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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

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

Introduction

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

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

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

Methods

Study sites and sampling

Intertidal surveys were carried out on four natural rocky shores on the north and south coasts of the southwest peninsula of England: Bude (50.836667, -4.556944) and Croyde (51.133889, -4.243889) on the north coast and, Bantham (50.276944, -3.884722) and South Milton Sands (50.253889, -3.861944) on the south coast. All sites share similar geology (Upper Palaeozoic, inter-bedded shales and sandstones) with strata tilted at 80º-90º (i.e., vertical dip) running perpendicular (i.e., east-west strike) to the shoreline and 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 ($0.25m^2$) 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 gulley 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

Results

Aspect and Community Structure

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

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

220   Unsurprisingly, algal assemblages varied across all four sites (PERMANOVA $_{Psu}F_{3,48}$ =

221   4.0475; $P < 0.001$), but while there was a seasonal effect ($_{Psu}F_{1,48}$ = 8.9749; P = 0.0385),

222   we also found a consistent influence of aspect on community composition ($_{Psu}F_{1,48}$ =

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 ($F_{1,26} = 0.6.4361$, $P = 0.0175$), 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

Discussion

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

15

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. Fucoids (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

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

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

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

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

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

Literature Cited

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573

Figure Legends

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

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

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

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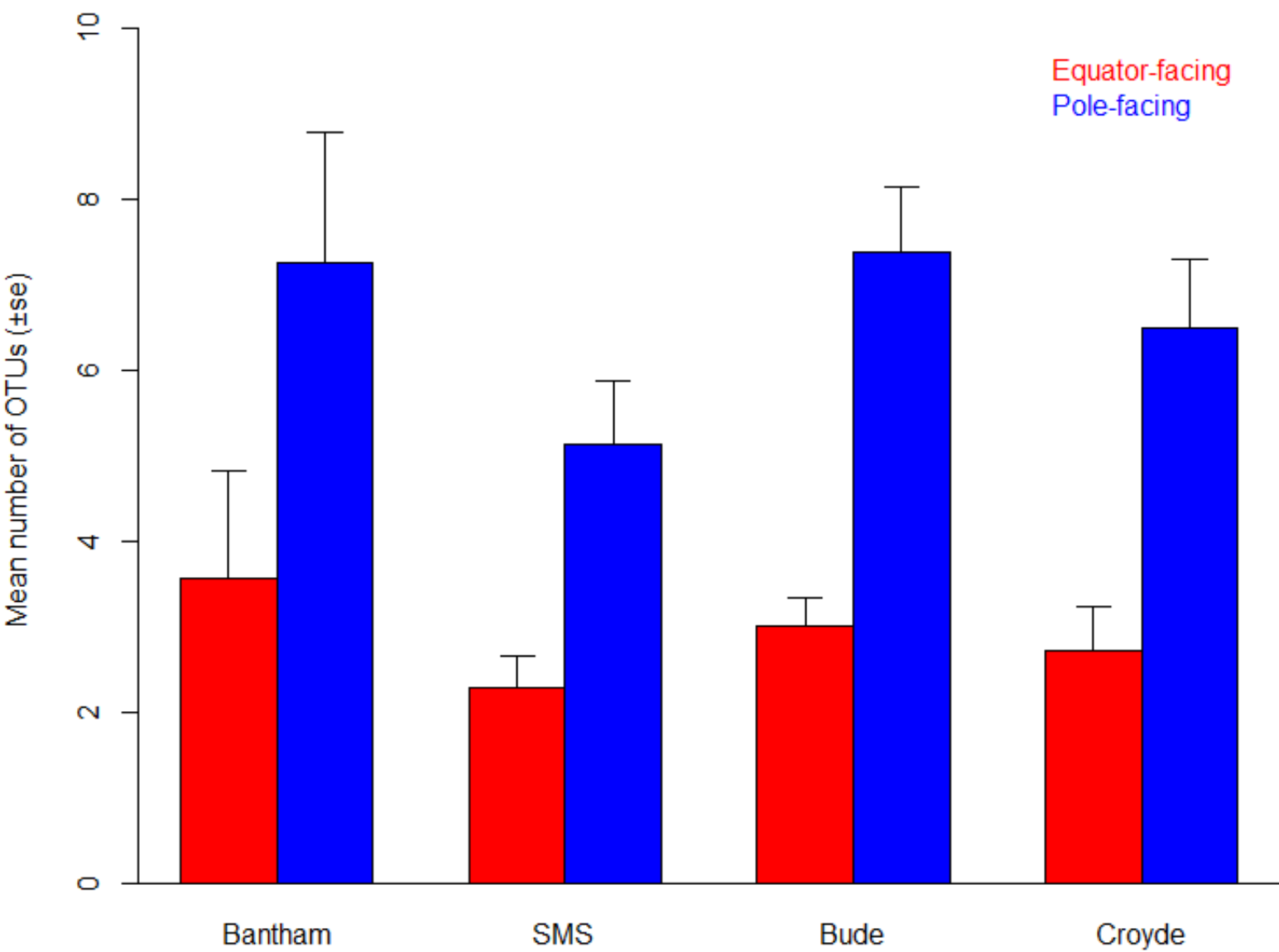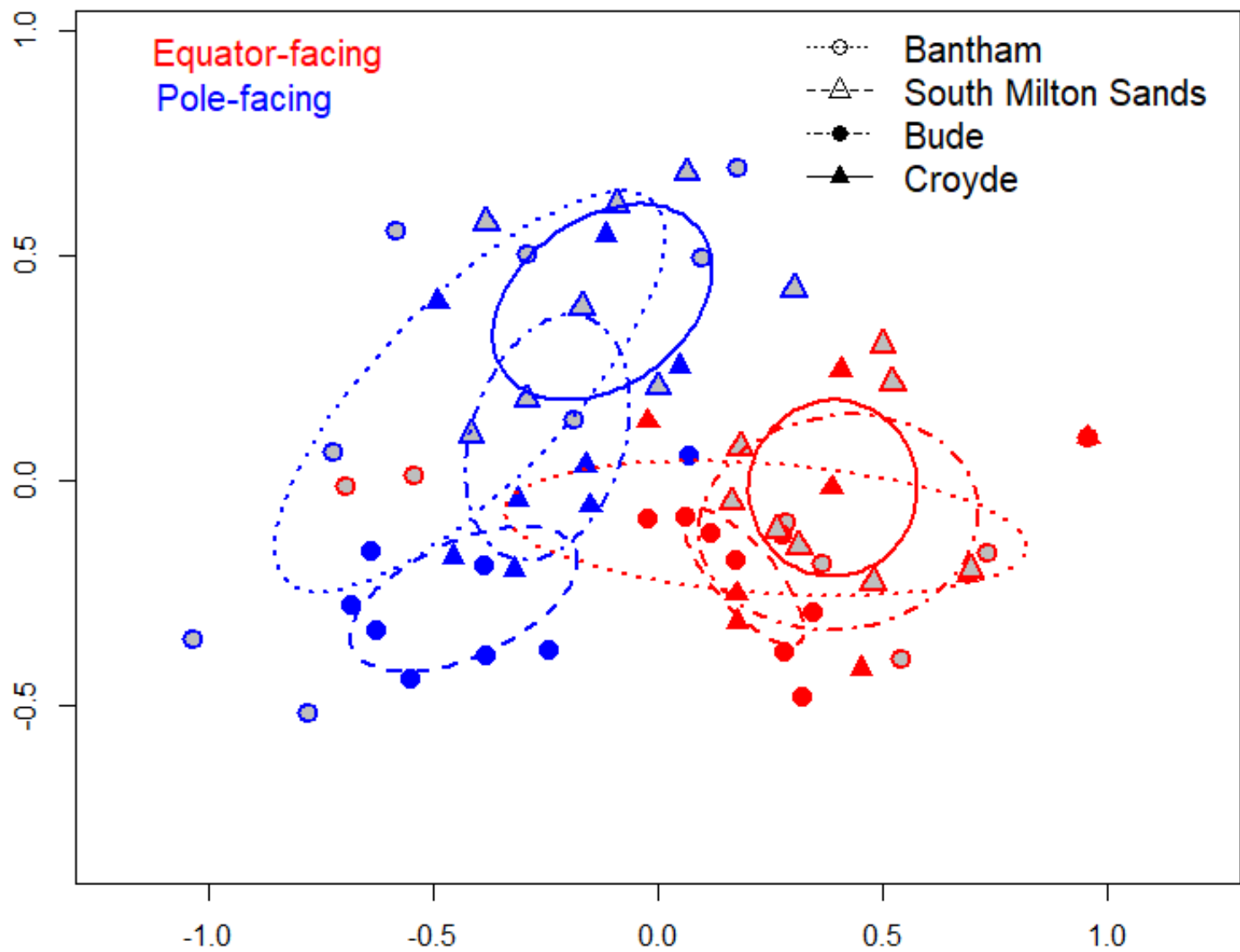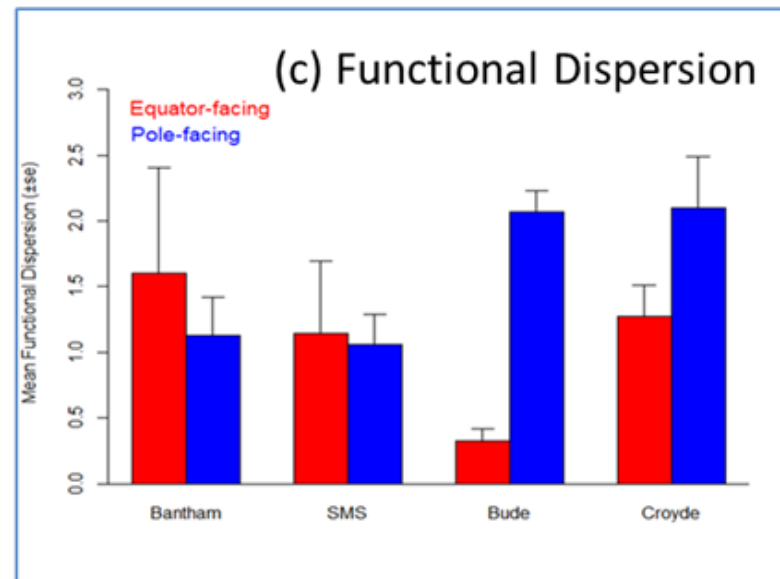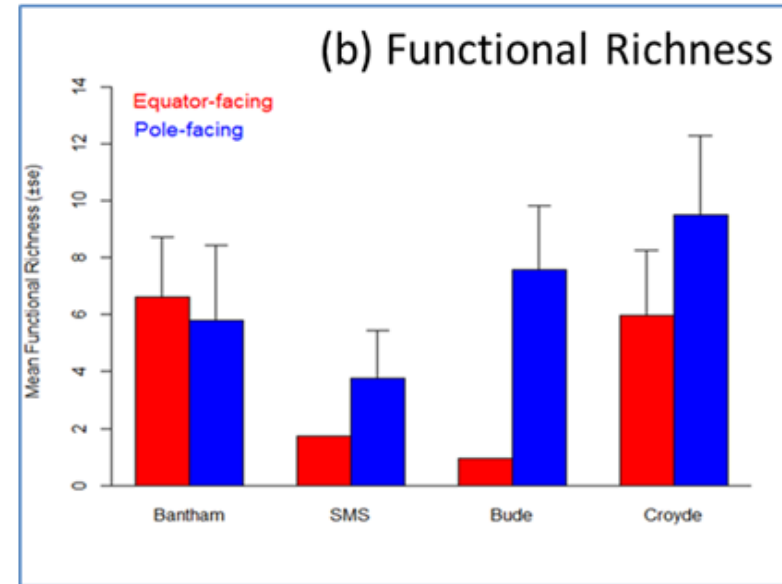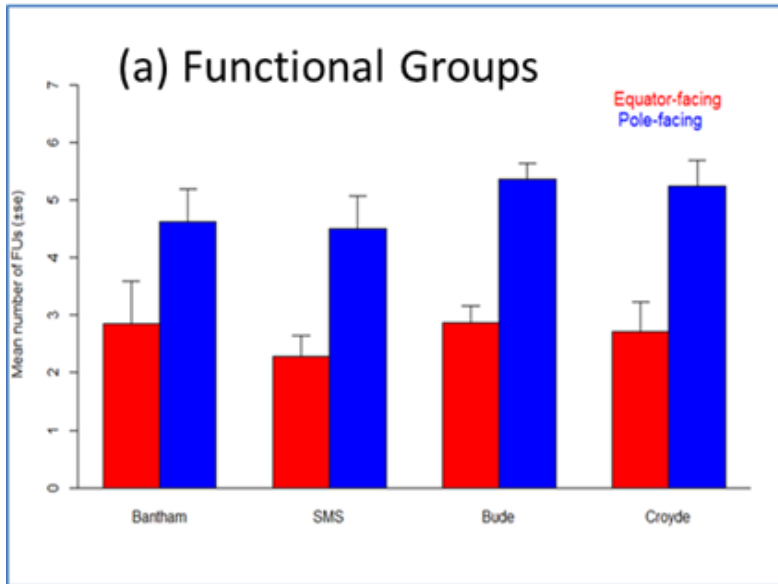
SOI Legend

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

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
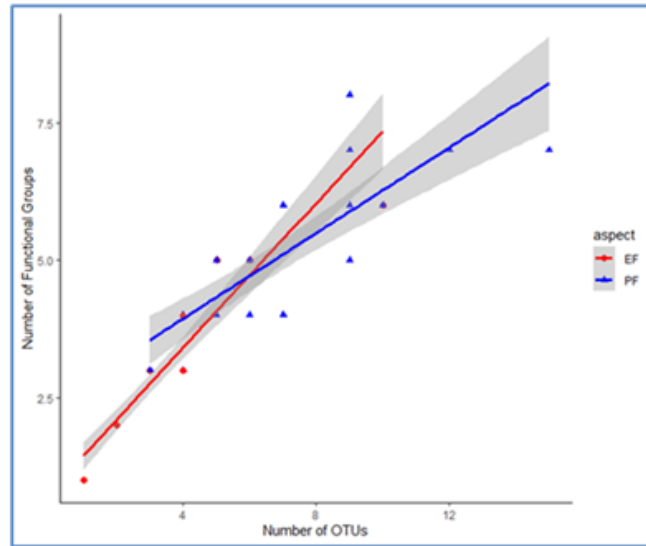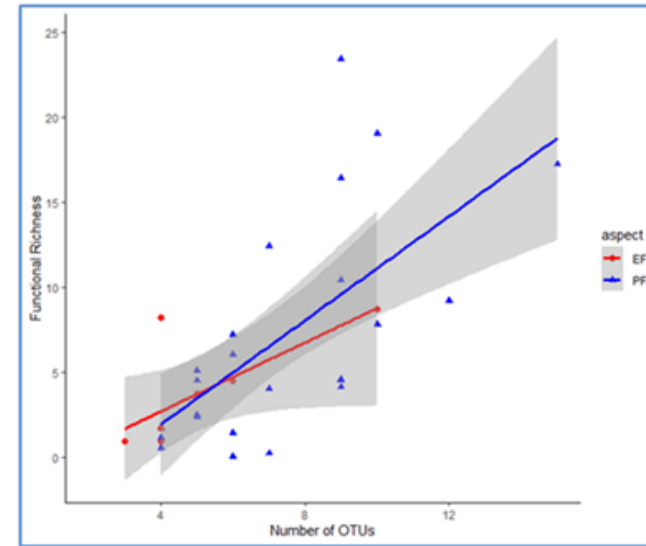610 respectively.

(a) Functional Groups

(b) Functional Richness

(c) Functional Dispersion

(a) Functional Groups

(b) Functional Richness

(c) Functional Dispersion