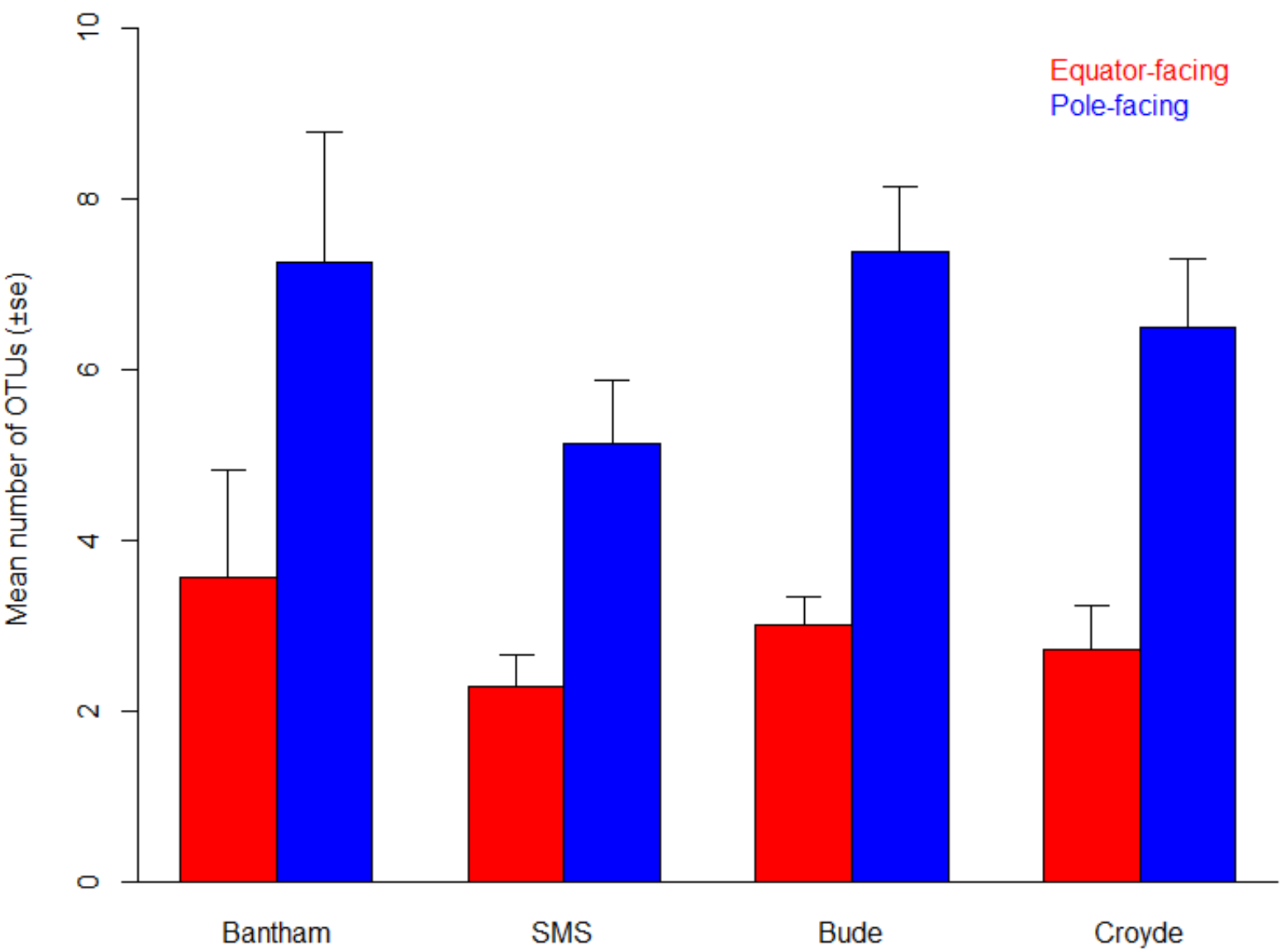
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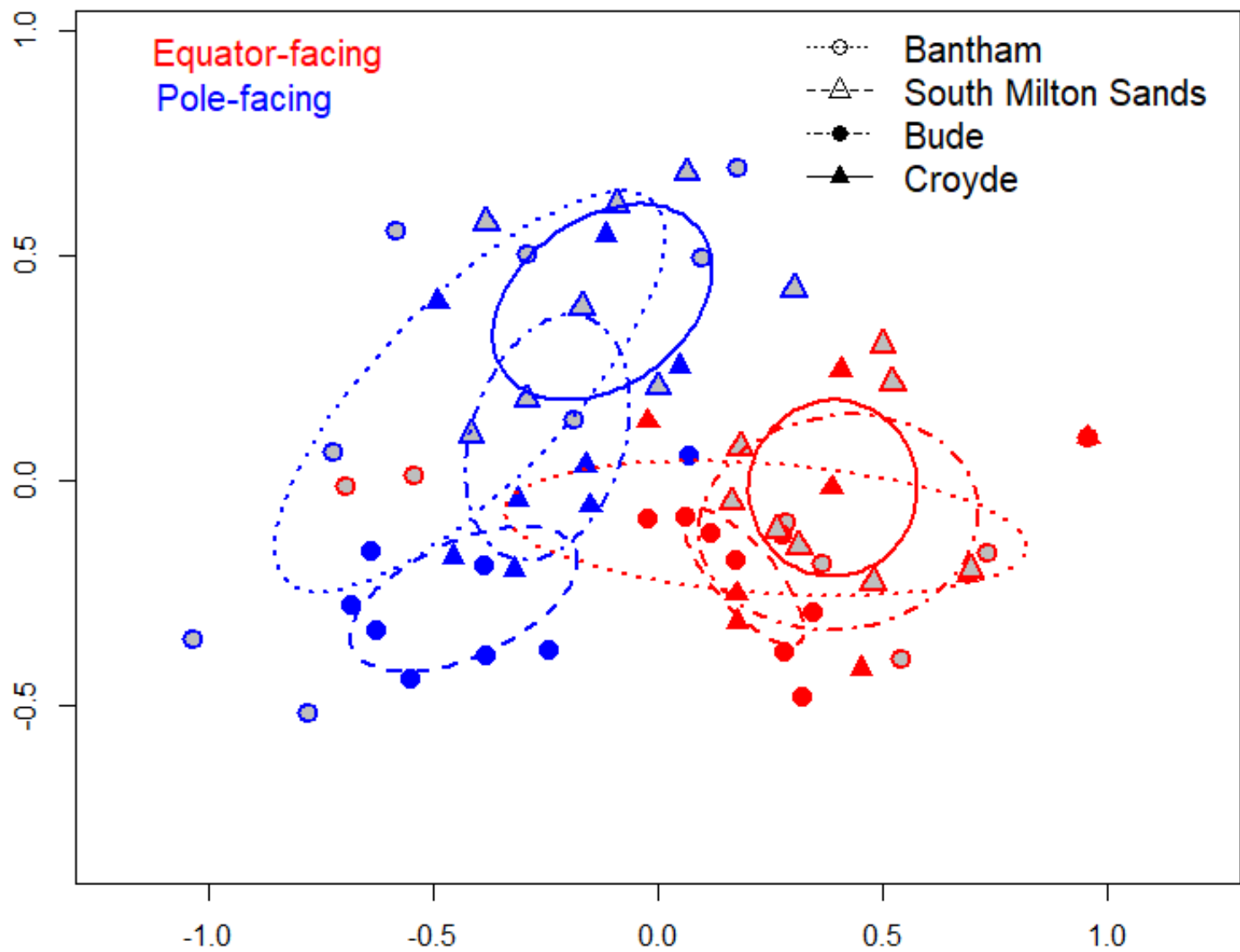
599 **SOI Legend**

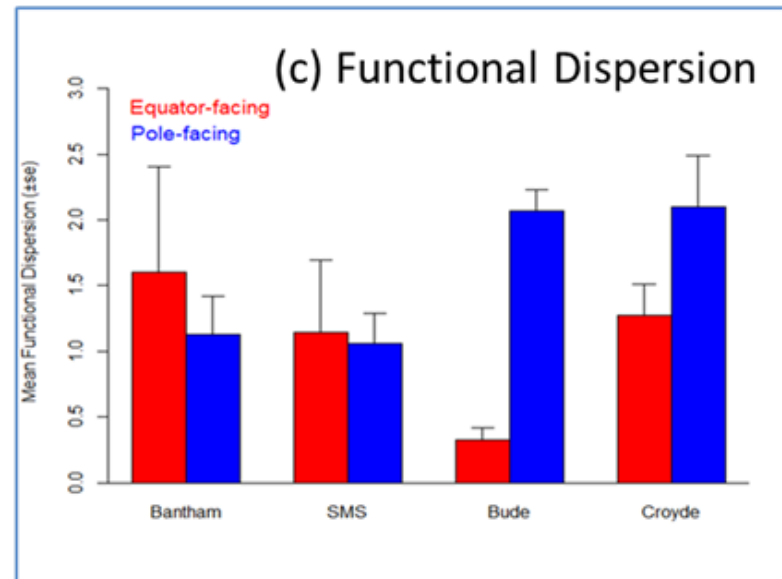
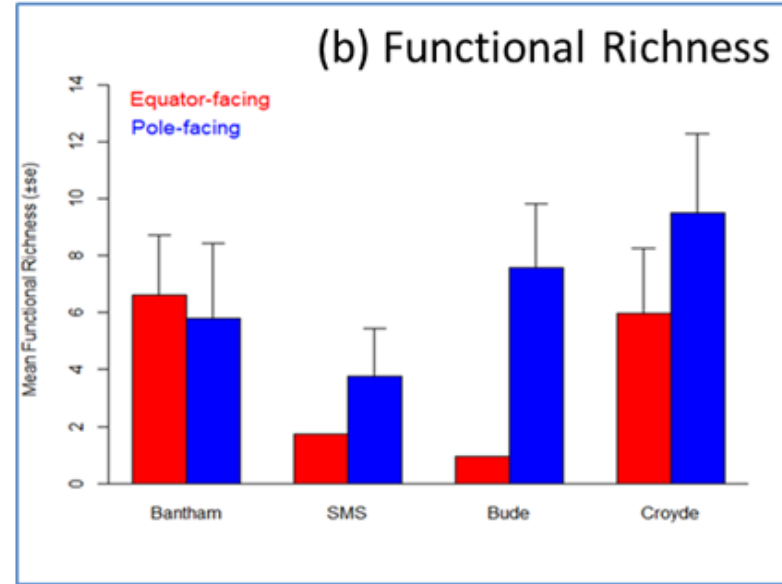
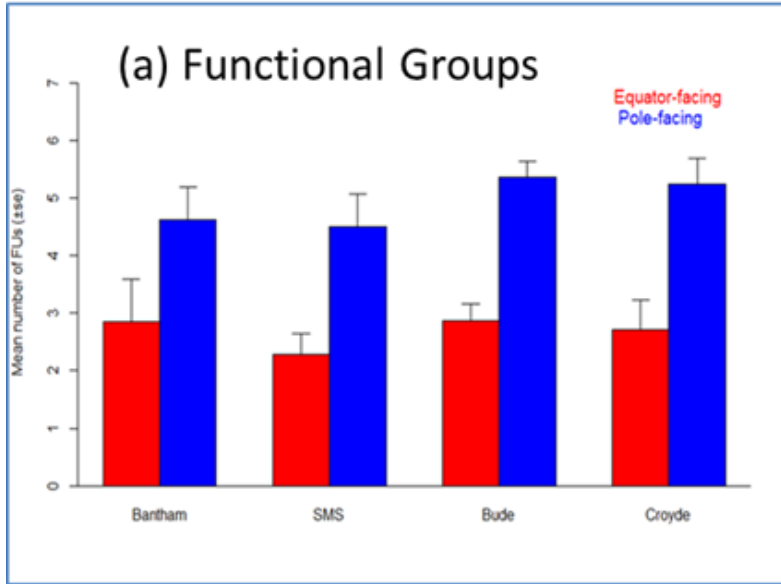
600 Table S1: Summary of variation in relative abundance (percentage cover) of macro-
601 algal species encountered in four paired gullies sited at four locations in SW England
602 according to aspect (PF - Pole facing and EF - Equator Facing), for summer 2016 and
603 winter 2017. Assignment of the ‘Putative Functional Group’ follows Mauffrey et al
604 (2020a).

605

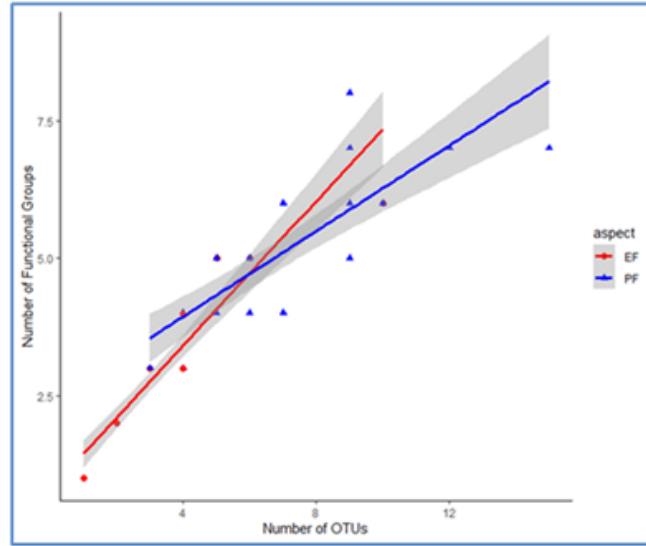
606 Figure S1. The influence of surface aspect on intertidal macroalgal communities
607 sampled at four sites (symbols and line types) across the SW peninsula of England in a)
608 summer 2016 and b) winter 2017. nMDS based upon Bray-Curtis dissimilarity matrix;
609 ellipses indicate standard deviations around group centroids, stresses = 0.145 and 0.124
610 respectively.



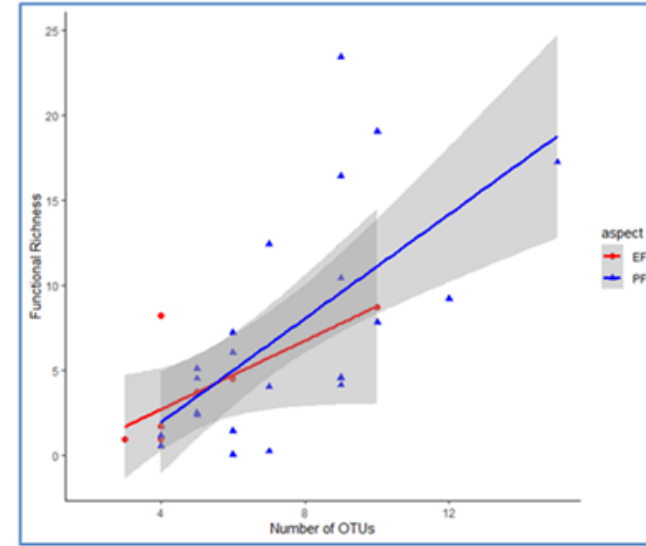




(a) Functional Groups



(b) Functional Richness



(c) Functional Dispersion

