Faculty of Science and Engineering

School of Biological and Marine Sciences

2024-01-01

The northsouth divide? Macroalgal functional trait diversity and redundancy varies with intertidal aspect

Amstutz, A

https://pearl.plymouth.ac.uk/handle/10026.1/22403

10.1093/aob/mcad183 Annals of Botany Oxford University Press (OUP)

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

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

Thank you for agreeing to review this paper for Annals of Botany. The Annals of Botany aims to be among the very top of plant science journals and as we receive over 1000 submissions every year we need to be very selective in deciding which papers we can publish. In making your assessment of the manuscript's suitability for publication in the journal please consider the following points.

Scientific Scope

Annals of Botany welcomes papers in all areas of plant science. Papers may address questions at any level of biological organization ranging from molecular through cells and organs, to whole organisms, species, communities and ecosystems. Its scope extends to all flowering and non-flowering taxa, and to evolutionary and pathology research. Many questions are addressed using comparative studies, genetics, genomics, molecular tools, and modeling.

To merit publication in Annals of Botany, contributions should be substantial, concise, written in clear English and combine originality of content with potential general interest.

- We want to publish papers where our reviewers are enthusiastic about the science: is this a paper that you would keep for reference, or pass on to your colleagues? If the answer is "no" then please enter a low priority score when you submit your report.
- We want to publish papers with novel and original content that move the subject forward, not papers that report incremental advances or findings that are already well known in other species. Please consider this when you enter a score for originality when you submit your report.

Notes on categories of papers:

All review-type articles should be novel, rigorous, substantial and "make a difference" to plant science. The purpose is to summarise, clearly and succinctly, the "cutting edge" of the subject and how future research would best be directed. Reviews should be relevant to a broad audience and all should have a strong conclusion and illustrations including diagrams.

- *Primary Research* articles should report on original research relevant to the scope of the journal, demonstrating an important advance in the subject area, and the results should be clearly presented, novel and supported by appropriate experimental approaches. The Introduction should clearly set the context for the work and the Discussion should demonstrate the importance of the results within that context. Concise speculation, models and hypotheses are encouraged, but must be informed by the results and by the authors' expert knowledge of the subject.
- *Reviews* should place the subject in context, add significantly to previous reviews in the subject area and moving forward research in the subject area. Reviews should be selective, including the most important and best, up-to-date, references, not a blow-by-blow and exhaustive listing.
- *Research in Context* should combine a review/overview of a subject area with original research, often leading to new ideas or models; they present a hybrid of review and research. Typically a Research in Context article contains an extended Introduction that provides a general overview of the topic before incorporating new research results with a Discussion proposing general models and the impact of the research.
- *Viewpoints* are shorter reviews, presenting clear, concise and logical arguments supporting the authors' opinions, and in doing so help to stimulate discussions within the topic.
- Botanical Briefings are concise, perhaps more specialised reviews and usually cover topical issues, maybe involving some controversy.

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

Amstutz A, Firth LB, Foggo A, Spicer JI, Hanley ME^{*}

School of Biological and Marine Sciences, University of Plymouth, Drakes

Circus, Plymouth, PL4 8AA, UK.

* Author for correspondence. Email: mehanley@plymouth.ac.uk

Running Title: Aspect and Seaweed Functional Traits

1 Abstract

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

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

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

30

31 Keywords:

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

35 Introduction

Globally, ecosystems face unprecedented pressures from a combination of habitat loss, 36 37 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 38 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 the notion of 'functional complementarity/redundancy'; i.e., how the impact of species 41 losses on ecosystem function and resilience may be compensated if functionally similar 42 43 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 44 studies have demonstrated the robustness of the functional redundancy concept, it is 45 apparent that assessment and prediction of the ecological consequences of 46 environmental change for the contribution of functional diversity to the BEF 47 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 BEF in field conditions is challenging. Manipulation of single and multiple key 51 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 (Pfisterer & Schmid, 2002; Allison, 2004; Grime et al., 2008; Vetter et al., 2020). 55 56 Although microbial microcosms offer a tractable way to manipulate, replicate and control species (functional) composition and multiple external environmental conditions 57

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

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

In terrestrial systems, variation in species distributions has long been associated with habitat orientation towards the sun (Cantlon, 1953; Nevo, 2012). Recent studies in marine intertidal systems also highlight considerable local differences in thermal conditions and species assemblages on Pole-Facing (PF) versus Equator-Facing (EF) surfaces (Seabra et al., 2011; Firth et al., 2016; Lima et al., 2016). Moreover, when compared at relatively local scales (i.e., PF and EF slopes are metres apart), other 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 (i.e., 'air') temperatures 1.6°C higher on EF than PF rock surfaces, with high extremes 83 (i.e., $> 30^{\circ}$ C) six times more frequent on EF-surfaces. Unsurprisingly, community 84 85 composition also varied with aspect, but the effect was apparent both within (e.g., more patellid and trochid grazing molluscs on PF-surfaces), as well as between (e.g., more 86 carnivorous dogwhelks on PF-surfaces, but fewer filter-feeding barnacles) trophic 87 88 levels. Moreover, Amstutz et al (2021) also observed aspect-related variation in reproductive phenology and thermal stress responses in two patellid limpet species. 89

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 not consider how functional traits within communities varied with aspect. Marine 94 macroalgae ('seaweeds') play a critical role in ecological structure and functioning in 95 the intertidal and coastal shelf environments (Ling et al., 2009; Johnson et al., 2011; 96 Pessarrodona et al., 2022), but are especially vulnerable to the physico-chemical 97 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 in sea surface temperatures (SSTs) and their effects upon subtidal algae. Given the 102 103 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; Bracewell et al., 2018; Jurgens et al., 2022), our ability to predict intertidal community 106 107 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 108 109 ACC-linked warming is likely to affect community assembly and process in intertidal macroalgal assemblages and subsequent shifts in the trait characteristics possessed by 110 seaweeds on cooler PF- and warmer EF-aspects. To do this, we investigated how 111 112 intertidal aspect (and the temperature variation associated with PF- and EF-slope orientation) influenced intertidal macroalgae communities, specifically testing the 113 predictions that (i) community composition and taxon richness vary between EF- and 114 115 PF-surfaces and that consequently, (ii) functional diversity, and thence redundancy, also vary with aspect. 116

117

118 Methods

119 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 80°-90° (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).

At each location, four gullies were haphazardly selected, but with the *proviso* that they 129 provided access to long sections of opposing PF and EF vertical rock surfaces at mid-130 131 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 (January/February) 2017, twelve 0.5 x 0.5 m $(0.25m^2)$ quadrats were haphazardly 133 positioned along each of four gullies at each site, such that PF- and EF-quadrats 134 opposed each other at the same relative shore height in each gully (a total 192 quadrats 135 136 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 estimated. 138

139 Analysis of Community Structure

We identified seaweeds in the field as accurately as possible, lumping problem taxa to genera where necessary (hereafter referred to as operational taxonomic units - OTUs – rather than 'species'). We estimated the number of OTUs in each gulley by averaging across quadrats, and tested for an effect of 'Aspect', 'Season' and 'Site' (fixed effects) using a Poisson error generalized linear model in R ver 4.0 (R Core Team 2021). The model was simplified using single term deletions based upon change in AIC >2; 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 4 th -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' \times 'Site' \times '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

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

164 First we used the extensive database of functional trait scores provided by Mauffrey et

al., (2020a,b) to calculate values of Functional Richness (*FRic*) (Villéger et al., 2008)

- 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 selected 11 of the 12 traits employed by Mauffrey et al., (2020b) (we excluded the 175 presence of pneumatocysts, as when sampled, none of our taxa possessed them). 176 177 Functional diversity measures were calculated based upon Euclidean distances using standardized, abundance-weighted trait scores (where relevant). Where OTUs at the 178 179 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 & Groothuis-Oudshoorn, 2011) provided that >70% of species scores were present. We 182 183 tested these measures of functional diversity using the same linear modelling approach applied to taxonomic species richness, transforming data to achieve homogeneity of 184 185 variances where necessary.

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

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

- 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.

198 **Results**

199 Aspect and Community Structure

Although total algal cover varied little on PF-slopes with season (circa 3%), on EF-200 slopes cover more than doubled between summer (circa 8%) and winter (circa 17%). 201 These values are, fairly typical of the moderately exposed, barnacle and limpet 202 203 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 204 incrustans and Lomentaria articulata) were also noticeably more common (i.e., more 205 206 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 record, but Fucus sp. (hereafter 'fucoids' - combined because individuals were often too 208 209 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 210 summer and 1.7% EF vs 0.8% PF in winter). Three entire gulley sites were devoid of 211 macroalgae, these were excluded from further analyses due to their disproportionate 212 213 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 $_{Psu}F_{3,48}$ = 4.0475; P < 0.001), but while there was a seasonal effect ($_{Psu}F_{1,48} = 8.9749$; P = 0.0385), 221 222 we also found a consistent influence of aspect on community composition $(P_{Su}F_{1.48} =$ 16.211; P = 0.0289). Contrasts of aspects within sites reinforced this picture (Fig 2, 223 224 Supplemental Figures 1a and b), indicating highly significant differences in algal assemblages between aspects in both seasons at Bude (t = 3.8256; P < 0.001), Croyde (t225 = 2.8244; P < 0.001), and South Milton (t = 3.0468; P < 0.001). The pattern of 226 227 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 detected no significant interactions between 'Site', 'Season' and 'Aspect'. Collectively, 229 230 there was strong support for our hypothesis that macroalgal community composition and species (OTU) richness vary between EF- and PF-surfaces. 231

232

233 Functional Trait Variation and Redundancy

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

By contrast, although there was a tendency towards higher Functional Richness (*FRic*) on PF- slopes at three sites (Figure 3b), we established that *FRic* did not vary with 'Aspect' ($F_{1,26} = 0.6286$, P = 0.435) or 'Site' ($F_{3,26} = 2.0277$, P = 0.1346). There was a seasonal effect ($F_{1,26} = 0.6.4361$, P = 0.0175), most likely attributed to the influence of homogeneous data for two of the sites, South Milton Sands and Bude on EF- slopes. There was no 'Site' × 'Aspect' interaction ($F_{3,26} = 2.2047$, P = 0.1115). For Functional Dispersion (*FDis*), there were no significant effects of 'Aspect' ($F_{1,40} = 2.4159$, P =0.1280), 'Season' (removed during model simplification) or 'Site' ($F_{2,40} = 0.7764$, P =0.4669) and no 'Site' × 'Aspect' interaction ($F_{2,40} = 2.0204$, P = 0.1454).

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

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

266 **Discussion**

267 Understanding variation in the functional diversity of primary producers across environmental gradients can provide essential information about how community 268 269 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, it seems likely that the difference in temperature regimes (i.e., 1.6°C annual average, 274 275 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 276 277 community. What we cannot disentangle is the relative importance of temperature on algal ecophysiology weighed against the role played by the various other intertidal 278 organisms that influence algal settlement, establishment, and persistence. For example, 279 280 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 Cirripedia (Southward, 1958; Wethey, 1983). It remains unclear however, whether 282 283 Chthamalus reduced the area available for macroalgal settlement because of an 284 ecophysiological tolerance of warmer slopes or was simply taking advantage of reduced algal cover. Similarly, higher limpet and trochid abundance on PF slopes (Firth et al., 285 2016; Amstutz et al., 2021) may signpost how ecophysiological responses in the grazer 286 community influence macroalgal species distributions and trait expression, or instead 287 reflect macroalgae abundance and food and shelter provision for the grazers. 288

289 While more research is needed to determine the ecological mechanisms explaining how and why algal abundance and distribution varies between PF- and EF-surfaces, our 290 291 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, the comparative accumulation rates of alpha (FRic) and beta (FDis) functional diversity, 295 296 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 greater functional redundancy, i.e., ecosystem function in the more diverse PF-aspects is 298 299 more robust to species loss since functionally similar macroalgae are present to compensate (Yachi & Loreau, 1999; Naeem, 2002; Safi et al., 2011; Seddon et al., 300 301 2016).

Given the relative paucity of OTUs on EF-aspects (few plots supported more than one 302 303 or two species of thermo-tolerant macroalgae), it is unsurprising that we found greater effective functional redundancy on the richer PF assemblages. Our understanding of 304 why these differences emerged can be informed by an examination of the OTU trait 305 306 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 desiccation/herbivory, capacity for resource retention, and allocation to structural rather 310 than photosynthetic tissues (Mauffrey et al., 2020a). Of these emergent trait 311 312 characteristics, resistance to desiccation and resource retention would seem to be the 313 most valuable for any alga experiencing comparatively high mean and extreme314 temperatures on EF-aspects.

Although representation varied with season (see SoI Table 1), PF-aspects were 315 generally dominated by OTUs assigned by Mauffrey et al., (2020a) to 'EFGs' 7, 8 or 9. 316 317 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 investment in photosynthetic over structural tissue. 'EFG 8' (Membranoptera alata and 319 320 Osmundea sp.) similarly possess traits associated with relatively rapid resource utilization (i.e., comparatively high STA, thallus Surface Area to Volume (SA:V) ratio 321 322 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 323 324 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 herbivory. 326

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 microscopic biofilms (Crothers 2001; Jenkins et al., 2001). Consequently, the 331 332 comparatively higher grazer abundance on PF-aspects may not directly impact established macroalgae (indeed, the most abundant species in our surveys, especially 333 PF-aspects, Lithophyllum incrustans, is a 'crustose' rhodophyte highly resistant to 334 surface grazing). This assertion does, however, raise an important point. If grazer 335

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).

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, our study highlights the value that local variation in aspect can play in our 343 344 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 when emersed, are we likely to understand how ACC affects shifts in species 349 350 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 351 responses (like photosynthesis) did not always match observed distributional shifts in 352 353 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., PF-aspects and higher latitude shores), a shift to a less species rich, desiccation-tolerant 357 358 (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.
- 367 Literature Cited
- Aguilera MA, Valdivia N, Broitman BR, Jenkins SR, Navarrete SA. 2020. Novel
 co-occurrence of functionally redundant consumers induced by range expansion
 alters community structure. *Ecology* 101: e03150.
- Allison G. 2004. The influence of species diversity and stress intensity on community
 resistance and resilience. *Ecological Monographs* 74: 117–134.
- Amstutz A, Firth LB, Spicer JI, Hanley ME. 2021. Facing up to climate change:
 community composition varies with aspect and surface temperature in the rocky
 intertidal. *Marine Environmental Research* 172: 105482.
- Banitz T, Chatzinotas A, Worrich A. 2020. Prospects for integrating disturbances,
 biodiversity and ecosystem functioning using microbial systems. *Frontiers in Ecology and Evolution* 8: 21.
- Barton MG, Clusella-Trullas S, Terblanche JS. 2019. Spatial scale, topography and
 thermoregulatory behaviour interact when modelling species' thermal niches.
 Ecography 42: 376-389.
- Bracewell SA, Clark G, Johnston EL. 2018. Habitat complexity effects on diversity
 and abundance differ with latitude: an experimental study over 20 degrees.
 Ecology 99: 1964-1974.
- Cantlon JE. 1953. Vegetation and microclimates on north and south slopes of
 Cushetunk Mountain, New Jersey, *Ecological Monographs* 23: 241–270.

- Cappelatti L, Mauffrey ARL, Griffin JN. 2020. Functional diversity of habitat
 formers declines scale-dependently across an environmental stress gradient.
 Oecologia 194: 135–149.
- 390 Cardinale BJ. 2011. Biodiversity improves water quality through niche partitioning.
 391 *Nature* 272: 86-89.
- 392 Crisp DJ. 1964. The effects of the severe winter of 1962-63 on marine life in Britain.
 393 *Journal of Animal Ecology* 33: 165-210.
- 394 Crothers JH. 2001. Common topshells: an introduction to the biology of *Osilinus* 395 *lineatus* with notes on other species in the genus. *Field Studies* 10: 115-160.
- 396 Davies AJ, Johnson MP, Maggs CA. 2007. Limpet grazing and loss of Ascophyllum
 397 nodosum canopies on decadal time scales. Marine Ecology Progress Series 339:
 398 131-141.
- 399 Diaz-Acosta L, Barreiro R, Provera I, Piñeiro-Corbeira C. 2021. Physiological
 400 response to warming in intertidal macroalgae with different thermal affinity.
 401 Marine Environmental Research 169: 105350.
- 402 Dolbeth M, Crespo D, Leston S, Solane M. 2019. Realistic scenarios of environmental
 403 disturbance lead to functionally important changes in benthic species 404 environment interactions. *Marine Environmental Research* 150: 104770.
- Fetzer I, Johst K, Schäwe R, Banitz T, Harms H, Chatzinotas A. 2015. The extent
 of functional redundancy changes as species' roles shift in different
 environments. *Proceedings of the National Academy of Sciences* 112:1488814893.
- Filbee-Dexter K, Wernberg T, Grace SP, et al. 2020. Marine heatwaves and the
 collapse of marginal North Atlantic kelp forests. *Scientific Reports* 10: 13388.
- 411 Firth LB, Williams GA. 2009. The influence of multiple environmental stressors on
 412 the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong.
 413 *Journal of Experimental Marine Biology and Ecology* 375: 70-75.
- 414 Firth LB, Knights AM, Bell SS. 2011. Air temperature and winter mortality:
 415 implications for the persistence of the invasive mussel, *Perna viridis* in the
 416 intertidal zone of the south-eastern United States. *Journal of Experimental*417 *Marine Biology and Ecology* 400: 250-256.

- 418 Firth LB, Mieszkowska N, Grant LM, et al. 2015. Historical comparisons reveal
 419 multiple drivers of decadal change of an ecosystem engineer at the range edge.
 420 *Ecology and Evolution* 5: 3210-3222.
- 421 Firth LB, White FJ, Schofield M, et al. 2016. Facing the future: the importance of
 422 substratum features for ecological engineering of artificial habitats in the rocky
 423 intertidal. *Marine and Freshwater Research* 67: 131-143.
- 424 Firth LB, Harris D, Blaze JA, et al. 2021. Specific niche requirements underpin
 425 multidecadal range edge stability, but may introduce barriers for climate change
 426 adaptation. *Diversity and Distributions* 27: 668-683.
- Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR. 2008.
 Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences USA* 105: 10028–10032.
- Harley CD, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, Graham
 MH. 2012. Effects of climate change on global seaweed communities. *Journal*of Phycology 48: 1064–1078.
- Harlin MM, Lindbergh JM. 1977. Selection of substrata by seaweeds: optimal surface
 relief. *Marine Biology* 40: 33-40.
- Hawkins SJ, Pack KE, Hyder K, Benedetti-Cecchi L, Jenkins SR. 2020. Rocky
 shores as tractable test systems for experimental ecology. *Journal of the Marine Biological Association of the United Kingdom* 100: 1017-1041.
- Helmuth B, Mieszkowska N, Moore P, Hawkins SJ. 2006. Living on the edge of two
 changing worlds: forecasting the responses of rocky intertidal ecosystems to
 climate change. *Annual Review of Ecology, Evolution and Systematics* 37: 373404.
- 442 Isbell F, Gonzalez A, Loreau M., et al. 2017. Linking the influence and dependence of
 443 people on biodiversity across scales. *Nature* 546: 65-72.
- Jenkins SR, Arenas F, Arrontes J, et al. 2001. European-scale analysis of seasonal
 variability in limpet grazing activity and microalgal abundance. *Marine Ecology Progress Series* 211: 193-203.
- Johnson MP, Hanley ME, Frost NJ, Moseley MWJ, Hawkins SJ. 2008. The
 persistent spatial patchiness of limpet grazing. *Journal of Experimental Marine Biology & Ecology* 365: 136-141.

- Johnson CR, Banks SC, Barrett NS, et al. 2011. Climate change cascades: Shifts in
 oceanography, species' ranges and subtidal marine community dynamics in
 eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* 400:
 17-32.
- Jurgens LJ, Ashlock LW, Gaylord B. 2022. Facilitation alters climate change risk on
 rocky shores. *Ecology* 103: e03596.
- Kühn P, Ratier Backes A, Römermann C, Bruelheide H, Haider S. 2020.
 Contrasting patterns of intraspecific trait variability in native and non-native
 plant species along an elevational gradient on Tenerife, Canary Islands. *Annals of Botany* 127: 565–576.
- 460 Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional
 461 diversity from multiple traits. *Ecology* 91: 299-305.
- 462 Laliberté E, Legendre P & Shipley B. 2014. FD: measuring functional diversity from
 463 multiple traits, and other tools for functional ecology. R package version 1.0-12.
- 464 Lenth RV. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R
 465 package version 1.5.3. <u>https://CRAN.R-project.org/package=emmeans</u>
- Lima FP., Ribeiro P, Queiroz N, Hawkins SJ, Santos AM. 2007. Do distributional
 shifts of northern and southern species of algae match the warming pattern? *Global Change Biology* 13: 2592–2604.
- 469 Lima FP, Gomes F, Seabra R, et al. 2016. Loss of thermal refugia near equatorial
 470 range limits. *Global Change Biology* 22: 254-263.
- 471 Ling SD, Johnson CR, Frusher SD, Ridgway K. 2009. Overfishing reduces resilience
 472 of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the*473 *National Academy of Sciences* 106: 22341-22345.
- 474 Lorenzen S. 2007. The limpet *Patella vulgata* L. at night in air: effective feeding on
 475 Ascophyllum nodosum monocultures and stranded seaweeds. *Journal of*476 *Molluscan Studies* 73: 267-274.
- 477 Martins, N, Coleman MA, Wernberg T, Roleda MY. 2023. Opening the black box of
 478 kelps: Response of early life stages to anthropogenic stressors. *Frontiers in* 479 *Marine Science* 9: doi.org/10.3389/fmars.2022.1133857.

- 480 Mauffrey ARL, Cappelatti L, Griffin JN. 2020a. Seaweed functional diversity
 481 revisited: confronting traditional groups with quantitative traits. *Journal of*482 *Ecology* 108: 2390–2405.
- 483 Mauffrey ARL, Cappelatti L, Griffin JN. 2020b. Data from: functional diversity of
 484 seaweeds revisited: confronting traditional groups with quantitative traits. *Dryad* 485 *Digital Repository*, https://doi.org/10.5061/dryad.nvx0k6dpn
- 486 Micheli F, Halpern BS. 2005. Low functional redundancy in coastal marine
 487 assemblages. *Ecology Letters* 8: 391–400.
- 488 Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being:
 489 Biodiversity Synthesis. World Resources Institute, Washington, DC.
- 490 Naeem S. 2002. Biodiversity equals instability?. Nature 416: 23-24.
- 491 Nevo E. 2012. "Evolution Canyon," a potential microscale monitor of global warming
 492 across life. *Proceedings of the. National Academy of Sciences, USA* 109: 2960–
 493 2965.
- 494 Notman GM, McGill RA, Hawkins SJ, Burrows MT. 2016. Macroalgae contribute to
 495 the diet of *Patella vulgata* from contrasting conditions of latitude and wave
 496 exposure in the UK. *Marine Ecology Progress Series* 549: 113-123.
- 497 Oksanen J, Blanchet FG, Friendly M, et al. 2020. Vegan: community ecology
 498 package. R package version 2:5–5 https://cran.r499 project.org/web/packages/vegan/index.html.
- 500 Parmesan C, Hanley ME. 2015. Plants and climate change: complexities and surprises.
 501 *Annals of Botany* 116: 849–864.
- Parmesan C, Morecroft MD, Trisurat Y, et al. 2022. Terrestrial and freshwater
 ecosystems and their services. In: Pörtner HO, Roberts DC, Tignor M, et al. eds. *Climate Change 2022: Impacts, Adaptation, and Vulnerability*. Contribution of
 Working Group II to the Sixth Assessment Report of the Intergovernmental
 Panel on Climate Change, Cambridge University Press.
- 507 Paul C, Hanley N, Meyer ST et al. 2020. On the functional relationship between
 508 biodiversity and economic value. *Scientific Advances* 6: eaax7712.
- 509 Pessarrodona A, Asis J, Filbee-Dexter K, et al., 2022. Global seaweed productivity.
 510 Scientific Advances 8: eabn2465.

- 511 Pfisterer AB, Schmid B. 2002. Diversity-dependent production can decrease the
 512 stability of ecosystem functioning. *Nature* 416: 84-86.
- **R Core Team 2021**. R: A language and environment for statistical computing. R
 Foundation for Statistical Computing, Vienna, Austria. https://www.Rproject.org/.
- 516 Safi K, Cianciaruso MV, Loyola RD, Brito D, Armour-Marshall K, Diniz-Filho
 517 JAF. 2011. Understanding global patterns of mammalian functional and
 518 phylogenetic diversity. *Philosophical Transactions of the Royal Society of*519 London. Series B, Biological Sciences 366: 2536–2544.
- Seabra R, Wethey DS, Santos AM, Lima FP. 2011. Side matters: microhabitat
 influence on intertidal heat stress over a large geographical scale. *Journal of Experimental Marine Biology and Ecology* 400: 200–208.
- Seabra R, Wethey DS, Santos AM, Gomes F, Lima FP. 2016. Equatorial range limits
 of an intertidal ectotherm are more linked to water than air temperature. *Global Change Biology* 22: 3320-3331.
- Seddon N, Mace GM, Naeem S, et al., 2016. Biodiversity in the Anthropocene:
 Prospects and policy. *Proceedings of the Royal Society B: Biological Sciences*283: 20162094.
- 529 Smale DA, Burrows MT, Moore P et al., 2013. Threats and knowledge gaps for
 530 ecosystem services provided by kelp forests: a northeast Atlantic perspective.
 531 *Ecology & Evolution* 3: 4016–4038.
- 532 Smale DA, Teagle H, Hawkins SJ, et al., 2022. Climate-driven substitution of
 533 foundation species causes breakdown of a facilitation cascade with potential
 534 implications for higher trophic levels. *Journal of Ecology* 110: 2132-2144.
- Southward AJ. 1958. Note on the temperature tolerance of some intertidal animals in
 relation to environmental temperature and geographic distribution. *Journal of the Marine Biological Association of the United Kingdom* 37: 49– 66.
- Underwood AJ, Jernakoff P. 1984. The effects of tidal height, wave-exposure,
 seasonality and rock-pools on grazing and the distribution of intertidal
 macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology* 75: 71-96.

- 542 Usinowicz J, Levine JM. 2018. Species persistence under climate change: a 543 geographical scale coexistence problem. *Ecology Letters* 21: 1589–1603.
- Vale CG, Arenas F, Barreiro R, Piñeiro-Corbeira C. 2021. Understanding the local
 drivers of beta-diversity patterns under climate change: The case of seaweed
 communities in Galicia, North West of the Iberian Peninsula. *Diversity & Distributions* 27: 1696-1705.
- van Buuren S, Groothuis-Oudshoorn K. 2011. mice: multivariate Imputation by
 Chained Equations in R. *Journal of Statistical Software* 45: 1–67.
- Venter O, Sanderson EW, Magrach, A., et al., 2016. Sixteen years of change in the
 global terrestrial human footprint and implications for biodiversity conservation.
 Nature Communications 7: 12558.
- 553 Vetter VMS, Kreyling J, Dengler J, et al., 2020. Invader presence disrupts the
 554 stabilizing effect of species richness in plant community recovery after drought.
 555 *Global Change Biology* 26: 3539-3551.
- Villéger S, Mason NWH, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*89: 2290–2301.
- Wernberg T, Thomsen MS, Tuya F., Kendrick GA. 2011. Biogenic habitat structure
 of seaweeds change along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology* 400: 264–271.
- Westerband AC, Funk JL, Barton KE 2021. Intraspecific trait variation in plants: a
 renewed focus on its role in ecological processes. *Annals of Botany* 127: 397–
 410.
- Westerband A, Knight TM, Barton KE. 2021. Intraspecific trait variation and
 reversals of trait strategies across key climate gradients in native Hawaiian
 plants and non-native invaders. *Annals of Botany* 127: 553–564.
- Wethey DS. 1983. Geographic limits and local zonation: the barnacles *Semibalanus*(*Balanus*) and *Chthamalus* in New England. *Biological Bulletin* 165: 330-341.
- 570 Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating
 571 environment: the insurance hypothesis. *Proceedings of the National Academy of*572 *Sciences USA* 96: 1463–1468.
- 573

574

Figure Legends

575

Figure 1: The influence of rock surface aspect on mean (\pm 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).

580

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.

585

Figure 3: The influence of rock surface aspect on mean (\pm 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.

591

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.

598

599 SOI Legend

Table S1: Summary of variation in relative abundance (percentage cover) of macroalgal 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).

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











(c) Functional Dispersion

