



Macroalgae exhibit diverse responses to human disturbances on coral reefs

Cannon, Sara; Donner, Simon; Liu, Angela; Gonzalez Espinosa, Pedro; Baird, Andrew; Baum, Julia; Bauman, Andrew; Beger, Maria; Benkwitt, Cassandra; Birt, Matthew; Chancerelle, Yannick; Cinner, Joshua; Crane, Nicole; Denis, Vianney; Depczynski, Martial; Fadli, Nur; Fenner, Douglas; Fulton, Christopher; Golbuu, Yimnang; Graham, Nicholas; Guest, James; Harrison, Hugo; Hobbs, Jean-Paul; Hoey, Andrew; Holmes, Thomas; Houk, Peter; Januchowski-Hartley, Fraser; Jompa, Jamaluddin; Kuo, Chao-Yang; Valentino Limmon, Gino; Lin, Yuting; McClanahan, Timothy; Muenzel, Dominic; Paddack, Michelle; Planes, Serge; Pratchett, Morgan; Radford, Ben; Reimer, James; Richards, Zoe; Ross, Claire; Rulmal Jr., John; Sommer, Brigitte; Williams, Gareth J.; Wilson, Shaun

Global Change Biology

DOI:

[10.1111/gcb.16694](https://doi.org/10.1111/gcb.16694)

Published: 01/06/2023

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Cannon, S., Donner, S., Liu, A., Gonzalez Espinosa, P., Baird, A., Baum, J., Bauman, A., Beger, M., Benkwitt, C., Birt, M., Chancerelle, Y., Cinner, J., Crane, N., Denis, V., Depczynski, M., Fadli, N., Fenner, D., Fulton, C., Golbuu, Y., ... Wilson, S. (2023). Macroalgae exhibit diverse responses to human disturbances on coral reefs. *Global Change Biology*, 29(12), 3318-3330. <https://doi.org/10.1111/gcb.16694>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

02. Jun. 2024

1 **Macroalgae exhibit diverse responses to human disturbances on coral reefs**

2 Sara E. Cannon,^{1*} Simon D. Donner,¹ Angela Liu,^{1,2} Pedro C. González Espinosa,^{1,3} Andrew H. Baird,⁴ Julia
3 K. Baum,⁵ Andrew G. Bauman,⁶ Maria Beger,^{7,8,9} Cassandra E. Benkwitt,¹⁰ Matthew J. Birt,¹¹ Yannick
4 Chancerelle,¹² Joshua E. Cinner,⁴ Nicole L. Crane,^{13,14} Vianney Denis,¹⁵ Martial Depczynski,^{11,29} Nur Fadli,¹⁶
5 Douglas Fenner,¹⁷ Christopher J. Fulton,^{11,29} Yimnang Golbuu,¹⁸ Nicholas A. J. Graham,¹⁰ James Guest,¹⁹
6 Hugo B. Harrison,^{4,20,21} Jean-Paul A. Hobbs,²¹ Andrew S. Hoey,⁴ Thomas H. Holmes,^{22,29} Peter Houk,²³ Fraser
7 A. Januchowski-Hartley,²⁴ Jamaluddin Jompa²⁵, Chao-Yang Kuo,^{4,26} Gino Valentino Limmon,^{27,28,29} Yuting
8 V. Lin,¹⁵ Timothy R. McClanahan,³⁰ Dominic Muenzel,⁷ Michelle J. Paddack,^{13,31} Serge Planes,¹² Morgan S.
9 Pratchett,⁴ Ben Radford,^{11,32} James Davis Reimer,^{33,34} Zoe T. Richards,^{35,36} Claire L. Ross,^{22,32} John Rulmal Jr.,^{13,37}
10 Brigitte Sommer,^{38,39} Gareth J. Williams,⁴⁰ Shaun K. Wilson^{22,32}

11 *Corresponding author: s.cannon@oceans.ubc.ca; 604-789-2433

- 14 1. Department of Geography, University of British Columbia, Vancouver, BC, Canada.
- 15 2. School of Geography and the Environment, University of Oxford, Oxford, UK.
- 16 3. Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, BC, Canada.
- 17 4. Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook
18 University, Townsville QLD, Australia.
- 19 5. Department of Biology, University of Victoria, Victoria, BC, Canada.
- 20 6. Department of Marine and Environmental Science, Nova Southeastern University, Dania Beach,
21 Florida, USA.
- 22 7. School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK.
- 23 8. Department of Aquatic Resources Management, Faculty of Fisheries and Marine Science,
24 Pattimura University, Indonesia.
- 25 9. Centre for Biodiversity and Conservation Science, University of Queensland, Australia.
- 26 10. Lancaster Environment Centre, Lancaster University, Lancaster, UK.
- 27 11. Australian Institute of Marine Science, Perth, Western Australia, Australia.
- 28 12. PSL Research University, CRIODE, UAR 3278 CNRS-EPHE-UPVD, Moorea French Polynesia
29 and the French Center for Excellence for Coral Reefs (LabEx Corail), France.
- 30 13. One People One Reef, Santa Cruz, CA, USA.
- 31 14. Department of Biology, Cabrillo College, Aptos, CA, USA.
- 32 15. Institute of Oceanography, National Taiwan University, Taipei, Taiwan.
- 33 16. Faculty of Marine and Fisheries, Universitas Syiah Kuala, Banda Aceh, Indonesia.
- 34 17. Coral Reef Consulting, Pago Pago, American Samoa.
- 35 18. Palau International Coral Reef Center, Koror, Palau.
- 36 19. School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne,
37 UK.
- 38 20. School of Biological Sciences, University of Bristol, Bristol, UK
- 39 21. School of Biological Sciences, The University of Queensland, Brisbane, QLD, Australia.
- 40 22. Marine Science Program, Biodiversity and Conservation Science, Department of Biodiversity
41 Conservation and Attractions, Kensington WA, Australia.
- 42 23. University of Guam Marine Laboratory, UOG Station, Mangilao, Guam.
- 43 24. Department of Biosciences, Swansea University, Swansea, UK.
- 44 25. Department of Marine Science and Fisheries, Hasanuddin University, Makassar, South Sulawesi,
45 Indonesia.
- 46 26. Biodiversity Research Center, Academia Sinica, Taipei, Taiwan.
- 47 27. Department of Marine Biology, Pattimura University, Ambon, Indonesia.
- 48 28. Maritime and Marine Science Centre of Excellence, Pattimura University, Ambon, Indonesia.
- 49 29. Centre for Collaborative Research on Aquatic Ecosystems in Eastern Indonesia.
- 50 30. Wildlife Conservation Society, Global Marine Programs, Bronx, NY, USA.

- 51 31. Santa Barbara City College, Santa Barbara, CA, USA.
52 32. Oceans Institute, University of Western Australia, Perth, WA, Australia.
53 33. Department of Marine Science, Chemistry and Biology, Faculty of Science, University of the
54 Ryukyus, Okinawa, Japan.
55 34. Tropical Biosphere Research Center, University of the Ryukyus, Okinawa, Japan.
56 35. Coral Conservation and Research Group, School of Molecular and Life Sciences, Curtin
57 University, Bently, WA Australia.
58 36. Collections and Research, Western Australian Museum, Perth, Western Australia, Australia.
59 37. Ulithi Falalop Community Action Program, Yap, Federated States of Micronesia.
60 38. School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia
61 39. School of Life Sciences, University of Technology Sydney, Sydney, NSW 2007, Australia.
62 40. School of Ocean Sciences, Bangor University, Anglesey, LL59 5AB, UK.
63

64 **Running Head: Macroalgae responses to local human disturbance**

65

66 **Abstract**

67 Scientists and managers rely on indicator taxa such as coral and macroalgal cover to evaluate the
68 effects of human disturbance on coral reefs, often assuming a universally positive relationship
69 between local human disturbance and macroalgae. Despite evidence that macroalgae respond to
70 local stressors in diverse ways, there have been few efforts to evaluate relationships between
71 specific macroalgae taxa and local human-driven disturbance. Using genus-level monitoring data
72 from 1,205 sites in the Indian and Pacific Oceans, we assess whether macroalgae percent cover
73 correlates with local human disturbance while accounting for factors that could obscure or
74 confound relationships. Assessing macroalgae at genus level revealed that no genera were
75 positively correlated with all human disturbance metrics. Instead, we found relationships
76 between the division or genera of algae and specific human disturbances that were not detectable
77 when pooling taxa into a single functional category, which is common to many analyses. The
78 convention to use percent cover of macroalgae as an indication of local human disturbance
79 therefore likely obscures signatures of local anthropogenic threats to reefs. Our limited
80 understanding of relationships between human disturbance, macroalgae taxa, and their responses
81 to human disturbances impedes the ability to diagnose and respond appropriately to these threats.

82

83 **Keywords: Macroalgae, Coral Reefs, Multiple Stressors, Indian Ocean, Pacific Ocean,**
84 **Local Human Disturbance, Coral Reef Health**

85 **Introduction**
86 Coral reefs are a highly diverse habitats within the tropical and sub-tropical seascape and provide
87 essential services to millions of people, even as anthropogenic stressors intensify (Williams et
88 al., 2019). Changes in the relative abundance of indicator taxa are often used to evaluate the
89 effects of disturbances and human stressors on coral reefs, two common indicators being
90 macroalgae and coral cover. In general, high cover of macroalgae is considered indicative of
91 degraded reefs while high cover of hard corals indicates healthy reefs (Bruno et al., 2009;
92 McCook, 1999; Vroom, 2011; Vroom et al., 2006). The perception that macroalgae cover is
93 indicative of reef health is driven by the theory that local anthropogenic stressors can promote
94 macroalgae proliferation through top-down or bottom-up processes (e.g. the Relative Dominance
95 Model; Littler and Littler, 1984, 2007). However, macroalgae-dominated reefs are not
96 necessarily unhealthy (Vroom, 2011; Vroom et al., 2006). Macroalgae support ecosystem
97 functioning and services (Fulton et al., 2019), contributing to carbonate production and providing
98 nursery habitat that supports adult fish populations (Sievers et al., 2020), including target species
99 for tropical reef fisheries (Wilson et al., 2022). Moreover, while macroalgae and corals compete
100 for space and macroalgae may impede coral recovery through shading, abrasion, or chemical
101 defenses (Littler et al., 2006; Littler & Littler, 2007; Mumby et al., 2006), there are also positive
102 interactions between corals and macroalgae. For example, macroalgae can provide refuge for
103 corals from predation by the Crown-of-Thorns seastar, *Acanthaster planci* (Clements and Hay,
104 2017). Macroalgal canopies can also protect corals from bleaching by limiting exposure to high
105 irradiance (Jompa and McCook, 1998; Smith et al., 2022).

106
107 Macroalgae is a broad term that can encompass multiple taxa with different morphology,
108 ecology, and biology. Consequently, comparisons of studies using the percent cover of
109 macroalgae as a proxy for local human-driven degradation often find conflicting results. For
110 example, Smith et al (2016) reported a significant positive relationship between populated
111 islands and macroalgae cover, concluding that human populations negatively affect reef health.
112 Conversely, Bruno and Valdivia (2016) failed to find a relationship between human populations
113 and macroalgae cover on reefs, concluding local signatures of degradation are being obscured by
114 climate-driven stressors.

115

116 Differences in how macroalgae are defined may have confounded comparisons between studies.
117 Smith et al (2016), for example, included turf algae and excluded erect, calcifying algae such as
118 *Halimeda*, while Bruno and Valdivia (2016) excluded turf algae but included *Halimeda* and
119 other erect, calcifying taxa. Clearly, scientists define macroalgae inconsistently, and the nature of
120 these definitions may obscure drivers of macroalgal cover.

121

122 Furthermore, environmental factors can influence macroalgal cover on reefs, such as exposure to
123 wind and waves (Gove et al., 2015; Page-Albins et al., 2012; Fabricius et al., 2023), seasonality
124 (Brown et al., 2018; Fulton et al., 2014), and sea surface temperature (SST) (Graba-Landry et al.,
125 2020; Tanaka et al., 2012). Studies endeavoring to assess links between local human disturbance
126 and macroalgae cover should therefore consider these environmental factors in analyses.

127 Macroalgae taxa also exhibit variability in their responses to local human and environmental
128 stressors, including temperature (Anton et al., 2020; Fabricius et al., 2023), fishing pressure
129 (Gilby et al., 2015), water pollution (Fabricius, 2005; McClanahan et al., 2004; McCook, 1999),
130 and sedimentation (Fabricius, 2005; Harris et al., 2021). Research investigating these taxon-
131 specific responses to local stressors are lacking for all but the most common macroalgae.

132

133 We re-examine the relationship between macroalgae cover and local human disturbance using
134 data from 1,205 sites in the Indian and Pacific Oceans collected between 2004 and 2020 (Figure
135 1). We define macroalgae as including erect calcifying genera but excluding turf or crustose
136 algae (Bruno et al., 2009; Steneck, 1988; Tebbet and Bellwood, 2019). We use this definition to
137 remain consistent with past studies (e.g. Bruno et al., 2009; Bruno and Valdivia, 2016; Steneck,
138 1988; Tebbett and Bellwood, 2019; Tebbett et al., 2023), and to make use of pre-existing survey
139 data in which turf algae was not identified consistently across surveys. The analyses test the
140 hypothesis that macroalgae percent cover is correlated with local human disturbance when
141 accounting for environmental factors that might have confounded the findings in previous studies
142 (Bruno and Valdivia, 2016; Smith et al., 2016). For all sites and within six biogeographic realms
143 (Costello et al., 2017; see Methods), we determined the suite of human disturbance and
144 environmental variables (Supplementary Table 1) that best explain the genus-level macroalgae
145 communities via canonical correspondence analysis (CCA) and stepwise ordination. Next, we fit
146 permutational analysis of variance (PERMANOVA) models to estimate the effects of each

147 variable on macroalgal communities. We then used Similarity Percentage Analysis (SIMPER) to
148 determine the taxa driving differences across biogeographic realms. Finally, we fit zero-inflated
149 generalized linear mixed models (GLMMs) to quantify the relationships between local human
150 disturbance and the common macroalgae genera and their divisions (red, green, brown).

151

152 **Materials and Methods**

153 We collated data from genus-level macroalgae benthic surveys conducted by the authors
154 (Supplementary Materials: Data Sources) from 1,205 individual tropical and subtropical coral
155 reef study sites across the Indian and Pacific Oceans between 2004 and 2020, covering a period
156 of 16 years. This dataset provides a snapshot of each site at a single time point and we did not
157 investigate temporal changes in macroalgal communities. As discussed below, we considered
158 temporal and methodological variables to account for differences across sites and surveys
159 (Supplementary Table 1). Of the 1,205 sites, 1,145 identified all macroalgae to the genus level,
160 while 60 surveys only identified macroalgae of the genus *Halimeda*. We did not include these
161 *Halimeda*-only surveys in the investigation of community drivers of macroalgae, but we
162 included them in the genus-specific analyses described below. All statistical modeling, figures,
163 and plots were done using R Statistical Software version 4.4.1 (R Core Team, 2021), R Studio
164 version 2021.09.0 Build 351 (RStudio Team, 2020), the R package ggplot2 (Wickham, 2016),
165 and Inkscape (Inkscape Project, 2020). The R code is available on GitHub
166 (https://github.com/secanno/Cannonet2023_Macroalgae). We created the map in QGIS version
167 3.24 (QGIS Development Team, 2022) using a base map from OpenStreetMap (OpenStreetMap
168 Foundation, 2021).

169

170 To limit the ability of confounding factors to obscure potential relationships between macroalgae
171 and local human disturbance, we identified and calculated 45 site-specific variables (in addition
172 to 15 variables representing human disturbance), representing drivers known to influence
173 macroalgae growth and distribution at multiple resolutions. These variables encompassed eight
174 categories: connectivity with other reefs, heat stress, human disturbance, methodological and site
175 descriptive variables, net primary productivity, seasonality, storms, and wind and wave exposure.
176 Because the estimates of these variables cover a wide geographic area, we conducted the analysis
177 for the entire dataset, and also separated the sites into marine biogeographic realms (Costello et

178 al., 2017) to test whether the macroalgae communities within realms were explained by different
179 variables. One of the realms, the offshore Indian Ocean, included just twelve sites, which we
180 added to the Indo-Pacific Seas and Indian Ocean realm. We also considered data contributors
181 and the survey methodologies as explanatory variables to account for differences in site selection
182 and sampling methodologies. Due to spatial constraints, we are unable to detail the methods and
183 justifications for each of the 60 explanatory variables that we considered in the main text of the
184 manuscript. Instead, Supplementary Table 1 contains a table describing each variable, including
185 its definition, source, spatial resolution, and justification for inclusion in the analysis.

186

187 We assessed multicollinearity during variable selection at two steps in the analysis. First, we
188 used the R package Hmisc (Harrell, Jr., 2021) to calculate the Pearson's r correlation coefficients
189 for all possible pairs of variables and eliminated any with r correlation values of greater than 0.7
190 within each of the eight covariate categories. When multiple variables were correlated within a
191 given category, we chose those with the lowest summed Pearson's r coefficient, eliminating 33
192 variables (Supplementary Table 2). Then, following Borcard et al. (2011), to select variables that
193 best explained the macroalgae community compositions, we conducted CCA and stepwise
194 variable selection using the R package vegan (Oksanen et al., 2020) for all sites combined and
195 independently for each of the six realms. We addressed multicollinearity in this second step by
196 eliminating any variables with a variable inflation factor (VIF) > 10 (Table 1) (Borcard et al.,
197 2011). We detail the variables selected by the CCAs and their VIF in Supplementary Table 3.

198

199 Using the R package vegan (Oksanen et al, 2020), we ran SIMPER (999 permutations) to
200 identify the macroalgae taxa driving differences across biogeographic realms. We also identified
201 variables with strong correlations to macroalgal community composition with principal
202 component analysis and by fitting seven PERMANOVAs: one for all the data combined and for
203 each of the six realms independently. Each PERMANOVA included the variables selected by the
204 CCA, excluding those with VIFs > 10 (Supplementary Table 3).

205

206 Last, we evaluated how local human disturbance, represented by variables detailed in
207 Supplementary Table 1, influenced the distribution of the most common genera of macroalgae.
208 To estimate the effects of five categories of local human disturbance on the most common

209 macroalgae taxa, their divisions, and for all macroalgae combined, we fit generalized linear
210 mixed models using the R package glmmTMB (Bolker et al., 2009) for the following equation:

211
212 *Percent of Macroalgae ~ cumulative human impact score + log(population density) + NDVI +*
213 *nutrients + market gravity + (I|Latitude:Longitude)*

214
215 We considered each of the five human disturbance variables fixed effects, the interaction
216 between latitude and longitude a random effect to account for spatial autocorrelation across sites.
217 The most common genera were defined as those comprising more than 1% of the total
218 macroalgae cover, either across the entire dataset or within one of the realms. The cumulative
219 human impact score is a metric for local human disturbance that includes small scale fishing
220 pressure, coastal population, industrial development, tourism, and two types of water pollution
221 (sedimentation and nitrogen from agriculture), while the normalized difference vegetation index
222 (NDVI) is a proxy for nearby development. For more details, including methods and
223 justifications for each of the model variables, please see Supplementary Table 1.

224
225 We compared zero and non-zero-inflated GLMM with gaussian and beta distributions. We
226 selected zero-inflated beta regression models because they best met the assumptions that the
227 residuals would exhibit homoscedasticity and be normally distributed, and that the data are not
228 autocorrelated. The human population variable was log-transformed to meet the assumptions.
229 We used diagnostic plots to test for normal distribution and equal variance of residuals with the
230 R package DHARMA (Hartig, 2022), and Moran's tests to test for spatial autocorrelation with
231 the package spdep (Bolker et al., 2009, Supplementary Materials 4). We also calculated the R²
232 values (marginal R², which represents only the fixed effects, and conditional R², which measures
233 the fit of the entire model) using the Nakagawa method (Nakagawa et al., 2017). Finally, to
234 enable comparing the model results across taxa, we used the R package ggeffects to calculate the
235 adjusted marginal effects for each of the explanatory variables (Lüdecke, 2018).

236
237

238 **Results**

239 Across these 1,205 sites, we identified 96 genera of macroalgae and total macroalgae cover
240 varied from zero to 88.2% per site, with a mean of 12.8% and a median of 6.8%. The calcified
241 green algae *Halimeda* occurred at the most sites (68.2%).

242

243 Macroalgal community compositions differed across realms (Figure 2). The genus *Halimeda* was
244 most common in all realms except for the offshore West Pacific and northwest Pacific, where
245 *Lobophora*, a brown fleshy alga, was the most common taxa. We describe the most common taxa
246 within each realm in detail in Supplementary Table 5, and the full SIMPER results comparing all
247 realms to each other in Supplementary Table 6.

248

249 The drivers of spatial differences in macroalgal community compositions differed when
250 considering the full model (containing all sites) or within each of the realms (Table 1,
251 Supplementary Table 7). A principal component analysis considering the potential drivers of
252 macroalgae distribution (Supplementary Table 1) found that the first three principal components
253 accounted for 46.32% of the variation in macroalgal communities (Supplementary Materials 8).
254 The full equations for all the PERMANOVAs were statistically significant with p-values < 0.01
255 for the model containing all sites, and models for each of the realms except the mid-tropical
256 North Pacific, which was not significant (p = 0.08). The explanatory power of each model
257 varied, and each of the independent variables had R² values less than 0.10. For all macroalgae
258 combined, the PERMANOVA accounted for 10% of the variation in macroalgae percent cover
259 across sites. The model for the Mid-Tropical North Pacific had the least explanatory power for
260 variation in macroalgal community composition (R² = 0.05), while the model for sites in the
261 Mid-South Tropical Pacific had the greatest (R² = 0.21).

262

263 The human disturbance metrics had the largest effects of all drivers contributing to the variation
264 in macroalgal communities in all realms. Of these human disturbance indicators, the normalized
265 difference vegetation index (NDVI, an indicator of development on land; see Methods) and
266 nutrients from agriculture had the greatest presence in the models, although nutrients were only
267 significant in two of six models, while NDVI was significant in three of the six. Three of the
268 models also included a categorical variable representing fisheries management (open-access,

269 restricted, or closed / no access), which had greater explanatory power than the other human
270 disturbance metrics (all of which had R^2 values less than 0.05). Of the biophysical indicators,
271 mean wave energy was another common driver of macroalgae community composition and was
272 significant in four out of six models. Except for fisheries management, all the variables had R^2
273 values that were less than or equal to 0.05.

274

275 The relationships between the percent cover and each of the human disturbance metrics varied
276 for different macroalgae genera (Figure 3) and divisions (Figure 4, Supplementary Materials 9).
277 The adjusted estimates indicated weak relationships between the percent cover of total
278 macroalgae and the human disturbance metrics (Supplementary Materials 10), with effect sizes
279 that were all less than one. When investigating potential relationships by genera or division,
280 however, some relationships between specific taxa and human disturbance became apparent that
281 were not evident for all macroalgae combined. Similarly, when considering the division of
282 macroalgae (red, green, or brown), relationships with human disturbance were less apparent than
283 they were for specific macroalgae taxa. Percent cover of all algae had a negative relationship
284 with three out of five human disturbance variables. Within the brown macroalgae division, most
285 taxa exhibited positive relationships with the log of the population density, and negative
286 relationships with NDVI and nutrients from agriculture. Only two of the brown macroalgae
287 genera exhibited strong relationships with the disturbance. The genus *Spatoglossum* was
288 positively correlated with the cumulative human impact score (which includes sedimentation,
289 nutrients from agriculture, tourism, industrial development, and small-scales fisheries pressure;
290 Andrello et al., 2021), log of population density, and market gravity, but was negatively
291 correlated with NDVI and nutrients from agriculture. By contrast, *Dictyopteris* was positively
292 correlated with the cumulative human impact score and NDVI, but negatively correlated with
293 market gravity and nutrients from agriculture.

294

295 Similarly, both the green and red macroalgae taxa also demonstrated weak relationships with
296 human disturbance when considered by division, with specific taxa showing stronger positive or
297 negative relationships. Most of the green macroalgae genera were negatively related to the log of
298 the population density (*Microdictyon* and *Udotea* were strongly and negatively correlated) but
299 were weakly related with the remaining human disturbance metrics. The red macroalgae taxa

300 were also negatively related to the log of the population density and NDVI. By contrast, the red
301 macroalgae genera *Ceratodictyon* and *Hypnea* were positively correlated with the population
302 density, although these relationships were weak.

303

304 **Discussion and Conclusions**

305 The percent cover of total macroalgae is not a robust indicator for local anthropogenic
306 disturbance in the Indian and Pacific Oceans, for two main reasons: (1) the drivers of macroalgae
307 communities are unclear, challenging to estimate, and differ across realms, and (2) different
308 macroalgae genera and divisions have distinct and often opposite responses to diverse types of
309 local human disturbance.

310

311 We find that multiple environmental factors, unrelated to local anthropogenic disturbance,
312 influenced macroalgae community compositions (connectivity, wind and wave exposure, storms,
313 net primary production and seasonality). Accounting for these environmental factors is
314 imperative if researchers and managers are to use macroalgae as an indicator of anthropogenic
315 impact on reefs. Otherwise, researchers risk attributing observed patterns in macroalgal
316 community composition to the wrong drivers. Furthermore, despite assessing 60 variables that
317 could influence macroalgae communities, the most parsimonious models included few variables,
318 and the PERMANOVAs all had R^2 values of less than 0.25. This indicates that the models were
319 still unable to account for most of the variation in macroalgal communities and highlights the
320 difficulty in identifying the drivers of ecological patterns (discussed further below).

321

322 In addition, the relative importance of the factors influencing macroalgal communities differed
323 across the biogeographical realms. The CCA identified 17 variables influencing macroalgae
324 distribution when considering all sites. However, each variable explained less than 3% of the
325 variation and collectively, the full equation only accounted for 10% of the variation. Many of
326 these variables were selected only when considering all sites collectively, but not when
327 examining the drivers of macroalgal communities by biogeographical realm. In the Coral Sea,
328 the CCA identified six variables as best describing the variation in macroalgal communities, half
329 of which (nutrients from agriculture, the kurtosis of chl-a, and the standard deviation of net
330 primary productivity) are related to nutrients, and the other half were related to storms and

331 exposure to wind and waves (number of storms greater than type 3, cyclone score, and mean
332 wave energy). These variables collectively accounted for 21% of the variation across sites in the
333 Coral Sea. In the mid-South Tropical Pacific, the PERMANOVA accounted for 18% of the
334 variation, and fisheries management and development (represented by NDVI) were important for
335 explaining variation in macroalgal communities, along with the depth of the surveys,
336 photosynthetic radiation, and the aspect of the site. By contrast, the heat stress metrics were not
337 important drivers of macroalgal communities, whether considering all sites collectively or within
338 the biogeographic realms. Collectively, the CCAs and PERMANOVA results show that
339 macroalgal communities are influenced by different factors depending on their location. Without
340 accounting for these factors, studies that compare the percent cover of macroalgae across broad
341 regions may obscure differences in community compositions, rather than revealing them.

342

343 The macroalgae genera we assessed also exhibited diverse and oftentimes opposing relationships
344 with different metrics of human disturbance. Combining all macroalgae into a single category, or
345 into divisions, obscured ecologically important relationships. In addition, the total macroalgae
346 cover metric was uniformly weakly explained by each of the human disturbance variables. The
347 cumulative human impact score did not have the strongest correlation with macroalgae cover.
348 This is most likely because this metric is a conglomeration of multiple stressors, and our analysis
349 clearly shows that many taxa respond more strongly to a specific anthropogenic stressor.
350 Moreover, the percent cover of many taxa will increase in response to one stressor but decline
351 when subjected to another, somewhat nullifying any response when responses from multiple
352 stressors are combined. This indicates that taxon-specific responses to individual human
353 pressures should be considered when evaluating local anthropogenic impacts on coral reefs.

354

355 The individual traits of the macroalgae genera may explain their relationships with the various
356 disturbance metrics, each of which represents a different form of localized disturbance. The
357 genus *Halimeda* was present at almost 70% of the sites and was the most common macroalga in
358 our dataset. As the most common calcifying alga on tropical reefs globally, *Halimeda*, produce
359 sediment on coral reefs and play an important role in reef accretion (Hillis-Colinvaux, 1980).
360 Our results suggest that *Halimeda* cover will increase with increasing cumulative human impacts
361 but will decline with increasing market gravity and nutrients from agriculture. While market

362 gravity was designed as a metric for fishing pressure (Cinner et al., 2018), it incorporates human
363 population size, and may therefore also reflect nutrient loading present in realms with high
364 human populations. The weak but negative correlation with nutrients from agriculture, is in
365 contrast with past findings showing that *Halimeda* growth is stimulated by nutrients (Delgado,
366 1994; Teichberg et al., 2013). Increasing market gravity might increase competition with other
367 macroalgae taxa that would otherwise be kept in check by herbivory, which could explain the
368 negative correlation. However, coral reef herbivores show low preferences for *Halimeda* and
369 some species are chemically defended (Hay et al., 1988; Paul and Van Alstyne, 1988).
370 Collectively, these results reveal a complex relationship between *Halimeda* and human
371 disturbance; it is more likely to grow where nutrients are high, but not necessarily where there is
372 high fishing pressure.

373

374 Complex relationships may also exist for other macroalgae taxa examined here, although
375 confirming these relationships is not possible with the current data and will require further
376 research as well as experiments that manipulate the extent of different stressors imposed on
377 macroalgae taxa. For example, we found that canopy-forming brown algae, which provide
378 important habitat for fish and support small-scale fisheries (Sievers et al., 2020; Wilson et al.,
379 2022), exhibit diverse responses to disturbance. For example, blooms of *Turbinaria* have been
380 linked to high nutrient concentrations on the Great Barrier Reef (McCook, 1999), which is
381 consistent with our results from across the Indian and Pacific Oceans. *Sargassum* was one of the
382 few taxa exhibiting a negative relationship with nutrients from agriculture, which aligns with
383 past research (e.g. McClanahan et al., 2004). However, it is in direct opposition of the Relative
384 Dominance Model (RDM), which posits that macroalgae cover on coral reefs is dictated by
385 human disturbance acting through top-down (e.g., fishing pressure) or bottom-up (e.g., nutrients)
386 processes (Littler and Littler, 1984, 2007).

387

388 While past research helps explain many of the relationships between specific macroalgae taxa
389 and our human disturbance variables, we also found unexpected relationships. The morphology
390 of *Turbinaria*, along with its chemical defenses, make it unpalatable to many herbivores (Bittick
391 et al., 2010) and we would not anticipate an increase in percent cover with increasing fishing
392 pressure (Davis, 2018). However, we found a positive correlation with market gravity. Other

393 studies have also reported that macroalgae taxa often do not respond as predicted to stressors
394 (McClanahan et al., 2004; McCook, 1999), again, underscoring how little these interactions are
395 understood. Unfortunately, studies investigating taxa-specific interactions with human
396 disturbance for tropical macroalgae are lacking for all but the most common taxa and often
397 report conflicting results (Ramseyer et al., 2021). Existing studies are primarily motivated by
398 negative interactions between corals and macroalgae (Fulton et al., 2019; Vroom, 2011).
399 Furthermore, because of the Relative Dominance Model's predictions, studies are usually limited
400 to investigating the effects of fishing pressure or nutrients (e.g. Adam et al., 2021; Holbrook et
401 al., 2022).

402

403 Our results show that the lack of correlation between total macroalgae cover and local human
404 disturbance may be in part because of the varied interactions between disturbance and individual
405 macroalgae taxa. Signatures of human disturbance that were undetectable using total macroalgae
406 cover may still be evident when identifying macroalgae at the genus level. In these cases, relying
407 on the assumption that macroalgae percent cover correlates with local disturbance may lead to
408 maladaptive interventions; for example, if managers assume that all macroalgae will respond
409 similarly to enhanced herbivory despite evidence to the contrary (Kelly et al., 2016), or
410 misidentify undisturbed reefs as degraded, this approach could lead to costly and ineffective
411 management interventions.

412

413 For reef-building corals, research has greatly improved our understanding of diverse and
414 complex responses to disturbance. Literature has documented differences in how corals respond
415 to bleaching, for example, because of their morphology, heterotrophic feeding ability,
416 physiology, and several other factors (Darling et al., 2012; Loya et al., 2001; Van Woesik et al.,
417 2011). Yet, the focus on coral in the literature demonstrates that scientists have failed to consider
418 how genera within diverse macroalgae assemblages may also respond to disturbance differently
419 and what this means for ecosystem function (Fulton et al., 2019). Like reef-building coral
420 communities, some taxa of macroalgae are susceptible to climate-driven stressors (Anton et al.,
421 2020; Graba-Landry et al., 2020). Our limited understanding of the relationships between both
422 human and climate disturbance and macroalgae taxa, and their importance in reef ecosystem

423 functioning, impedes our ability to respond to the many threats facing coral reef ecosystems as a
424 whole (Vroom, 2011).

425

426 This study builds on previous research that has called the RDM and the subsequent assertions
427 that macroalgae is correlated with local human disturbance an oversimplification (Fulton et al.,
428 2019; McCook, 1999; Vroom, 2011) with potentially negative implications for management
429 (McCook, 1999; Vroom, 2011), and that has criticized the widespread reliance on macroalgae as
430 an indicator of reef health or degradation (Bruno et al., 2009; Vroom, 2011). Despite these
431 critiques, researchers and managers continue to use total macroalgae cover to provide proxy
432 estimates on the health of coral reefs and how they are affected by people (Bruno and Valdivia,
433 2016; Smith et al., 2016). A key limitation to this and other research on macroalgae distribution
434 (Keith et al., 2014; Tebbett et al., 2023) is the lack of available survey data identifying
435 macroalgae at the genus level. Most of the survey data we analyzed were collected to investigate
436 the status and/or health of coral reefs, and site selection may have excluded parts of the reef with
437 higher macroalgae cover. In addition, the sampling was uneven across realms, and the reliance
438 on large-scale, low-resolution global databases to calculate site-specific independent variables
439 may have affected our ability to account for local drivers of macroalgal communities because of
440 differences in scale. Despite these limitations, this study demonstrates that the links between
441 macroalgae cover and human disturbance are uncertain, which undermines the usefulness of total
442 macroalgae cover as a way of estimating local, human-driven degradation.

443

444 Strategic management of coral reefs is increasingly vital as the climate continues to warm
445 (Darling et al., 2019). Evaluating how coral reefs are being affected by disturbance is an
446 indispensable part of research and management, but the most common metrics used in that work
447 are based on an oversimplified and poorly tested paradigm. We have shown here that total
448 macroalgae cover does not correlate well with local human disturbance but that evaluating
449 macroalgae cover at the genus-level shows more promise as a management and assessment tool.
450 Genus-level data might also provide greater understanding of the drivers of macroalgae and how
451 they influence overall ecosystem functioning. Investments in further research on macroalgae at
452 finer taxonomic resolutions, including genus-specific interactions with human-driven stressors,
453 may be important for future coral reef conservation. In addition, as others have argued, testing

454 long-standing paradigms in marine ecology will be increasingly necessary to make good
455 predictions as climate change intensifies (Williams et al., 2019), demonstrating the need for
456 enhanced monitoring to improve our ability to assess climate-driven changes in benthic
457 communities. We hope that by demonstrating that total macroalgae cover is only weakly
458 correlated with human disturbance and is not an effective way to estimate coral reef health in the
459 Indian and Pacific Oceans, this work catalyzes much-needed consideration of how we define reef
460 health and the effects of local human disturbance, especially under rapidly changing
461 environmental conditions.

462

463 **Acknowledgments**

464 The authors are grateful to the editors and two anonymous reviewers for their careful reading of
465 earlier drafts and their constructive input. Please see the Supplementary Acknowledgements for
466 full acknowledgments. The authors have no conflicts of interest.

467

468 **Citations**

- 469 Adam, T. C., Burkepile, D. E., Holbrook, S. J., Carpenter, R. C., Claudet, J., Loiseau, C.,
470 Thiault, L., Brooks, A. J., Washburn, L., & Schmitt, R. J. (2021). Landscape-scale
471 patterns of nutrient enrichment in a coral reef ecosystem: Implications for coral to algae
472 phase shifts. *Ecological Applications*, 31(1), e2227. <https://doi.org/10.1002/eap.2227>
- 473 Anton, A., Randle, J. L., Garcia, F. C., Rossbach, S., Ellis, J. I., Weinzierl, M., & Duarte, C. M.
474 (2020). Differential thermal tolerance between algae and corals may trigger the
475 proliferation of algae in coral reefs. *Global Change Biology*, 26(8), 4316–4327.
<https://doi.org/10.1111/gcb.15141>
- 477 Bittick, S. J., Bilotti, N. D., Peterson, H. A., & Stewart, H. L. (2010). *Turbinaria ornata* as an
478 herbivory refuge for associate algae. *Marine Biology*, 157(2), 317–323.
<https://doi.org/10.1007/s00227-009-1319-6>
- 480 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., &
481 White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology
482 and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135.
<https://doi.org/10.1016/j.tree.2008.10.008>
- 484 Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical Ecology with R* (R. Gentleman, K.
485 Hornick, & G. G. Parmigiani, Eds.). Springer. <https://doi.org/10.1007/978-1-4419-7976-6>
- 486 Brown, K. T., Bender-Champ, D., Kubicek, A., van der Zande, R., Achlatis, M., Hoegh-
487 Gulberg, O., & Dove, S. G. (2018). The Dynamics of Coral-Algal Interactions in Space
488 and Time on the Southern Great Barrier Reef. *Frontiers in Marine Science*, 5, 181.
<https://doi.org/10.3389/fmars.2018.00181>
- 490 Bruno, J. F., & Valdivia, A. (2016). Coral reef degradation is not correlated with local human
491 population density. *Scientific Reports*, 6(July), 29778. <https://doi.org/10.1038/srep29778>
- 492 Bruno, J. F., Precht, W. F., Vroom, P. S., & Aronson, R. B. (2014). Coral reef baselines: How

- 493 much macroalgae is natural? *Marine Pollution Bulletin*, 80(1–2), 24–29.
494 <https://doi.org/10.1016/j.marpolbul.2014.01.010>
- 495 Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., McClanahan,
496 T. R., Barnes, M. L., Kittinger, J. N., Hicks, C. C., D'Agata, S., Hoey, A. S., Gurney, G.
497 G., Feary, D. A., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G. J., ...
498 Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains.
499 *Proceedings of the National Academy of Sciences*, 115(27), E6116–E6125.
500 <https://doi.org/10.1073/pnas.1708001115>
- 501 Clements, C. S., & Hay, M. E. (2017). Size matters: Predator outbreaks threaten foundation
502 species in small Marine Protected Areas. *PLOS One*, 12(2), e0171569.
503 <https://doi.org/10.1371/journal.pone.0171569>
- 504 Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., & Chaudhary, C. (2017).
505 Marine biogeographic realms and species endemicity. *Nature Communications*, 8(1),
506 Article 1. <https://doi.org/10.1038/s41467-017-01121-2>
- 507 Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., & Côté, I. M. (2012).
508 Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*,
509 15(12), 1378–1386. <https://doi.org/10.1111/j.1461-0248.2012.01861.x>
- 510 Darling, E. S., McClanahan, T. R., Maina, J., Gurney, G. G., Graham, N. A. J., Januchowski-
511 Hartley, F., Cinner, J. E., Mora, C., Hicks, C. C., Maire, E., Puotinen, M., Skirving, W. J.,
512 Adjeroud, M., Ahmadia, G., Arthur, R., Bauman, A. G., Beger, M., Berumen, M. L.,
513 Bigot, L., ... Mouillot, D. (2019). Social–environmental drivers inform strategic
514 management of coral reefs in the Anthropocene. *Nature Ecology & Evolution*, 3(9),
515 1341–1350. <https://doi.org/10.1038/s41559-019-0953-8>
- 516 Davis, S. L. (2018). Associational refuge facilitates phase shifts to macroalgae in a coral reef
517 ecosystem. *Ecosphere*, 9(5), e02272. <https://doi.org/10.1002/ecs2.2272>
- 518 Delgado, O. (1994). Nutrient-limited productivity of calcareous versus fleshy macroalgae in a
519 eutrophic, carbonate-rich tropical marine environment. *Coral Reefs*, 13, 151–159.
520 <https://doi.org/10.1007/BF00301191>
- 521 Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs:
522 Review and synthesis. *Marine Pollution Bulletin*, 50(2), 125–146.
523 <https://doi.org/10.1016/j.marpolbul.2004.11.028>
- 524 Fabricius, K. E., Crossman, K., Jonker, M., Mongin, M., & Thompson, A. (2023). Macroalgal
525 cover on coral reefs: Spatial and environmental predictors, and decadal trends in the
526 Great Barrier Reef. *PloS One*, 18(1), e0279699.
527 <https://doi.org/10.1371/journal.pone.0279699>
- 528 Fulton, C. J., Depczynski, Martial., Holmes, T. H., Noble, M. M., Radford, B., Wernberg, T., &
529 Wilson, S. K. (2014). Sea temperature shapes seasonal fluctuations in seaweed biomass
530 within the Ningaloo coral reef ecosystem. *Limnology and Oceanography*, 59(1), 156–
531 166. <https://doi.org/10.4319/lo.2014.59.1.0156>
- 532 Fulton, C. J., Abesamis, R. A., Berkström, C., Depczynski, M., Graham, N. A. J., Holmes, T. H.,
533 Kulbicki, M., Noble, M. M., Radford, B. T., Tano, S., Tinkler, P., Wernberg, T., &
534 Wilson, S. K. (2019). Form and function of tropical macroalgal reefs in the
535 Anthropocene. *Functional Ecology*, 33, 989–999. <https://doi.org/10.1111/1365-2435.13282>
- 536 Gilby, B. L., Maxwell, P. S., Tibbetts, I. R., & Stevens, T. (2015). Bottom-Up Factors for Algal
537 Productivity Outweigh No-Fishing Marine Protected Area Effects in a Marginal Coral

- 539 Reef System. *Ecosystems*, 18(6), 1056–1069. <https://doi.org/10.1007/s10021-015-9883-8>

540 Gove, J. M., Williams, G. J., McManus, M. A., Clark, S. J., Ehses, J. S., & Wedding, L. M.
541 (2015). Coral reef benthic regimes exhibit non-linear threshold responses to natural
542 physical drivers. *Marine Ecology Progress Series*, 522, 33–48.
<https://doi.org/10.3354/meps11118>

543 Graba-Landry, A. C., Loffler, Z., McClure, E. C., Pratchett, M. S., & Hoey, A. S. (2020).
544 Impaired growth and survival of tropical macroalgae (*Sargassum* spp.) at elevated
545 temperatures. *Coral Reefs*, 39(2), 475–486. <https://doi.org/10.1007/s00338-020-01909-7>

546 Harrell, Jr., F. E. (2021). *Hmisc: Harrell Miscellaneous* (4.6-0) [R Programming; R Statistical
547 Software]. <https://CRAN.R-project.org/package=Hmisc>

548 Harris, R. J., Wilson, S. K., & Fulton, C. J. (2021). Interactive effects of sediments and urchins
549 on the composition and structure of tropical macroalgal assemblages. *Marine Biology*,
550 168(9), 144. <https://doi.org/10.1007/s00227-021-03953-5>

551 Hartig, F. (2022). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
552 Regression Models* (R package version 0.4.6). [https://CRAN.R-
553 project.org/package=DHARMA](https://CRAN.R-project.org/package=DHARMA)

554 Hay, M. E., Paul, V. J., Lewis, S. M., Gustafson, K., Tucker, J., & Trindell, R. N. (1988). Can
555 tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth,
556 nitrogen content, herbivory, and chemical versus morphological defenses. *Oecologia*,
557 75(2), 233–245. <https://doi.org/10.1007/BF00378604>

558 Hillis-Colinvaux, L. (1980). Ecology and Taxonomy of Halimeda: Primary Producer of Coral
559 Reefs. In *Advances in Marine Biology* (Vol. 17, pp. 1–327). Elsevier.
[https://doi.org/10.1016/S0065-2881\(08\)60303-X](https://doi.org/10.1016/S0065-2881(08)60303-X)

560 Holbrook, S. J., Wencelius, J., Dubel, A. K., Adam, T. C., Cook, D. C., Hunter, C. E., Lauer, M.,
561 Lester, S. E., Miller, S. D., Rassweiler, A., & Schmitt, R. J. (2022). Spatial covariation in
562 nutrient enrichment and fishing of herbivores in an oceanic coral reef ecosystem.
563 *Ecological Applications: A Publication of the Ecological Society of America*, 32(3),
564 e2515. <https://doi.org/10.1002/eaap.2515>

565 Inkscape Project. (2020). *Inkscape*.

566 Jompa, J., & McCook, L. J. (1998). Seaweeds save the reef?!: *Sargassum* canopy decreases coral
567 bleaching on inshore reefs. *Reef Research*, 8, 5.

568 Keith, S. A., Kerswell, A. P., & Connolly, S. R. (2014). Global diversity of marine macroalgae:
569 Environmental conditions explain less variation in the tropics: Global diversity of marine
570 macroalgae. *Global Ecology and Biogeography*, 23(5), 517–529.
<https://doi.org/10.1111/geb.12132>

571 Kelly, E. L. A., Eynaud, Y., Clements, S. M., Gleason, M., Sparks, R. T., Williams, I. D., &
572 Smith, J. E. (2016). Investigating functional redundancy versus complementarity in
573 Hawaiian herbivorous coral reef fishes. *Oecologia*, 182(4), 1151–1163.
<https://doi.org/10.1007/s00442-016-3724-0>

574 Littler, M. M., & Littler, D. S. (1984). Models of tropical reef biogenesis: The contribution of
575 algae. In F. Round & D. Chapman (Eds.), *Progress in Phycological Research* (Vol. 3, pp.
576 323–364). Biopress.

577 Littler, M. M., & Littler, D. S. (2007). Assessment of coral reefs using herbivory/nutrient assays
578 and indicator groups of benthic primary producers: A critical synthesis, proposed
579 protocols, and critique of management strategies. *Aquatic Conservation: Marine and
580 Freshwater Ecosystems*, 17, 195–215. <https://doi.org/10.1002/aqc.790>

- 585 Loya, Y., Sakai, K., Nakano, Y., & Woesik, R. V. (2001). Coral bleaching: The winners and the
586 losers. *Ecology Letters*, 4, 122–131. <https://doi.org/10.1046/j.1461-0248.2001.00203.x>
- 587 M McClanahan, T. R., Sala, E., Mumby, P. J., & Jones, S. (2004). Phosphorus and nitrogen
588 enrichment do not enhance brown frondose “macroalgae.” *Marine Pollution Bulletin*,
589 48(1–2), 196–199. <https://doi.org/10.1016/j.marpolbul.2003.10.004>
- 590 McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and
591 management consequences for the Great Barrier Reef. *Coral Reefs*, 18(4), 357–367.
592 <https://doi.org/10.1007/s003380050213>
- 593 Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R^2
594 and intra-class correlation coefficient from generalized linear mixed-effects models
595 revisited and expanded. *Journal of The Royal Society Interface*, 14(134), 20170213.
596 <https://doi.org/10.1098/rsif.2017.0213>
- 597 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R.,
598 O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H.
599 (2020). *vegan: Community Ecology Package* (2.5-7) [R]. <https://CRAN.R-project.org/package=vegan>
- 600 OpenStreetMap Foundation. (2021). *OpenStreetMap* [Map]. OpenStreetMap.
601 www.OpenStreetMap.org/copyright
- 602 Page-Albins, K. N., Vroom, P. S., Hoeke, R., Albins, M. A., & Smith, C. M. (2012). Patterns in
603 Benthic Coral Reef Communities at Pearl and Hermes Atoll along a Wave-Exposure
604 Gradient. *Pacific Science*, 66(4), 481–496. <https://doi.org/10.2984/66.4.6>
- 605 Paul, V. J., & Van Alstyne, K. L. (1988). Chemical defense and chemical variation in some
606 tropical Pacific species of *Halimeda* (Halimedaceae; Chlorophyta). *Coral Reefs*, 6(3),
607 263–269. <https://doi.org/10.1007/BF00302022>
- 608 QGIS Development Team. (2022). *QGIS Geographic Information System*. Open Source
609 Geospatial Foundation Project. (3.24). <https://qgis.org>
- 610 R Core Team. (2021). *R: A Language and Environment for Statistical Computing* (4.4.1). R
611 Foundation for Statistical Computing. <https://www.R-project.org>
- 612 Ramseyer, T., Tronholm, A., Turner, T., Brandt, M., & Smith, T. (2021). Elevated nutrients and
613 herbivory negatively affect *Dictyota* growth dynamics. *Marine Ecology Progress Series*,
614 671, 81–95. <https://doi.org/10.3354/meps13788>
- 615 RStudio Team. (2020). *RStudio: Integrated Development for R*. RStudio, PBC.
616 <http://www.rstudio.com>
- 617 Sievers, K. T., McClure, E. C., Abesamis, R. A., & Russ, G. R. (2020). Non-reef habitats in a
618 tropical seascapes affect density and biomass of fishes on coral reefs. *Ecology and
619 Evolution*, 10(24), 13673–13686. <https://doi.org/10.1002/ece3.6940>
- 620 Smith, H. A., Prenzlau, T., Whitman, T., Fulton, S. E., Borghi, S., Logan, M., Heron, S. F., &
621 Bourne, D. G. (2022). Macroalgal canopies provide corals limited protection from
622 bleaching and impede post-bleaching recovery. *Journal of Experimental Marine Biology
623 and Ecology*, 553, 151762. <https://doi.org/10.1016/j.jembe.2022.151762>
- 624 Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., Lewis, L., Obura, D.,
625 Rohwer, F., Sala, E., Vroom, P. S., & Sandin, S. (2016). Re-evaluating the health of coral
626 reef communities: Baselines and evidence for human impacts across the central Pacific.
627 *Proceedings of the Royal Society B: Biological Sciences*, 283(1822), 20151985.
628 <https://doi.org/10.1098/rspb.2015.1985>
- 629 Steneck, R. S. (1988). Herbivory on Coral Reefs: A Synthesis. *Proceedings of the 6th*
- 630

- 631 *International Coral Reef Symposium, 1*, 37–49.
- 632 Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G., & Hiraoka, M. (2012). Warming off
633 southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds.
634 *Ecology and Evolution*, 2(11), 2854–2865. <https://doi.org/10.1002/ece3.391>
- 635 Tebbett, S. B., & Bellwood, D. R. (2019). Algal turf sediments on coral reefs: What's known and
636 what's next. *Marine Pollution Bulletin*, 149, 110542.
637 <https://doi.org/10.1016/j.marpolbul.2019.110542>
- 638 Tebbett, S. B., Connolly, S. R., & Bellwood, D. R. (2023). Benthic composition changes on coral
639 reefs at global scales. *Nature Ecology & Evolution*, 7(1), Article 1.
640 <https://doi.org/10.1038/s41559-022-01937-2>
- 641 Teichberg, M., Fricke, A., & Bischof, K. (2013). Increased physiological performance of the
642 calcifying green macroalga *Halimeda opuntia* in response to experimental nutrient
643 enrichment on a Caribbean coral reef. *Aquatic Botany*, 104, 25–33.
644 <https://doi.org/10.1016/j.aquabot.2012.09.010>
- 645 Van Woesik, R., Sakai, K., Ganase, A., & Loya, Y. (2011). Revisiting the winners and the losers
646 a decade after coral bleaching. *Marine Ecology Progress Series*, 434, 67–76.
647 <https://doi.org/10.3354/meps09203>
- 648 Vroom, P. S. (2011). “Coral Dominance”: A Dangerous Ecosystem Misnomer? *Journal of*
649 *Marine Biology*, 2011, 1–8. <https://doi.org/10.1155/2011/164127>
- 650 Vroom, P. S., Page, K. N., Kenyon, J. C., & Brainard, R. E. (2006). Algae-Dominated Reefs:
651 Numerous reports suggest that reefs must be dominated by coral to be healthy, but many
652 thriving reefs depend more on algae. *American Scientist*, 94, 430–437.
653 <https://doi.org/10.1511/2006.61.1004>
- 654 Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
655 <https://ggplot2.tidyverse.org>
- 656 Williams, G. J., Graham, N. A., Jouffray, J.-B., Norström, A. V., Nyström, M., Gove, J. M.,
657 Heenan, A., & Wedding, L. M. (2019). Coral reef ecology in the Anthropocene.
658 *Functional Ecology*, 33(6), 1014–1022. <https://doi.org/10.1111/1365-2435.13290>
- 659 Wilson, S. K., Fulton, C. J., Graham, N. A. J., Abesamis, R., Berkström, C., Coker, D. J.,
660 Depczynski, M., Evans, R. D., Fisher, R., Goetze, J., Hoey, A., Holmes, T. H., Kulbicki,
661 M., Noble, M., Robinson, J. P. W., Bradley, M., Åkerlund, C., Barrett, L. T., Bucol, A.
662 A., ... Tinkler, P. (2022). The contribution of macroalgae-associated fishes to small-scale
663 tropical reef fisheries. *Fish and Fisheries*, faf.12653. <https://doi.org/10.1111/faf.12653>
- 664

665 **Tables**

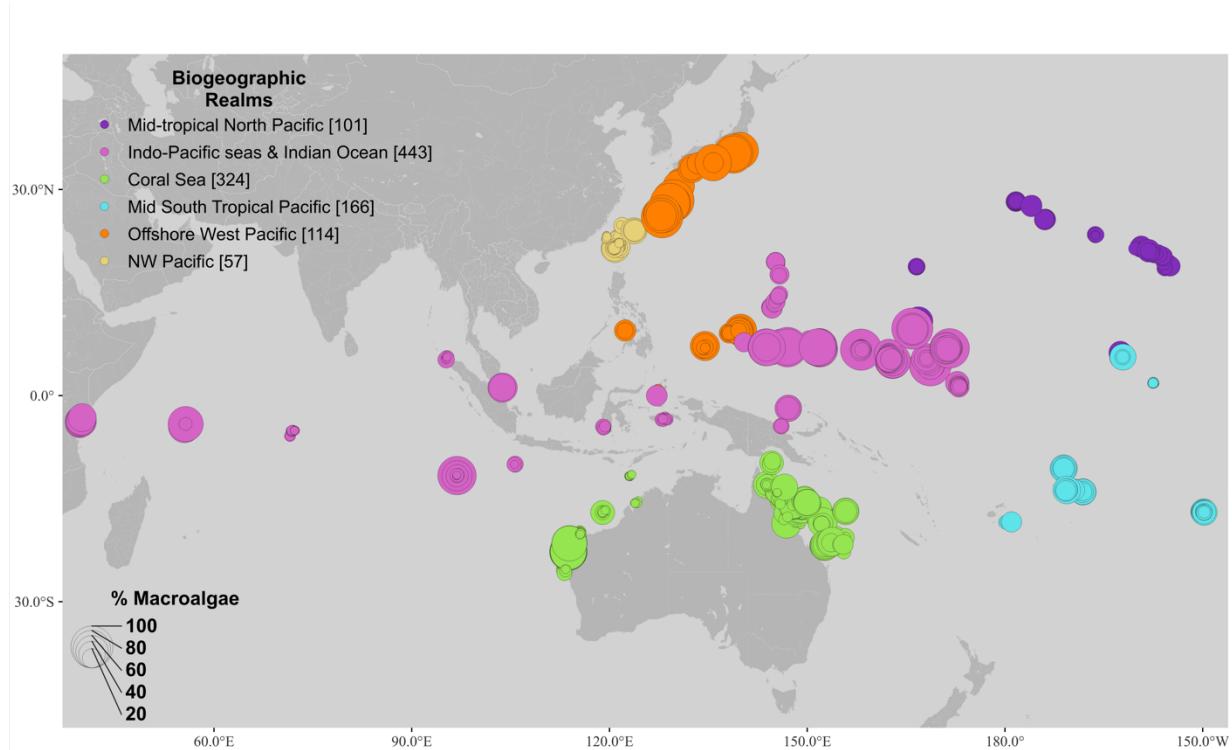
666 **Table 1.** Variables that best explained macroalgal communities (CCA results) and had variable inflation
 667 factors of less than 10, shown with their pseudo-R² values (PERMANOVA results). Values in bold are
 668 statistically significant at $\alpha = 0.05$, while those in italics are significant at $\alpha = 0.10$. Empty cells indicate that
 669 variables were not selected as best explaining the macroalgal communities by the CCA and were not included
 670 in the PERMANOVAs.

Variable Type	Variable	All Data	Mid-tropical N. Pacific	Indo-Pacific seas & Indian Ocean	Coral Sea	Mid South Tropical Pacific	Offshore West Pacific	NW Pacific
<i>R² (full equation)</i>		0.10	0.05	0.12	0.21	0.18	0.07	0.16
Connectivity	Reef Area (15km)			0.05				
	Reef Area (200km)	0.00		0.01				
Human Disturbance	Cum. Human Impact	0.01						
	Fisheries Management	0.01				0.08		0.09
	NDVI	0.00		0.02		0.02	0.03	
	Nutrients (Agriculture)	0.00	0.03		0.04			0.04
	Market Gravity							
Methodology & Sampling	Depth	0.00		0.02		0.04		
	Habitat	0.02						
	Latitude							
Net Primary Productivity	Chl-a (kurtosis)	0.00		0.01	0.02			0.02
	NPP (sd)	0.00			0.05			
Seasonality	Month of survey (by SST)	0.03						
	PAR average (survey mo.)	0.00				0.04		
	SST mean (survey mo.)			0.01				
Storms	# Storms \geq Type 3	0.00	0.02		0.01			
	Cyclone Score				0.02			
Heat stress	MaxDHW	0.00						
	MMM	0.00						
	SST _{SD}	0.00						
Wind and Wave Exposure	Aspect	0.00				0.00	0.01	
	Wave energy (mean)	0.00		0.00	0.04		0.02	
	Wind and Wave Exposure						0.01	0.01

671

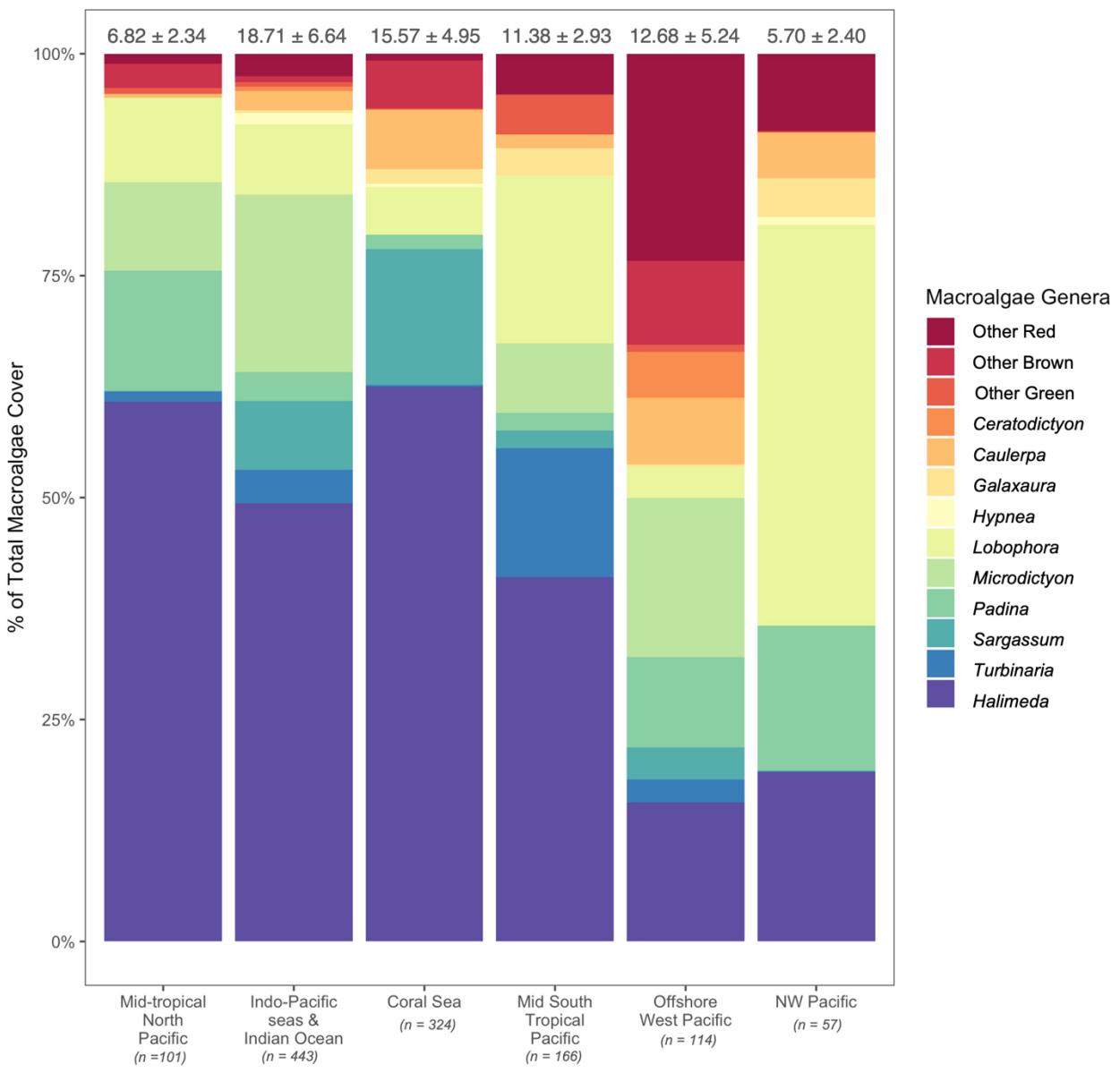
672

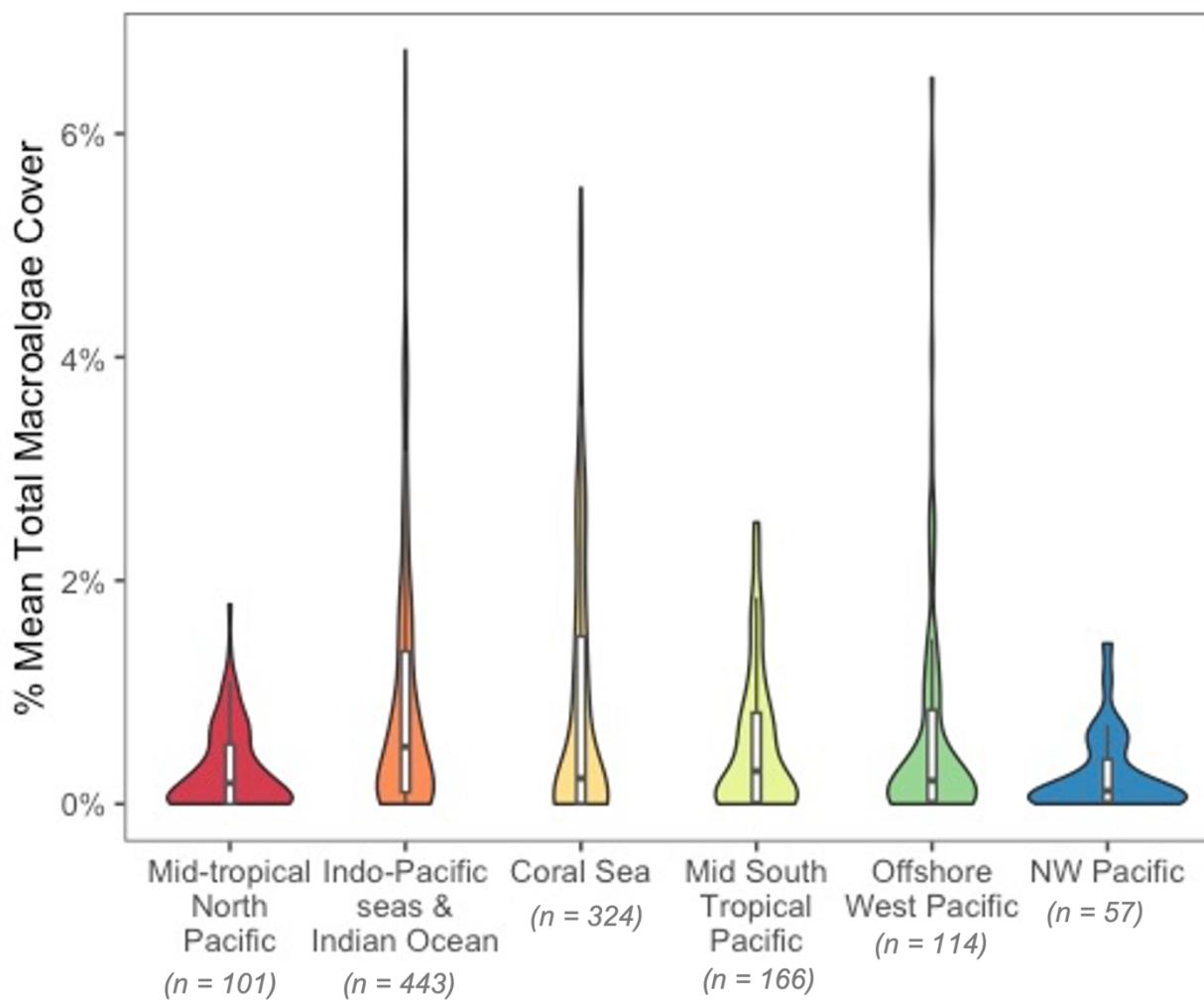
673 **Figures**



674
675 **Figure 1. Map of 1,205 study sites across the Indian and Pacific Oceans, by biogeographic**
676 **realm (as described in Costello et al., 2017). The size of the points represents the total**
677 **percent cover of macroalgae at each site. Map lines do not necessarily depict accepted**
678 **national boundaries.**

679





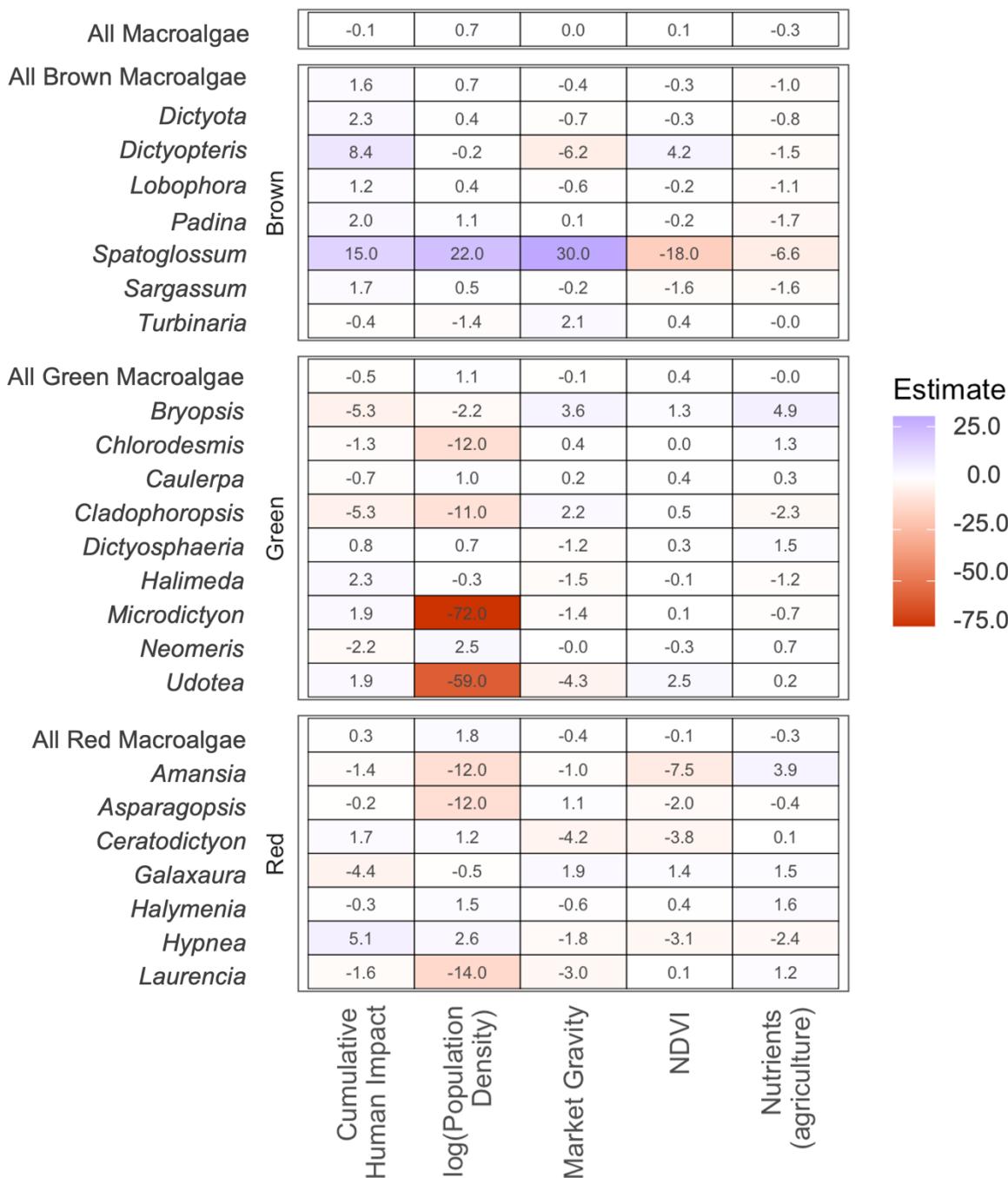
681
682
683

b.

Figure 2. (a) Top ten most common macroalgae taxa by biogeographic realm, with mean and standard deviation at the top of each bar. (b) Mean total macroalgae cover by site,

684 grouped by biogeographic realms.

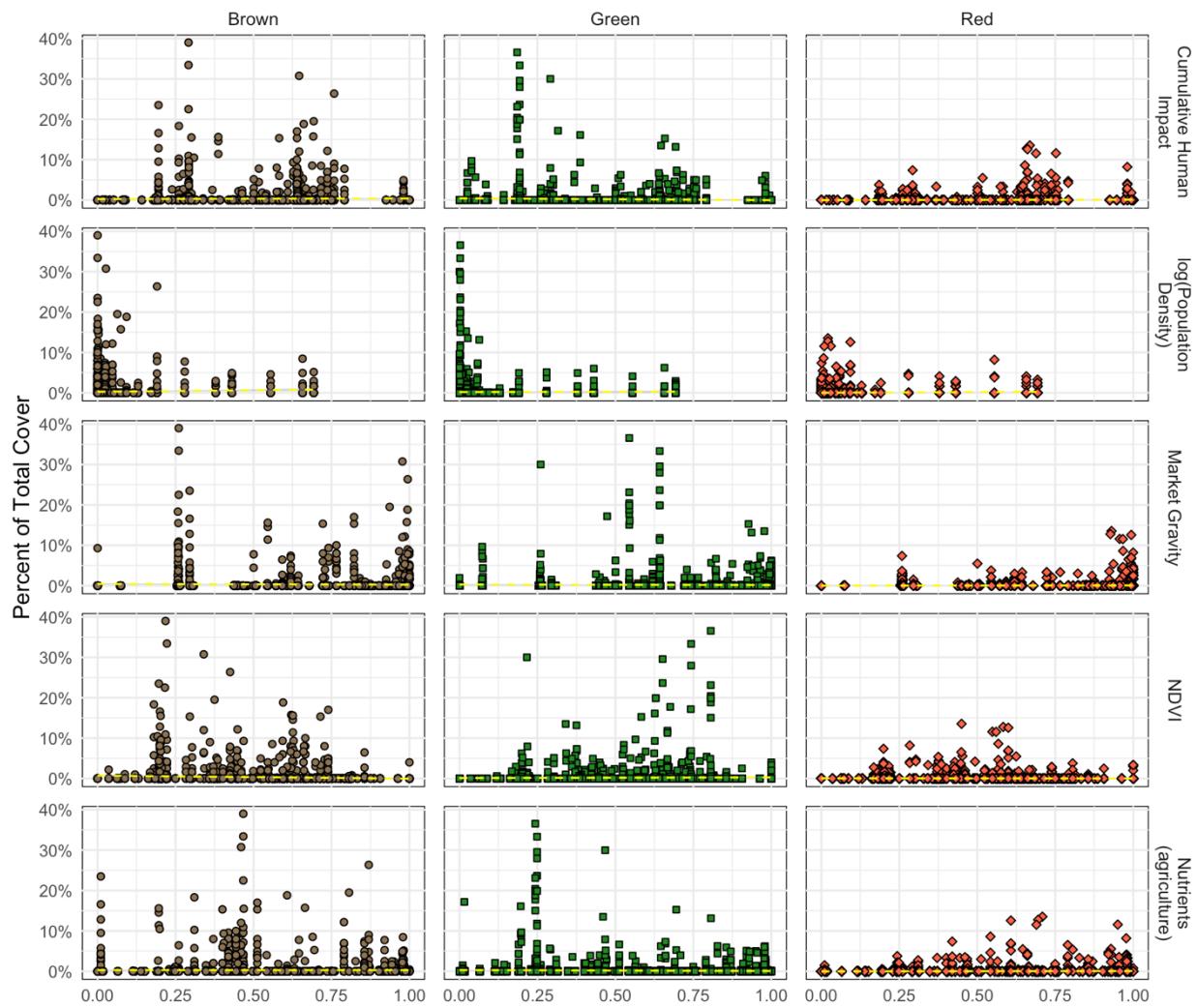
685



686

687

688 **Figure 3. Estimated parameters for fixed effects from the GLMMs.** *Estimates for NDVI
689 have been multiplied by -1 to account for this variable's inverse relationship with disturbance.
690



691
692

693 **Figure 4. The percent cover of macroalgae genera grouped into three divisions (brown,**
694 **green, and red), as they relate to five human disturbance variables.** The dashed yellow line is
695 the trendline. The disturbance variables have been normalized and range between zero and one
696 (see *Methods*).
697
698

699

700 **Supplementary Material: Data owners and contact information for requesting access for each dataset included in the analysis.**

Site Location	Data Region(s)	Data Owner(s)	Contact Name	Contact Email
Australia	Ashmore Reef & Great Barrier Reef	Richards	Zoe Richards	zoe.richards@curtin.edu.au
Australia	Cocos (Keeling) Islands	Hobbs	J.P. Hobbs	jp.hobbs@uq.edu.au
Australia	Coral Sea	Harrison, Hobbs, Hoey, and Pratchett	Andrew Hoey	Andrew.hoey1@jcu.edu.au
Australia	Great Barrier Reef	Pratchett and Hobbs	Morgan Pratchett	morgan.pratchett@jcu.edu
Australia	Great Barrier Reef	Baird and Kuo	Andrew Baird	andrew.baird@jcu.edu.au
Australia	Ningaloo	Birt, Depczynski, Fulton, Holmes, Radford, and Wilson	Shaun Wilson	shaun.wilson@dbca.wa.gov.au

Site Location	Data Region(s)	Data Owner(s)	Contact Name	Contact Email
Australia	Ningaloo, Rowley Shoals, Shark Bay, Montebello and Barrow Islands	Ross and Holmes	Claire Ross	claire.ross@dcba.wa.gov.au
Chagos Archipelago		Benkwitt, Graham, and Wilson	Nick Graham	nick.graham@lancaster.ac.uk
Federated States of Micronesia	Chuuk, Yap, Pohnpei, Kosrae	Houk	Peter Houk	peterhouk@gmail.com
Federated States of Micronesia	Yap and Chuuk Outer Islands	Paddack, Crane, and Rulmal, Jr.	Michelle Paddack	michelle.paddack@gmail.com
Fiji	Lau	Graham, Pratchett, and Wilson	Shaun Wilson	shaun.wilson@dbca.wa.gov.au
French Polynesia	Moorea	Planes and Chancerelle	Serge Planes	planes@univ-perp.fr
Indonesia	Aceh	Baird, Fadli, and Hoey	Andrew Baird	andrew.baird@jcu.edu.au
Indonesia	Spermonde, Ambon, and Halmahera	Beger, Muenzel, Jompa, Limmon	Maria Beger	m.beger@leeds.ac.uk

Site Location	Data Region(s)	Data Owner(s)	Contact Name	Contact Email
Japan		Beger, Reimer, Sommer	Maria Beger	m.beger@leeds.ac.uk
Kenya		McClanahan	Tim McClanahan	tmclanahan@wcs.org
Kiribati	Gilbert Islands, Tarawa and Abaiang Atolls	Cannon and Donner	Sara Cannon	s.cannon@oceans.ubc.ca
Kiribati	Kirimati	Baum	Julia Baum	baum@uvic.ca
Marshall Islands	Majuro and Arno Atolls	Cannon and Donner	Sara Cannon	s.cannon@oceans.ubc.ca
Marshall Islands	Rongelap, Ebon, Namdrik, and Wotho Atolls	Houk	Peter Houk	peterhouk@gmail.com
Palau		Golbuu	Yimnang Golbuu	ygolbuu@picrc.org
Papua New Guinea		Bauman, Cinner, and Januchowski-Hartley	Andrew Bauman	abauman@nova.edu
Philippines		Bauman and Januchowski-Hartley	Andrew Bauman	abauman@nova.edu
Seychelles		Graham and Wilson	Shaun Wilson	shaun.wilson@dbca.wa.gov.au

Site Location	Data Region(s)	Data Owner(s)	Contact Name	Contact Email
Singapore		Bauman and Guest	Andrew Bauman	abauman@nova.edu
Taiwan		Denis and Lin	Vianney Denis	vianney.denis@gmail.com
USA	American Samoa	Fenner	Douglas Fenner	douglasfennertassi@gmail.com
USA	Guam, Hawaii, Northern Marianas, American Samoa, Pacific Remote Island Areas	NOAA	Not applicable	NOAA National Centers for Environmental Information (http://ncei.noaa.gov)
USA	Pacific Remote Islands Area	Williams	Gareth Williams	g.j.williams@bangor.ac.uk

702 **Extended Funding and Acknowledgments**

703

704 **Australia.** Funding was provided to Z. Richards by the Western Australian Museum and
705 Woodside Energy for Ashmore and Hibernia Reef data collected during the Kimberley
706 Woodside Collection Project. Lizard Island fieldwork was funded by ARC Linkage Project
707 LP160101508, The Isobel Bennett Fellowship and the Lizard Island Reef Research Fellowship
708 awarded to Z. Richards. Funding for data from the Coral Sea Marine Park was provided by the
709 Director of National Parks, Australia (ASH, MSP, HBH, AHB), and we thank staff at Parks
710 Australia for assistance, particularly M. Russell. Funding for Ningaloo Reef was provided by the
711 Australian Institute of Marine Science and Department of Biodiversity, Conservation and
712 Attractions and we would like to acknowledge the Baiyungu, Thalanyji and Yinigurdira People
713 of this region. Funding for Rowley Shoals, Shark Bay and Montebello and Barrow Islands was
714 provided by the Department of Biodiversity, Conservation and Attractions. Funding for data
715 from the Townsville section of the Great Barrier Reef was provided by the ARC Centre of
716 Excellence for Coral Reef Studies (AHB, C-YK). Funding was provided to J. Hobbs for data
717 collected at Christmas and Cocos Islands by Parks Australia. Funding for data collected in Fiji
718 was provided to S. Wilson by National Geographic Grant #7941-05, and funding for data from
719 Singapore was provided to A. Bauman from the AXA Research Fund (154-000-649-507) and the
720 National Research Foundation, Prime Minister's Office, Singapore under the Marine Science
721 Research and Development Programme (MSRDP-P03). Fieldwork in Manus and Madang
722 Provinces in Papua New Guinea was supported by funding awarded to Joshua Cinner through the
723 Australian Research Council CE140100020, FT160100047, P110101540, and DP0877905), the
724 Pew Charitable Trust, the Paul M. and the Angell Family Foundation.

725

726 **Canada.** Funding for data from the Gilbert Islands, Kiribati and Majuro and Arno Atolls,
727 Republic of the Marshall Islands was provided to S. Cannon by a Natural Sciences &
728 Engineering Research Council of Canada (NSERC) Vanier Canada Doctoral Scholarship, and to
729 S. Donner by a Natural Sciences and Engineering Research Council of Canada Discovery Grant
730 (www.nserc-crsng.gc.ca, RGPIN-2019-04056). Field assistance in the Gilbert Islands was
731 provided by E. Aram, T. Beiateuea, A. Kiareti, and M. Peter. Field assistance in Majuro and
732 Arno was provided by K. DeBrum, D. Thompson, and E. Reed. Funding for data from
733 Kiritimati, Kiribati was provided to J.K. Baum by an NSERC Discovery Grant, a Rufford
734 Foundation grant, and the Canadian Foundation for Innovation.

735

736 **France.** Funding was provided to the Service d'Observation Corail, mainly by the IR ILICO, the
737 INSU-CNRS, the French Minister for Ecology and EPHE via the Institute for Coral reefs of the
738 Pacific. The Service d'Observation Corail (<http://observatoire.criobe.pf>) monitors coral reefs in
739 the south pacific and makes data available to the community.

740

741 **Japan.** Research was funded by grants from the Japanese Society for the Promotion of Science
742 (JSPS) 'Zuno-Junkan' grant entitled "Studies on origin and maintenance of marine biodiversity
743 and systematic conservation planning" to JDR, the Australian Research Council Centre of
744 Excellence for Environmental Decisions (CE110001014) and an EU Marie Slodowska Curie
745 Fellowship (TRIM-DLV-747102) to MB, and a Chancellor's Postdoctoral Research Fellowship
746 from the University of Technology Sydney to BS. We specifically thank Dr. T Naruse,
747 University of the Ryukyus for accommodation at Iriomote-jima Island, Okinawa, as well as Mr.

748 S Dewa, Diving Service Umiannai in Kagoshima and Mr. K Nomura,Kushimoto Marine Park
749 Center in Wakayama for arranging field surveys. We also thank Diving Service Toneriko at
750 Iriomote-jima Island, Okinoshima Diving Service Marine Snow at Tateyama,Nakagi Marine
751 Center at Shimoda, Yakushima Diving Service Morito-Umi at Yakushima Island, and Relax
752 Diving Service and Aquadive Koholloa at Amami-Oshima Island for logistical support.
753

754 **Kenya.** This work was supported by the Wildlife Conservation Society and supported by a
755 number of organizations, including the Pew Charitable Trust, Tiffany & Co. Foundation, and the
756 Western Indian Ocean Marine Science for Management Program. Clearance to do research in
757 Kenya was provided by Kenya's Office of Science and Technology and in the parks by Kenya
758 Wildlife Services. Many people assisted with the monitoring, notably R. Arthur, M. Azali, E.
759 Darling, C. Hicks, A. T. Kamukuru, R. Kiambo, J. Kosgei, B. Kaunda-Arara, J.Kawaka, R.
760 Machaku, H. Machano Ali, S. Mangi, J. Maina, J.Mariara, R. Moothien-Pillay, J. Mutere, N. A.
761 Muthiga, S. Mwacheriya, J. Ndagala, R. Odenya, J. Omukoto, and M. J. Rodrigues.
762

763 **Micronesia.** Data were collected by all authors in a collaborative partnership with the
764 Micronesia coral-reef and fisheries monitoring network ([https://micnesiareefmonitoring.com/](https://micronesiareefmonitoring.com/)).
765 Data were deposited into the Micronesia Reef Monitoring online database that hosts data,
766 provides data access, and offers collaboration with interested individuals and organizations
767 (<https://micnesiareefmonitoring.com/>). Data are also publicly available through the National
768 Oceanic and Atmospheric Administration National Center for Environmental Information
769 website (<https://www.coris.noaa.gov/search/catalog/main/home.page>) under accession number
770 0162463.
771

772 **Palau.** Funding for the Palau International Coral Reef Center's (PICRC) long-term coral reef
773 monitoring program was provided by the Government of Palau, the JICA Technical Assistance
774 Program (PICRC strengthening project) and the NOAA-Coral Reef Conservation Program, Pew
775 Fellowship in Marine Conservation. The David & Lucile Packard Foundation supported the
776 initial design and setup of the monitoring program at PICRC. We thank the numerous research
777 assistants and researchers who have been involved in PICRC's long-term coral reef monitoring
778 program over the last 20 years.
779

780 **Taiwan.** Funding was provided to V. Denis by grants from the Ministry of Science and
781 Technology of Taiwan (MOST 104-2611-M-002-020-MY2, 106-2611-M-002-008, 107-2611-M-
782 002-011, 108-2611-M-002-013, and 109-2611-M-002-017), and to Y.V. Lin by a graduate
783 research grant from the Ocean Affairs Councils of Taiwan (OAC-UNIV-108-004). Fieldwork
784 was possible under permits nos. 1083544868 and 1080123287 issued by New Taipei City and
785 Taitung County governments, respectively. The Academia Sinica Green Island Marine Research
786 Station provides logistic support at Ludao. Field assistance was provided by M.-J Ho at Ludao,
787 Functional Reef Ecology Lab Members: J.-W. Chen, Q. Chen, W.V. Hsiao, C. B. Wang, T.-H.T
788 Hsu, N. Sturaro and all diving instructors ensuring safety underwater.
789

790 **United Kingdom.** For data collected from the Philippines, funding was provided to F
791 Januchowski-Hartley by the Welsh European Funding Office and European Regional
792 Development Fund through a Sêr Cymru co-fund fellowship (Project Number: 80761-SU-
793 135)Government (80761-SU-135). Field assistance in the Philippines was provided by Dionn

794 Hubag and the Philippines Reef and Rainforest Conservation Foundation, Inc. Funding for data
795 from Spermonde, Ambon, and Halmahera, Indonesia came from grants by the UK Newton Fund
796 and Natural Environment Research Council (NERC) to M. Beger [grant number NE/S006931/1]
797 and a grant from the Indonesian Ministry of Research and Technology/National Agency for
798 Research and Innovation to J Jompa [grant number 7/AMD/E1/KP.PTNBH/2020]. Field
799 assistance was provided by Halwi, R. Purnama, C. Djakiman, and M. DeBrauwer. Funding for
800 the data from Aceh, Indonesia was provided by the ARC Centre of Excellence for Coral Reef
801 Studies (AHB). Research from the Seychelles was supported by a Royal Society University
802 Research Fellowship awarded to N Graham (UF140691), the Australian Research Council, and
803 the Leverhulme Trust. We thank the Seychelles Fishing Authority, Seychelles National Parks
804 Authority, Nature Seychelles, and Global Vision International for logistical support. Funding for
805 data collected from the Chagos Archipelago was provided to N. Graham by the Australian
806 Research Council, Royal Society and the Bertarelli Foundation and contributed to the Bertarelli
807 Programme in Marine Science.

808

809 **United States.** Field and logistical assistance was provided by J. Smith of Scripps Research
810 Institute, University of California San Diego for data collected from Palmyra and Kingman
811 Atolls. Funding for data from the outer islands of Yap and Chuuk, Federated States of
812 Micronesia was provided to N. Crane, M.J. Paddack and J. Rulmal by a National Science
813 Foundation grant (Grant 1546374 and 1622339) NOAA (Award # NA15NMF4270336),
814 Interior/Office of Insular Affairs (CRI-Ulithi1-2), and the David and Lucile Packard Foundation
815 and the Pacific Rim Research Program (UCSC). We are deeply grateful for the people of Ulithi
816 Atoll and the outer Islands of Yap, FSM, who continue to sustainably nurture their reefs for
817 future generations.

818

Supplementary Table 1. Description of variables thought to influence total macroalgae percent cover on coral reefs.

	Name	Resolution and/or Units	Description and Reasoning	Source
Connectivity			<i>Connections between coral reefs can influence local ecological communities through larval dispersal with impacts for resilience and management (Magris et al., 2016). Some macroalgae may travel long distances during various parts of their life cycles. Additionally, the ability of hard coral taxa to compete with macroalgae after disturbances may be influenced by coral larval supply (Beyer et al., 2018).</i>	
1	Connectivity Score	5 km resolution, no units	A metric estimating the level of connectivity of sites to other reefs, including outgoing larval settlement (including self-recruitment) and larval export estimated via a larval connectivity model (Beyer et al., 2018).	Andreollo et al., 2021, Beyer et al., 2018
2	Reef Area (15 km)	Number of reefs cells falling within a 15-km buffer multiplied by the area of a cell (0.25 km ²).	15-km is the upper range of larval dispersion distances for most reef fishes, which can influence macroalgae percent cover through herbivory (Green et al., 2015).	Yeager et al., 2017
3	Reef Area (200 km)	Number of reefs cells falling within a 200-km buffer multiplied by the area of a cell (0.25 km ²).	200-km is the upper range of larval dispersal distances for large-bodied fish species (Green et al., 2015). Some macroalgae can also disperse across large distances.	Yeager et al., 2017
Geography			<i>Geography influences the oceanography and climate of a given reef. These variables will also account for geographical bias in the dataset and spatial autocorrelation across sites.</i>	
4	Latitude	Decimal degrees	We used the latitude and longitude to account for spatial autocorrelation in the dataset.	Data contributors
5	Longitude	Decimal degrees	We used the latitude and longitude to account for spatial autocorrelation in the dataset.	Data contributors

	Name	Resolution and/or Units	Description and Reasoning	Source
6	Land area-15	0.25 km ² grid cell resolution, 15km radius, expressed in km ²	Land area within a 15-km radius of each site. Nutrient inputs from land-derived sources are commonly detectable within primary producers up to 15 km from shore (Lapointe and Clark 1992).	Yeager <i>et al.</i> , 2017
7	Land area-50	0.25 km ² grid cell resolution, 50 km radius, expressed in km ²	Land area within a 50 km radius of each site. Rivers can transport nutrients from land-use activities 50 km or more from the coast.	Yeager <i>et al.</i> , 2017
8	SST _{CV}	5 km resolution, no units	The coefficient of variation for sea surface temperature represents the range of temperature values at a given site.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
9	Number of DHW > 4	5 km resolution, no units	Degree heating weeks greater than 4 represent a bleaching warning as defined by Coral Reef Watch, indicating that coral bleaching is possible.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
10	Number of DHW > 8	5 km resolution, no units	When degree heating weeks exceed 8, Coral Reef Watch issues a bleaching warning, indicating that coral bleaching is likely.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
11	SST _{kurt}	5 km resolution, no units	The kurtosis of SST is the distribution by frequency, with positive values indicating a steeper distribution than normal, and negative values indicating a broader distribution than normal.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
12	MaxDHW (all)	5 km resolution, no units	The maximum Degree Heating Weeks, a metric for cumulative heat stress, in the entire time period (between 1995 and 2020).	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)

	Name	Resolution and/or Units	Description and Reasoning	Source
13	Mean of annual maxDHW	5 km resolution, no units	The mean of the highest DHW from each year between 1995 and 2020.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
14	MMM	5 km resolution, expressed in °C	The Maximum Monthly Mean is the highest value among the 12 monthly mean SST climatologies at a given site. Prolonged SSTs that are 1°C greater than the MMM may induce coral bleaching (Liu et al., 2018).	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
15	Overall Climate Score	5 km resolution, No units	A metric for the heat stress experienced at each site, incorporating historic, recent, and estimated future heat stress and trends (Beyer et al., 2018)	Andrello et al., 2021; Beyer et al., 2018
16	Historic Climate Stress Score	5 km resolution, No units	A metric for the historic heat stress experienced at each site, from 1985 - 2017 (Beyer et al., 2018)	Andrello et al., 2021; Beyer et al., 2018
17	SST _{sd}	5 km resolution, expressed in °C	The standard deviation of SST represents the amount that sea surface temperatures.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
18	SST _{skew}	5 km resolution, expressed in °C	The skewness of SST indicates whether the frequency of daily temperatures are normally distributed or skewed towards lower or higher temperature values.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
Human Disturbance	<i>Scientists use macroalgae as a metric for estimating reef health and may assume that coral reefs with high macroalgae percent cover are degraded (Littler and Littler, 2007). We collected a wide range of variables representing several aspects of human disturbance on coral reefs to test this assumption and whether macroalgae percent cover is useful as an indication of coral reef ecosystem health.</i>			

	Name	Resolution and/or Units	Description and Reasoning	Source
19	Cumulative Human Impact Score	5 km resolution, No units	An estimate of cumulative human impacts on coral reefs, including small scale fishing pressure, coastal population, industrial development, tourism, and two types of water pollution (sedimentation and nitrogen from agriculture).	Andrello <i>et al.</i> , 2021
20	Market Gravity	10 km grid cells; expressed as the number of people / (travel time to nearest market in hours) ²	The population of a major market divided by the squared travel time between a reef site and market, representing fishing pressure (Cinner et al., 2018). Fishing pressure can increase herbivory on coral reefs, which may increase macroalgae percent cover.	Andrello et al., 2021; Cinner <i>et al.</i> , 2018
21	HII-100	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 100-km radius around each site. HII incorporates population density, land use and infrastructure, and human aspects (including coastlines, roads, railroads, and rivers), which are known to predict local human impacts on coral reefs (Baumann et al., 2022).	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
22	HII-10	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 10-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)

	Name	Resolution and/or Units	Description and Reasoning	Source
23	HII-25	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 25-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
24	HII-50	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 50-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
25	HII-70	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 70-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
26	Population density	0.25 km ² grid cell resolution, Number of people within a 20-km radius of each site per 1,256 km ²	As human population densities increase, associated threats, including coastal development, nutrient pollution, and fishing pressure, may also increase. A 20-km radius represents the distance travelled by most subsistence fishers (Clark et al., 2002, Chuenpagdee et al., 2006) and the scale at which land-use change has the largest impact on nutrient loading (Yeager et al., 2017).	Yeager <i>et al.</i> , 2017

	Name	Resolution and/or Units	Description and Reasoning	Source
27	Population density	0.25 km ² grid cell resolution, Number of people within a 50-km radius of each site per 7,850 km ²	A 50-km radius represents the upper limit of small-scale or semi-commercial coastal fisheries (Chuenpagdee et al., 2006), and watershed-scale impacts of nutrient loading and sedimentation (Delvin and Brodie, 2005).	Yeager <i>et al.</i> , 2017
28	Scaled mean NDVI	1 km radius (3.14 km ² area) resolution, no units	The mean Normalized Difference Vegetation Index of land within a 1-km radius circle around each site, and an indication of nearby development. We calculated the NDVI values using LandSat8 data from the United States Geological Survey. We scaled mean NDVI values for each site to between 0 and 1 within each of the contributed datasets to account for climate-driven variation in vegetation across sites and regions. Coastal development can influence water quality by increasing the amount of sediment and nutrients from land.	Please see Cannon et. al. (2019, 2021) for detailed methods
29	Number of Ports	5 km resolution, no units	A proxy for pressures from industrial development, including dredging. Includes all ports within 5km ² as this is the maximum likely distance of dredging impacts (Wenger <i>et al.</i> , 2020).	Andreollo et al., 2021
30	Nutrients from agriculture	5 km resolution, no units	An estimate of nitrogen pollution produced via a settlement plume model. This metric will underestimate nitrogen pollution because it does not include eutrophication caused by wastewater discharge (Andreollo et al., 2021).	Nitrogen delivery to coral reefs from agriculture, from Andreollo et al (2021)

	Name	Resolution and/or Units	Description and Reasoning	Source
31	Population (coastal)	5 km resolution, no units	An estimate of the number of people living within a 5 km buffer of each coral reef cell using a global data layer of 2020 human populations.	Andrello et al., 2021
32	Tourism	5 km resolution, no units	The estimated number of tourist trip equivalents for global coral reefs using tourism activity from 2005 – 2012. Intensive tourist use can cause physical injury to corals, sediment-associated tissue necrosis, and disease (Lamb <i>et al.</i> , 2014), all of which may increase macroalgae percent cover.	Andrello et al., 2021
33	Sedimentation	5 km resolution, expressed as tons of sediment per km ²	Estimated sediment exposure as predicted by a sediment plume model described in Andrello et al. (2021).	Andrello et al., 2021
Methodology & Site Characteristics		<i>We included methodology and site characteristics here because they may account for any sampling noise associated with the data, for example from methodological differences or geographic bias. Site features such as the type of habitat and depth may also influence the benthic communities present at each site (Magris <i>et al.</i>, 2016).</i>		
34	Contributor	Categorical	The person(s) contributing a dataset to the analysis. We included this to account for any methodological differences driving sampling noise associated with the data.	Contributors
35	Depth	Meters	Depth of the ecological survey in meters. Depth influences the amount of light available for photosynthesis, local temperature, and exposure to wind and waves.	Contributors

	Name	Resolution and/or Units	Description and Reasoning	Source
36	Habitat	Categorical	Whether the survey site was located on a backreef, reef crest, reef flat, reef slope, or another habitat (such as terrace reefs and those in a channel). Each habitat type has different physical features that influence exposure to drivers of benthic community compositions. For example, sites on a reef crest experience higher wind and wave exposure than those on a backreef.	Contributors
37	Management	Categorical	Whether sites were open to fishing with no restrictions (open access), fishing was allowed but with restrictions (restricted access) or fishing was banned (no access) (Darling <i>et al.</i> , 2019). Fishing pressure can decrease herbivory on coral reefs and might trigger increases in some taxa of macroalgae.	Contributors
38	Methods	Categorical	Whether the survey used a point intercept transect, line intercept transect, or photo quadrat method. Methodological differences may account for potential noise in the dataset (Darling <i>et al.</i> , 2019).	Contributors
Net Primary Productivity	<i>Net primary productivity (NPP) on coral reefs is determined by light, water temperature, and nutrient availability (Yeager <i>et al.</i>, 2017). Many taxa of macroalgae may be nutrient-limited (Littler and Littler, 2007) and increasing nutrient availability (represented by NPP or chl_a) may drive increasing percent cover of macroalgae.</i>			
39	Chl _a CV	4 km ² monthly resolution, no units	Chlorophyll-a concentration (chl _a) is widely used to indicate net primary productivity (Siegel <i>et al.</i> , 2005). The coefficient of variation (CV) represents the variation in NPP.	MODIS-Ocean Color Data from NASA (2014)

	Name	Resolution and/or Units	Description and Reasoning	Source
40	Kurtosis of chl _a	4 km ² monthly resolution, no units	The distribution of chl _a concentration by frequency at each site, with positive values indicating a steeper distribution than normal, and negative values indicating a broader distribution than normal.	MODIS-Ocean Color Data from NASA (2014)
41	Mean chl _a	4 km ² monthly resolution, Mg m ⁻³	The average monthly chl _a value at each site.	MODIS-Ocean Color Data from NASA (2014)
42	Chl _a SD	4 km ² monthly resolution, no units	The standard deviation of chl _a representing the amount of variation in chl _a concentration experienced at each site.	MODIS-Ocean Color Data from NASA (2014)
43	Skewness of Chl _a	4 km ² monthly resolution, no units	The skewness of chl _a indicates whether the frequency of daily temperatures are normally distributed or skewed towards lower or higher temperature values.	MODIS-Ocean Color Data from NASA (2014)
44	Mean Chl _a for the year of survey	4 km ² monthly resolution, Mg m ⁻³	The average chl _a for the year of the survey.	MODIS-Ocean Color Data from NASA (2014)
45	NPP _{max}	mg C m ⁻² day ⁻¹	Mean annual maximum net primary productivity of carbon	Yeager <i>et al.</i> , 2017
46	NPP _{mean}	mg C m ⁻² day ⁻¹	Overall mean net primary productivity of carbon	Yeager <i>et al.</i> , 2017
47	NPP _{min}	mg C m ⁻² day ⁻¹	Mean annual minimum net primary productivity of carbon	Yeager <i>et al.</i> , 2017
48	NPP _{SD}	mg C m ⁻² day ⁻¹	Intra-annual standard deviation of the net primary productivity of carbon	Yeager <i>et al.</i> , 2017

	Name	Resolution and/or Units	Description and Reasoning	Source
Seasonality	<i>Several studies have found that macroalgae communities can be seasonal in nature, with blooms occurring at regular annual intervals, and that light and/or ocean temperatures may drive seasonal growth cycles (Fulton et al., 2014; Brown et al., 2020).</i>			
49	Mean SST of survey month	5 km	The average sea surface temperature of the month when the surveys were conducted.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2018)
50	Mean PAR of survey month	4 km	Average photosynthetically available radiation of the survey month.	MODIS-Ocean Color Data from NASA (2014)
51	Rank of survey month by SST	Month	The month of the survey corrected by the months ranked from hottest to coldest.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2018)
Storms and Cyclones	<i>Tropical storms and cyclones drive strong wind and waves that have the potential to break corals. They may also cause high storm surges that wash debris from land onto reefs, causing further damage. In some cases, macroalgae cover on coral reefs has increased immediately following storms that caused severe damage to corals.</i>			
52	Average number of storms	Annual	The average number of total storms per year passing within 100 km of each site. 100 km is the estimated maximum distance at which storms can cause damage to coral reefs (Fabricius et al., 2008).	Storm tracks for all storms after 1989 from NOAA National Centers for Environmental Information (NCEI) International Best Track Archive for Climate Stewardship (IBTrACS) (Knapp et al., 2018) and extracted in ArcMap.

	Name	Resolution and/or Units	Description and Reasoning	Source
53	Number of storms (class tropical storms or stronger)	Total number of tropical storms or greater passing within 100 km of each site as defined by Saffir-Simpson Hurricane Scale, in the 10 years preceding each survey.	The total number of tropical storms or greater passing within 100 km of each site as defined by Saffir-Simpson Hurricane Scale, in the 10 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.
54	Number of storms of type 3 or stronger	Total number of Type 3 storms or greater passing within 100 km of each site in 10 years	The total number of storms of Type 3 or greater passing within 100 km of each site as defined by the Saffir Simpson Hurricane Scale, in the 10 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.
55	Number of tropical storms or stronger	Total number of tropical storms or greater passing within 100 km of each site in 5 years	The total number of tropical storms or greater passing within 100 km of each site as defined by Saffir-Simpson Hurricane Scale, in the 5 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.
56	Number of storms of type 3 or stronger	Total number of Type 3 storms or greater passing within 100 km of each site in 10 years	The total number of storms of Type 3 or greater passing within 100 km of each site as defined by the Saffir Simpson Hurricane Scale, in the 5 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.

	Name	Resolution and/or Units	Description and Reasoning	Source
57	Cyclone Score	5 km resolution, No units	A metric for cyclone activity from 1985 – 2014 incorporating three damaging aspects of cyclones for coral reefs: average annual days of exposure, the maximum annual number of days of exposure to cyclones (winds of gale force or higher), and the inverse of the return time interval of at least one day of exposure per year (Beyer <i>et al.</i> , 2018).	Andreollo <i>et al.</i> , 2021; Beyer <i>et al.</i> , 2018
Wind and wave exposure	<i>Wind and wave exposure can drive benthic community compositions by selecting for taxa that can withstand the local environment (Page-Albins <i>et al.</i>, 2012).</i>			
58	Aspect	Decimal degrees	The direction from each site to the greatest depth in the surrounding area. Because there were too many sites to measure the direction each site faced manually, we assumed that greater depths indicated the open ocean and used the direction between the site and the greatest depth in the bathymetry layer in ArcGIS. We randomly spot-checked the sites manually to ensure accuracy.	Calculated in ArcGIS.
59	Mean wave energy	3-hour temporal resolution for a span of 31 years (1979-2009). Expressed in kW m ⁻¹	Wave energy flux (the power transmitted per unit of wavefront width), overall mean.	Yeager <i>et al.</i> , 2017

	Name	Resolution and/or Units	Description and Reasoning	Source
60	Wind and Wave Exposure	Decimal degrees	The angle of each site (using the Aspect) to the prevailing wind.	Calculated with data from NCDC Blended Sea Winds (Zhang, Reynolds and Bates, 2006) using the methods described in Cannon et al. (2021)

820

821 **Supplementary Citations**

- 822 Andrello, M. *et al.* (2021) ‘A global map of human pressures on tropical coral reefs’, *Conservation Letters* [Preprint]. doi:10.1111/conl.12858.
- 823 Baumann, J.H. *et al.* (2022) ‘Remoteness does not enhance coral reef resilience’, *Global Change Biology*, 28(2), pp. 417–428.
824 doi:10.1111/gcb.15904.
- 825 Beyer, H.L. *et al.* (2018) ‘Risk-sensitive planning for conserving coral reefs under rapid climate change’, *Conservation Letters*, 11(6), p. e12587.
826 doi:10.1111/conl.12587.
- 827 Brown, K.T. *et al.* (2020) ‘Seasonal shifts in the competitive ability of macroalgae influence the outcomes of coral–algal competition’, *Royal Society Open Science*, 7(12), p. 201797. doi:10.1098/rsos.201797.
- 828 Cannon, S.E. *et al.* (2019) ‘The relationship between macroalgae taxa and human disturbance on central Pacific coral reefs’, *Marine Pollution Bulletin* [Preprint]. doi:10.1016/j.marpolbul.2019.05.024.
- 829 Cannon, S.E. *et al.* (2021) ‘Coral reefs in the Gilbert Islands of Kiribati: Resistance, resilience, and recovery after more than a decade of multiple
830 stressors’, *PLOS One* [Preprint]. doi:10.1371/journal.pone.0255304.
- 831 Darling, E.S. *et al.* (2012) ‘Evaluating life-history strategies of reef corals from species traits’, *Ecology Letters*, 15(12), pp. 1378–1386.
832 doi:10.1111/j.1461-0248.2012.01861.x.
- 833 Darling, E.S. *et al.* (2019) ‘Social–environmental drivers inform strategic management of coral reefs in the Anthropocene’, *Nature Ecology &
834 Evolution*, 3(9), pp. 1341–1350. doi:10.1038/s41559-019-0953-8.

- 837 Fabricius, K.E. *et al.* (2008) ‘Disturbance gradients on inshore and offshore coral reefs caused by a tropical cyclone’, *Limnology and*
838 *Oceanography*, 52(2), pp. 690–704.
- 839 Fulton, C.J. *et al.* (2014) ‘Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem’, *Limnology*
840 *and Oceanography*, 59(1), pp. 156–166. doi:10.4319/lo.2014.59.1.0156.
- 841 Fulton, C.J. *et al.* (2018) ‘Form and function of tropical macroalgal reefs in the Anthropocene’, *Functional Ecology*, 33, pp. 989–999.
842 doi:10.1111/1365-2435.13282.
- 843 Green, A.L. *et al.* (2015) ‘Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design’,
844 *Biological Reviews*, 90(4), pp. 1215–1247. doi:10.1111/brv.12155.
- 845 Kleypas, J.A., Danabasoglu, G. and Lough, J.M. (2008) ‘Potential role of the ocean thermostat in determining regional differences in coral reef
846 bleaching events’, *Geophysical Research Letters*, 35(3), p. L03613. doi:10.1029/2007GL032257.
- 847 Knapp, K.R. *et al.* (2018) ‘International Best Track Archive for Climate Stewardship (IBTrACS) Project, Version 4’. NOAA National Centers for
848 Environmental Information. doi:10.25921/82TY-9E16.
- 849 Lamb, J.B. *et al.* (2014) ‘Scuba diving damage and intensity of tourist activities increases coral disease prevalence’, *Biological Conservation*, 178,
850 pp. 88–96. doi:10.1016/j.biocon.2014.06.027.
- 851 Littler, M.M. and Littler, D.S. (2007) ‘Assessment of coral reefs using herbivory/nutrient assays and indicator groups of benthic primary
852 producers: a critical synthesis, proposed protocols, and critique of management strategies’, *Aquatic Conservation: Marine and Freshwater*
853 *Ecosystems*, 17, pp. 195–215. doi:10.1002/aqc.
- 854 Magris, R.A. *et al.* (2016) ‘Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs’, *Ecography*,
855 39(7), pp. 649–664. doi:10.1111/ecog.01507.
- 856 NOAA Coral Reef Watch (2020) *Methodology, Product Description, and Data Availability of NOAA Coral Reef Watch’s Version 3.1 Daily*
857 *Global 5km Satellite Coral Bleaching Heat Stress Monitoring Products*. Silver Spring: NOAA Satellite and Information Service. Available at:
858 <https://coralreefwatch.noaa.gov/product/5km/methodology.php>.
- 859 Page-Albins, K.N. *et al.* (2012) ‘Patterns in Benthic Coral Reef Communities at Pearl and Hermes Atoll along a Wave-Exposure Gradient’, *Pacific*
860 *Science*, 66(4), pp. 481–496. doi:10.2984/66.4.6.
- 861 Siegel, D.A. *et al.* (2005) ‘Colored dissolved organic matter and its influence on the satellite-based characterization of the ocean biosphere’,
862 *Geophysical Research Letters*, 32(20). doi:10.1029/2005GL024310.

- 863 Wenger, A.S. *et al.* (2020) ‘Best-practice forestry management delivers diminishing returns for coral reefs with increased land-clearing’, *Journal*
864 *of Applied Ecology*, 57(12), pp. 2381–2392. doi:10.1111/1365-2664.13743.
- 865 Yeager, L.A. *et al.* (2017) ‘Marine Socio-Environmental Covariates: queryable global layers of environmental and anthropogenic variables for
866 marine ecosystem studies’, *Ecology*, 98(7), pp. 1976–1976. doi:10.1002/ecy.1884.
- 867 Zhang, H.-M., Reynolds, R.W. and Bates, J.G. (2006) ‘Blended and gridded high resolution global sea surface wind speed and climatology from
868 multiple satellites: 1987–present’, in. *14th Conference on Satellite Meteorology and Oceanography*, Atlanta, Georgia: American Meteorological
869 Society. Available at: <https://ams.confex.com/ams/Annual2006/webprogram/Paper100004.html>.
- 870
- 871
- 872
- 873
- 874
- 875

876 **Supplementary Table 2. Correlation Coefficients.**

	aspect	WWE	NDVI	MeanChlaSurveyY4	Pop50km	Pop20km	
aspect	1.00	-0.01	-0.03		-0.04	-0.06	-0.05
WWE	-0.01	1.00	0.10		-0.72	-0.75	-0.87
NDVI	-0.03	0.10	1.00		-0.09	-0.17	-0.13
MeanChlaSurveyYear	-0.04	-0.72	-0.09	1.00	0.62	0.62	0.67
Population50km	-0.06	-0.75	-0.17	0.62	1.00	0.78	
Population20km	-0.05	-0.87	-0.13	0.67	0.78	1.00	
MeanChlaAllYears	-0.06	-0.66	-0.07	0.97	0.59	0.59	
ChlaSD	-0.04	-0.26	-0.08	0.68	0.26	0.26	
ChlaKurtosis	-0.05	0.04	-0.14	0.10	-0.01	-0.02	
ChlaCV	0.01	-0.06	0.00	-0.04	0.02	0.02	
HII100km	-0.03	-0.38	-0.28	0.53	0.63	0.47	
HII75km	-0.03	-0.44	-0.30	0.56	0.71	0.54	
HII50km	-0.03	-0.48	-0.31	0.56	0.75	0.59	
HII25km	-0.02	-0.36	-0.30	0.43	0.56	0.50	
HII10km	0.03	-0.06	-0.29	0.08	0.27	0.21	
LandArea15km	0.05	-0.07	-0.29	0.22	0.22	0.19	
LandArea50km	0.01	-0.29	-0.28	0.54	0.47	0.40	
NPP_max	-0.02	-0.63	-0.18	0.74	0.68	0.61	
NPP_mean	-0.02	-0.70	-0.15	0.82	0.70	0.65	
NPP_min	-0.04	-0.62	-0.13	0.78	0.64	0.57	
NPP_sd	-0.01	-0.60	-0.17	0.61	0.63	0.60	
ReefArea15km	-0.06	0.04	0.28	0.01	-0.07	-0.05	
ReefArea200km	-0.04	-0.03	0.25	0.18	0.01	0.02	
MeanWaveEnergy	0.05	0.09	0.00	-0.26	-0.17	-0.13	
MMM	-0.14	-0.15	-0.03	-0.02	0.06	0.13	
sdSST	0.06	0.05	0.17	0.28	0.11	-0.01	

	aspect	WWE	NDVI	MeanChlaSurveyY4	Pop50km	Pop20km
cvSST	0.06	0.05	0.15	0.27	0.11	-0.02
kurtSST	-0.07	-0.11	-0.28	-0.08	0.04	0.09
MeanNumAnnualStorms	0.00	0.10	0.23	-0.01	0.07	-0.08
NumStorms5Yrs_TropPlus	-0.02	0.07	0.13	-0.07	-0.07	-0.08
NumStorms5Yrs_Cat3Plus	-0.02	0.04	-0.07	-0.04	0.01	-0.02
NumStorms10Yrs_TropPlus	0.00	0.07	0.16	-0.01	-0.01	-0.07
NumStorms10Yrs_Cat3Plus	-0.02	0.04	-0.01	-0.04	-0.03	-0.04
maxDHW	0.00	0.14	0.09	-0.07	-0.22	-0.17
AnnualMeanMaxDHW	0.06	0.11	0.22	-0.08	-0.15	-0.14
DHW_over_4	0.04	0.11	0.17	-0.11	-0.16	-0.13
DHW_over_8	0.00	0.06	0.02	-0.04	-0.11	-0.08
MeanSST_surveymonth	-0.01	-0.05	-0.01	-0.06	0.02	0.04
RankMonth_SST	0.01	-0.04	-0.05	-0.01	0.03	0.03
Depth	0.03	0.08	0.03	-0.23	-0.08	-0.11
MeanPARSurveyMonth	-0.09	0.05	0.16	-0.06	-0.02	-0.03
Latitude	-0.06	-0.03	-0.27	-0.15	0.17	0.08
Longitude	0.04	0.00	0.22	0.09	0.01	0.00
OverallClimateScore	-0.06	-0.11	0.03	0.15	0.13	0.15
ConnectivityScore	-0.10	0.02	0.15	0.09	0.02	0.03
CycloneScore	-0.03	-0.10	-0.09	0.10	-0.05	0.08
HistoricHeatStress	-0.04	-0.12	-0.13	0.05	0.19	0.16
MarketGravity	-0.05	-0.17	-0.30	0.20	0.34	0.26
SedimentationScore	0.02	-0.12	-0.35	0.18	0.24	0.18
NutrientScore	-0.01	-0.25	-0.30	0.37	0.43	0.32
Ports	-0.04	-0.09	-0.17	0.02	0.05	0.07
TourismValue	0.01	-0.06	-0.30	0.10	0.18	0.11
CumulativeHumanImpacts	-0.03	-0.19	-0.49	0.22	0.35	0.28

	MeanChlaAllYears	ChlaSD	ChlaKurtosis	ChlaCV	HII100km	HII75km	HII50km
aspect	-0.06	-0.04	-0.05	0.01	-0.03	-0.03	-0.03
WWE	-0.66	-0.26	0.04	-0.06	-0.38	-0.44	-0.48
NDVI	-0.07	-0.08	-0.14	0.00	-0.28	-0.30	-0.31
MeanChlaSurveyYear	0.97	0.68	0.10	-0.04	0.53	0.56	0.56
Population50km	0.59	0.26	-0.01	0.02	0.63	0.71	0.75
Population20km	0.59	0.26	-0.02	0.02	0.47	0.54	0.59
MeanChlaAllYears	1.00	0.75	0.11	-0.05	0.51	0.54	0.54
ChlaSD	0.75	1.00	0.42	-0.31	0.37	0.38	0.39
ChlaKurtosis	0.11	0.42	1.00	-0.44	0.15	0.17	0.21
ChlaCV	-0.05	-0.31	-0.44	1.00	-0.09	-0.09	-0.08
HII100km	0.51	0.37	0.15	-0.09	1.00	0.98	0.91
HII75km	0.54	0.38	0.17	-0.09	0.98	1.00	0.97
HII50km	0.54	0.39	0.21	-0.08	0.91	0.97	1.00
HII25km	0.42	0.38	0.27	-0.08	0.76	0.82	0.90
HII10km	0.07	0.08	0.12	0.05	0.50	0.54	0.60
LandArea15km	0.21	0.22	0.26	-0.16	0.56	0.59	0.62
LandArea50km	0.52	0.44	0.29	-0.17	0.83	0.86	0.87
NPP_max	0.71	0.44	0.14	-0.12	0.64	0.68	0.67
NPP_mean	0.80	0.43	0.09	-0.03	0.63	0.66	0.66
NPP_min	0.77	0.42	0.10	-0.01	0.59	0.62	0.61
NPP_sd	0.58	0.36	0.10	-0.14	0.53	0.57	0.58
ReefArea15km	0.03	0.00	-0.02	0.01	-0.13	-0.14	-0.17
ReefArea200km	0.20	0.13	-0.04	0.07	0.08	0.04	-0.03
MeanWaveEnergy	-0.27	-0.23	-0.13	0.13	-0.25	-0.24	-0.22
MMM	-0.01	0.00	0.07	-0.15	-0.09	-0.08	-0.07
sdSST	0.31	0.23	-0.12	0.11	0.26	0.23	0.19
cvSST	0.31	0.23	-0.11	0.11	0.27	0.24	0.20
kurtSST	-0.10	-0.05	0.22	-0.17	-0.07	-0.05	-0.01

	MeanChlaAllYears	ChlaSD	ChlaKurtosis	ChlaCV	HII100km	HII75km	HII50km
MeanNumAnnualStorms	0.00	-0.03	-0.16	0.05	0.05	0.02	0.03
NumStorms5Yrs_TropPlus	-0.06	-0.05	-0.15	0.06	-0.04	-0.06	-0.07
NumStorms5Yrs_Cat3Plus	-0.03	-0.04	-0.08	0.07	0.13	0.10	0.09
NumStorms10Yrs_TropPlus	0.01	-0.03	-0.16	0.05	0.02	0.00	-0.01
NumStorms10Yrs_Cat3Plus	-0.03	-0.06	-0.09	0.09	0.08	0.05	0.04
maxDHW	-0.06	-0.08	-0.11	0.18	-0.32	-0.33	-0.32
AnnualMeanMaxDHW	-0.06	-0.07	-0.07	0.20	-0.19	-0.20	-0.21
DHW_over_4	-0.09	-0.09	-0.09	0.15	-0.23	-0.24	-0.25
DHW_over_8	-0.04	-0.06	-0.06	0.19	-0.19	-0.18	-0.16
MeanSST_surveymonth	-0.08	-0.10	0.03	-0.14	-0.06	-0.07	-0.07
RankMonth_SST	-0.04	-0.07	0.02	-0.05	-0.02	-0.01	0.02
Depth	-0.22	-0.19	-0.09	0.16	-0.07	-0.10	-0.13
MeanPARSurveyMonth	-0.07	-0.03	-0.04	0.01	-0.06	-0.07	-0.06
Latitude	-0.16	-0.10	0.07	-0.08	0.14	0.14	0.18
Longitude	0.10	0.10	0.03	-0.19	0.04	0.01	-0.01
OverallClimateScore	0.15	0.14	0.05	-0.20	0.25	0.25	0.21
ConnectivityScore	0.10	0.10	0.05	-0.05	0.21	0.17	0.11
CycloneScore	0.09	0.09	0.14	-0.09	-0.11	-0.07	-0.09
HistoricHeatStress	0.04	0.06	0.02	-0.23	0.23	0.23	0.23
MarketGravity	0.21	0.20	0.13	-0.09	0.52	0.53	0.52
SedimentationScore	0.17	0.17	0.20	0.05	0.46	0.48	0.51
NutrientScore	0.37	0.30	0.19	-0.05	0.71	0.72	0.69
Ports	0.01	0.00	-0.01	0.02	-0.04	-0.02	0.00
TourismValue	0.10	0.11	0.03	0.03	0.37	0.38	0.38
CumulativeHumanImpacts	0.21	0.21	0.17	-0.01	0.58	0.60	0.62

	HII25km	HII10km	LandArea15km	LandArea50km	NPP_max	NPP_mean
aspect	-0.02	0.03	0.05	0.01	-0.02	-0.02
WWE	-0.36	-0.06	-0.07	-0.29	-0.63	-0.70
NDVI	-0.30	-0.29	-0.29	-0.28	-0.18	-0.15
MeanChlaSurveyYear	0.43	0.08	0.22	0.54	0.74	0.82
Population50km	0.56	0.27	0.22	0.47	0.68	0.70
Population20km	0.50	0.21	0.19	0.40	0.61	0.65
MeanChlaAllYears	0.42	0.07	0.21	0.52	0.71	0.80
ChlaSD	0.38	0.08	0.22	0.44	0.44	0.43
ChlaKurtosis	0.27	0.12	0.26	0.29	0.14	0.09
ChlaCV	-0.08	0.05	-0.16	-0.17	-0.12	-0.03
HII100km	0.76	0.50	0.56	0.83	0.64	0.63
HII75km	0.82	0.54	0.59	0.86	0.68	0.66
HII50km	0.90	0.60	0.62	0.87	0.67	0.66
HII25km	1.00	0.79	0.79	0.81	0.52	0.49
HII10km	0.79	1.00	0.76	0.52	0.20	0.16
LandArea15km	0.79	0.76	1.00	0.76	0.38	0.32
LandArea50km	0.81	0.52	0.76	1.00	0.62	0.61
NPP_max	0.52	0.20	0.38	0.62	1.00	0.94
NPP_mean	0.49	0.16	0.32	0.61	0.94	1.00
NPP_min	0.43	0.11	0.29	0.59	0.85	0.96
NPP_sd	0.46	0.19	0.31	0.48	0.94	0.81
ReefArea15km	-0.17	-0.19	-0.12	-0.14	-0.10	-0.07
ReefArea200km	-0.11	-0.23	-0.19	0.02	0.07	0.11
MeanWaveEnergy	-0.21	-0.07	-0.25	-0.27	-0.20	-0.17
MMM	-0.04	-0.05	-0.10	-0.18	0.03	-0.05
sdSST	0.13	0.04	0.08	0.23	0.25	0.29
cvSST	0.14	0.05	0.10	0.24	0.24	0.29
kurtSST	0.03	0.00	0.09	-0.02	-0.03	-0.07

	HII25km	HII10km	LandArea15km	LandArea50km	NPP_max	NPP_mean
MeanNumAnnualStorms	0.04	0.07	0.00	-0.03	-0.10	-0.06
NumStorms5Yrs_TropPlus	-0.01	0.07	-0.06	-0.11	-0.14	-0.13
NumStorms5Yrs_Cat3Plus	0.12	0.14	0.03	0.03	-0.07	-0.06
NumStorms10Yrs_TropPlus	0.01	0.07	-0.02	-0.05	-0.07	-0.05
NumStorms10Yrs_Cat3Plus	0.06	0.08	-0.02	-0.01	-0.08	-0.07
maxDHW	-0.27	-0.21	-0.15	-0.22	-0.20	-0.16
AnnualMeanMaxDHW	-0.17	-0.16	-0.11	-0.15	-0.12	-0.06
DHW_over_4	-0.21	-0.17	-0.14	-0.19	-0.15	-0.10
DHW_over_8	-0.12	-0.10	-0.10	-0.11	-0.08	-0.04
MeanSST_surveymonth	-0.06	-0.08	-0.02	-0.07	-0.04	-0.09
RankMonth_SST	0.01	-0.04	-0.04	-0.01	0.01	-0.02
Depth	-0.10	0.01	-0.21	-0.25	-0.17	-0.19
MeanPARSurveyMonth	-0.05	0.01	-0.13	-0.15	0.00	-0.05
Latitude	0.26	0.31	0.19	0.04	-0.11	-0.17
Longitude	0.02	-0.03	0.14	0.08	-0.07	-0.05
OverallClimateScore	0.10	0.03	0.02	0.19	0.22	0.18
ConnectivityScore	0.06	-0.07	-0.05	0.12	0.08	0.06
CycloneScore	-0.16	-0.24	-0.07	0.02	0.17	0.15
HistoricHeatStress	0.17	0.16	0.08	0.13	0.13	0.07
MarketGravity	0.48	0.40	0.34	0.39	0.44	0.36
SedimentationScore	0.55	0.53	0.51	0.47	0.28	0.25
NutrientScore	0.62	0.45	0.47	0.61	0.54	0.51
Ports	0.02	0.11	0.05	-0.03	0.05	0.02
TourismValue	0.35	0.40	0.32	0.32	0.20	0.16
CumulativeHumanImpacts	0.62	0.61	0.53	0.51	0.41	0.34

	NPP_min	NPP_sd	ReefArea15km	ReefArea200km	MeanWaveEnergy	MMM
aspect	-0.04	-0.01	-0.06	-0.04	0.05	-0.14
WWE	-0.62	-0.60	0.04	-0.03	0.09	-0.15
NDVI	-0.13	-0.17	0.28	0.25	0.00	-0.03
MeanChlaSurveyYear	0.78	0.61	0.01	0.18	-0.26	-0.02
Population50km	0.64	0.63	-0.07	0.01	-0.17	0.06
Population20km	0.57	0.60	-0.05	0.02	-0.13	0.13
MeanChlaAllYears	0.77	0.58	0.03	0.20	-0.27	-0.01
ChlaSD	0.42	0.36	0.00	0.13	-0.23	0.00
ChlaKurtosis	0.10	0.10	-0.02	-0.04	-0.13	0.07
ChlaCV	-0.01	-0.14	0.01	0.07	0.13	-0.15
HII100km	0.59	0.53	-0.13	0.08	-0.25	-0.09
HII75km	0.62	0.57	-0.14	0.04	-0.24	-0.08
HII50km	0.61	0.58	-0.17	-0.03	-0.22	-0.07
HII25km	0.43	0.46	-0.17	-0.11	-0.21	-0.04
HII10km	0.11	0.19	-0.19	-0.23	-0.07	-0.05
LandArea15km	0.29	0.31	-0.12	-0.19	-0.25	-0.10
LandArea50km	0.59	0.48	-0.14	0.02	-0.27	-0.18
NPP_max	0.85	0.94	-0.10	0.07	-0.20	0.03
NPP_mean	0.96	0.81	-0.07	0.11	-0.17	-0.05
NPP_min	1.00	0.67	-0.03	0.14	-0.16	-0.11
NPP_sd	0.67	1.00	-0.17	-0.03	-0.13	0.12
ReefArea15km	-0.03	-0.17	1.00	0.51	-0.36	0.12
ReefArea200km	0.14	-0.03	0.51	1.00	-0.23	-0.12
MeanWaveEnergy	-0.16	-0.13	-0.36	-0.23	1.00	-0.30
MMM	-0.11	0.12	0.12	-0.12	-0.30	1.00
sdSST	0.29	0.17	-0.03	0.36	0.02	-0.56
cvSST	0.30	0.16	-0.04	0.35	0.03	-0.60
kurtSST	-0.09	0.00	0.04	-0.35	-0.28	0.55

	NPP_min	NPP_sd	ReefArea15km	ReefArea200km	MeanWaveEnergy	MMM
MeanNumAnnualStorms	-0.08	-0.09	0.01	-0.08	-0.09	-0.07
NumStorms5Yrs_TropPlus	-0.15	-0.10	-0.04	-0.03	0.03	0.01
NumStorms5Yrs_Cat3Plus	-0.08	-0.07	0.01	0.17	-0.07	-0.04
NumStorms10Yrs_TropPlus	-0.07	-0.05	-0.08	-0.02	0.02	-0.06
NumStorms10Yrs_Cat3Plus	-0.08	-0.08	-0.01	0.22	-0.06	-0.07
maxDHW	-0.14	-0.24	0.09	-0.07	0.01	-0.13
AnnualMeanMaxDHW	-0.05	-0.15	0.06	0.02	0.09	-0.16
DHW_over_4	-0.09	-0.17	0.03	-0.08	0.12	-0.14
DHW_over_8	-0.05	-0.11	0.06	-0.09	0.01	-0.16
MeanSST_surveymonth	-0.11	-0.02	0.11	0.01	-0.23	0.26
RankMonth_SST	-0.04	0.02	-0.05	0.12	-0.06	-0.23
Depth	-0.22	-0.10	-0.12	-0.01	0.32	-0.08
MeanPARSurveyMonth	-0.07	0.04	0.07	0.06	0.08	0.15
Latitude	-0.21	-0.06	0.05	-0.27	-0.38	0.44
Longitude	-0.04	-0.13	0.44	0.28	-0.63	0.14
OverallClimateScore	0.17	0.22	0.06	0.36	-0.05	0.16
ConnectivityScore	0.06	0.03	0.23	0.60	-0.29	0.11
CycloneScore	0.18	0.15	0.03	0.08	0.06	0.09
HistoricHeatStress	0.04	0.17	-0.03	0.07	-0.07	0.21
MarketGravity	0.32	0.44	-0.08	0.05	-0.12	0.12
SedimentationScore	0.22	0.24	-0.17	-0.12	-0.03	0.05
NutrientScore	0.47	0.47	-0.17	0.03	-0.12	-0.01
Ports	0.00	0.09	-0.07	-0.13	0.10	0.12
TourismValue	0.12	0.21	-0.15	-0.04	-0.07	-0.04
CumulativeHumanImpacts	0.29	0.41	-0.21	-0.16	-0.08	0.13

	sdSST	cvSST	kurtSST	MeanNumAnnualStorms	NumStorms5Yrs_TropPlus
aspect	0.06	0.06	-0.07	0.00	-0.02
WWE	0.05	0.05	-0.11	0.10	0.07
NDVI	0.17	0.15	-0.28	0.23	0.13
MeanChlaSurveyYear	0.28	0.27	-0.08	-0.01	-0.07
Population50km	0.11	0.11	0.04	0.07	-0.07
Population20km	-0.01	-0.02	0.09	-0.08	-0.08
MeanChlaAllYears	0.31	0.31	-0.10	0.00	-0.06
ChlaSD	0.23	0.23	-0.05	-0.03	-0.05
ChlaKurtosis	-0.12	-0.11	0.22	-0.16	-0.15
ChlaCV	0.11	0.11	-0.17	0.05	0.06
HII100km	0.26	0.27	-0.07	0.05	-0.04
HII75km	0.23	0.24	-0.05	0.02	-0.06
HII50km	0.19	0.20	-0.01	0.03	-0.07
HII25km	0.13	0.14	0.03	0.04	-0.01
HII10km	0.04	0.05	0.00	0.07	0.07
LandArea15km	0.08	0.10	0.09	0.00	-0.06
LandArea50km	0.23	0.24	-0.02	-0.03	-0.11
NPP_max	0.25	0.24	-0.03	-0.10	-0.14
NPP_mean	0.29	0.29	-0.07	-0.06	-0.13
NPP_min	0.29	0.30	-0.09	-0.08	-0.15
NPP_sd	0.17	0.16	0.00	-0.09	-0.10
ReefArea15km	-0.03	-0.04	0.04	0.01	-0.04
ReefArea200km	0.36	0.35	-0.35	-0.08	-0.03
MeanWaveEnergy	0.02	0.03	-0.28	-0.09	0.03
MMM	-0.56	-0.60	0.55	-0.07	0.01
sdSST	1.00	1.00	-0.87	0.46	0.35
cvSST	1.00	1.00	-0.86	0.45	0.34
kurtSST	-0.87	-0.86	1.00	-0.41	-0.37

	sdSST	cvSST	kurtSST	MeanNumAnnualStorms	NumStorms5Yrs_TropPlus
MeanNumAnnualStorms	0.46	0.45	-0.41	1.00	0.77
NumStorms5Yrs_TropPlus	0.35	0.34	-0.37	0.77	1.00
NumStorms5Yrs_Cat3Plus	0.35	0.34	-0.31	0.43	0.64
NumStorms10Yrs_TropPlus	0.49	0.48	-0.47	0.84	0.95
NumStorms10Yrs_Cat3Plus	0.44	0.43	-0.39	0.47	0.61
maxDHW	-0.02	-0.01	0.10	0.00	-0.05
AnnualMeanMaxDHW	0.17	0.16	-0.11	-0.01	-0.04
DHW_over_4	0.07	0.07	-0.02	-0.07	-0.10
DHW_over_8	0.03	0.03	0.09	-0.10	-0.12
MeanSST_surveymonth	-0.25	-0.26	0.30	-0.07	-0.10
RankMonth_SST	0.09	0.10	-0.08	-0.01	-0.09
Depth	0.08	0.07	-0.18	0.07	0.12
MeanPARSurveyMonth	0.02	0.00	-0.11	0.02	-0.01
Latitude	-0.43	-0.42	0.54	0.14	0.02
Longitude	0.07	0.08	0.03	0.26	0.06
OverallClimateScore	0.04	0.03	-0.16	-0.14	-0.07
ConnectivityScore	0.19	0.18	-0.17	-0.09	-0.09
CycloneScore	-0.42	-0.42	0.38	-0.83	-0.63
HistoricHeatStress	-0.07	-0.07	-0.03	0.06	0.07
MarketGravity	0.15	0.14	-0.04	-0.17	-0.12
SedimentationScore	-0.04	-0.02	0.11	-0.08	-0.01
NutrientScore	0.20	0.21	-0.05	-0.09	-0.06
Ports	-0.11	-0.12	0.09	-0.06	0.02
TourismValue	0.15	0.15	-0.13	0.08	0.11
CumulativeHumanImpacts	0.00	0.00	0.10	-0.12	-0.04

	NumStorms5Yrs_Cat3Plus	NumStorms10Yrs_TropPlus	NumStorms10Yrs_Cat3Plus
aspect	-0.02	0.00	-0.02
WWE	0.04	0.07	0.04
NDVI	-0.07	0.16	-0.01
MeanChlaSurveyYear	-0.04	-0.01	-0.04
Population50km	0.01	-0.01	-0.03
Population20km	-0.02	-0.07	-0.04
MeanChlaAllYears	-0.03	0.01	-0.03
ChlaSD	-0.04	-0.03	-0.06
ChlaKurtosis	-0.08	-0.16	-0.09
ChlaCV	0.07	0.05	0.09
HII100km	0.13	0.02	0.08
HII75km	0.10	0.00	0.05
HII50km	0.09	-0.01	0.04
HII25km	0.12	0.01	0.06
HII10km	0.14	0.07	0.08
LandArea15km	0.03	-0.02	-0.02
LandArea50km	0.03	-0.05	-0.01
NPP_max	-0.07	-0.07	-0.08
NPP_mean	-0.06	-0.05	-0.07
NPP_min	-0.08	-0.07	-0.08
NPP_sd	-0.07	-0.05	-0.08
ReefArea15km	0.01	-0.08	-0.01
ReefArea200km	0.17	-0.02	0.22
MeanWaveEnergy	-0.07	0.02	-0.06
MMM	-0.04	-0.06	-0.07
sdSST	0.35	0.49	0.44
cvSST	0.34	0.48	0.43
kurtSST	-0.31	-0.47	-0.39

	NumStorms5Yrs_Cat3Plus	NumStorms10Yrs_TropPlus	NumStorms10Yrs_Cat3Plus
MeanNumAnnualStorms	0.43	0.84	0.47
NumStorms5Yrs_TropPlus	0.64	0.95	0.61
NumStorms5Yrs_Cat3Plus	1.00	0.59	0.87
NumStorms10Yrs_TropPlus	0.59	1.00	0.64
NumStorms10Yrs_Cat3Plus	0.87	0.64	1.00
maxDHW	-0.13	-0.06	-0.14
AnnualMeanMaxDHW	-0.10	-0.02	-0.09
DHW_over_4	-0.13	-0.09	-0.11
DHW_over_8	-0.11	-0.13	-0.14
MeanSST_surveymonth	-0.01	-0.13	-0.01
RankMonth_SST	0.09	-0.07	0.14
Depth	0.19	0.11	0.19
MeanPARSurveyMonth	-0.14	-0.02	-0.09
Latitude	0.21	-0.04	0.12
Longitude	0.05	0.10	0.06
OverallClimateScore	0.06	-0.07	0.07
ConnectivityScore	0.16	-0.08	0.21
CycloneScore	-0.56	-0.68	-0.58
HistoricHeatStress	0.18	0.06	0.16
MarketGravity	0.17	-0.08	0.16
SedimentationScore	0.16	-0.04	0.08
NutrientScore	0.16	-0.04	0.10
Ports	-0.05	0.00	-0.06
TourismValue	0.27	0.12	0.24
CumulativeHumanImpacts	0.20	-0.05	0.12

	maxDHW	AnnualMeanMaxDHW	DHW_over_4	DHW_over_8	MeanSST_surveymonth
aspect	0.00	0.06	0.04	0.00	-0.01
WWE	0.14	0.11	0.11	0.06	-0.05
NDVI	0.09	0.22	0.17	0.02	-0.01
MeanChlaSurveyYear	-0.07	-0.08	-0.11	-0.04	-0.06
Population50km	-0.22	-0.15	-0.16	-0.11	0.02
Population20km	-0.17	-0.14	-0.13	-0.08	0.04
MeanChlaAllYears	-0.06	-0.06	-0.09	-0.04	-0.08
ChlaSD	-0.08	-0.07	-0.09	-0.06	-0.10
ChlaKurtosis	-0.11	-0.07	-0.09	-0.06	0.03
ChlaCV	0.18	0.20	0.15	0.19	-0.14
HII100km	-0.32	-0.19	-0.23	-0.19	-0.06
HII75km	-0.33	-0.20	-0.24	-0.18	-0.07
HII50km	-0.32	-0.21	-0.25	-0.16	-0.07
HII25km	-0.27	-0.17	-0.21	-0.12	-0.06
HII10km	-0.21	-0.16	-0.17	-0.10	-0.08
LandArea15km	-0.15	-0.11	-0.14	-0.10	-0.02
LandArea50km	-0.22	-0.15	-0.19	-0.11	-0.07
NPP_max	-0.20	-0.12	-0.15	-0.08	-0.04
NPP_mean	-0.16	-0.06	-0.10	-0.04	-0.09
NPP_min	-0.14	-0.05	-0.09	-0.05	-0.11
NPP_sd	-0.24	-0.15	-0.17	-0.11	-0.02
ReefArea15km	0.09	0.06	0.03	0.06	0.11
ReefArea200km	-0.07	0.02	-0.08	-0.09	0.01
MeanWaveEnergy	0.01	0.09	0.12	0.01	-0.23
MMM	-0.13	-0.16	-0.14	-0.16	0.26
sdSST	-0.02	0.17	0.07	0.03	-0.25
cvSST	-0.01	0.16	0.07	0.03	-0.26
kurtSST	0.10	-0.11	-0.02	0.09	0.30

	maxDHW	AnnualMeanMaxDHW	DHW_over_4	DHW_over_8	MeanSST_surveymonth
MeanNumAnnualStorms	0.00	-0.01	-0.07	-0.10	-0.07
NumStorms5Yrs_TropPlus	-0.05	-0.04	-0.10	-0.12	-0.10
NumStorms5Yrs_Cat3Plus	-0.13	-0.10	-0.13	-0.11	-0.01
NumStorms10Yrs_TropPlus	-0.06	-0.02	-0.09	-0.13	-0.13
NumStorms10Yrs_Cat3Plus	-0.14	-0.09	-0.11	-0.14	-0.01
maxDHW	1.00	0.71	0.67	0.85	0.06
AnnualMeanMaxDHW	0.71	1.00	0.94	0.78	-0.05
DHW_over_4	0.67	0.94	1.00	0.75	-0.03
DHW_over_8	0.85	0.78	0.75	1.00	0.01
MeanSST_surveymonth	0.06	-0.05	-0.03	0.01	1.00
RankMonth_SST	-0.09	-0.26	-0.27	-0.12	0.41
Depth	-0.02	0.09	0.10	0.04	-0.04
MeanPARSurveyMonth	-0.05	0.00	-0.03	0.02	0.05
Latitude	0.02	-0.21	-0.15	0.02	0.28
Longitude	0.01	-0.02	-0.05	-0.06	0.20
OverallClimateScore	-0.78	-0.67	-0.66	-0.78	-0.02
ConnectivityScore	-0.26	-0.10	-0.16	-0.23	0.08
CycloneScore	0.04	0.06	0.10	0.11	0.00
HistoricHeatStress	-0.82	-0.91	-0.85	-0.84	0.04
MarketGravity	-0.46	-0.23	-0.21	-0.20	-0.03
SedimentationScore	-0.23	-0.18	-0.20	-0.16	-0.05
NutrientScore	-0.34	-0.19	-0.23	-0.19	-0.06
Ports	-0.01	-0.08	-0.07	-0.02	0.06
TourismValue	-0.31	-0.28	-0.27	-0.24	-0.03
CumulativeHumanImpacts	-0.40	-0.33	-0.31	-0.23	-0.02

	Rank	Month	SST	Depth	MeanPAR	SurveyMonth	Latitude	Longitude
aspect			0.01	0.03		-0.09	-0.06	0.04
WWE			-0.04	0.08		0.05	-0.03	0.00
NDVI			-0.05	0.03		0.16	-0.27	0.22
MeanChlaSurveyYear			-0.01	-0.23		-0.06	-0.15	0.09
Population50km			0.03	-0.08		-0.02	0.17	0.01
Population20km			0.03	-0.11		-0.03	0.08	0.00
MeanChlaAllYears			-0.04	-0.22		-0.07	-0.16	0.10
ChlaSD			-0.07	-0.19		-0.03	-0.10	0.10
ChlaKurtosis			0.02	-0.09		-0.04	0.07	0.03
ChlaCV			-0.05	0.16		0.01	-0.08	-0.19
HII100km			-0.02	-0.07		-0.06	0.14	0.04
HII75km			-0.01	-0.10		-0.07	0.14	0.01
HII50km			0.02	-0.13		-0.06	0.18	-0.01
HII25km			0.01	-0.10		-0.05	0.26	0.02
HII10km			-0.04	0.01		0.01	0.31	-0.03
LandArea15km			-0.04	-0.21		-0.13	0.19	0.14
LandArea50km			-0.01	-0.25		-0.15	0.04	0.08
NPP_max			0.01	-0.17		0.00	-0.11	-0.07
NPP_mean			-0.02	-0.19		-0.05	-0.17	-0.05
NPP_min			-0.04	-0.22		-0.07	-0.21	-0.04
NPP_sd			0.02	-0.10		0.04	-0.06	-0.13
ReefArea15km			-0.05	-0.12		0.07	0.05	0.44
ReefArea200km			0.12	-0.01		0.06	-0.27	0.28
MeanWaveEnergy			-0.06	0.32		0.08	-0.38	-0.63
MMM			-0.23	-0.08		0.15	0.44	0.14
sdSST			0.09	0.08		0.02	-0.43	0.07
cvSST			0.10	0.07		0.00	-0.42	0.08
kurtSST			-0.08	-0.18		-0.11	0.54	0.03

	RankMonth_SST	Depth	MeanPARSurveyMonth	Latitude	Longitude
MeanNumAnnualStorms	-0.01	0.07	0.02	0.14	0.26
NumStorms5Yrs_TropPlus	-0.09	0.12	-0.01	0.02	0.06
NumStorms5Yrs_Cat3Plus	0.09	0.19	-0.14	0.21	0.05
NumStorms10Yrs_TropPlus	-0.07	0.11	-0.02	-0.04	0.10
NumStorms10Yrs_Cat3Plus	0.14	0.19	-0.09	0.12	0.06
maxDHW	-0.09	-0.02	-0.05	0.02	0.01
AnnualMeanMaxDHW	-0.26	0.09	0.00	-0.21	-0.02
DHW_over_4	-0.27	0.10	-0.03	-0.15	-0.05
DHW_over_8	-0.12	0.04	0.02	0.02	-0.06
MeanSST_surveymonth	0.41	-0.04	0.05	0.28	0.20
RankMonth_SST	1.00	-0.02	0.06	0.07	0.03
Depth	-0.02	1.00	0.10	0.04	-0.18
MeanPARSurveyMonth	0.06	0.10	1.00	-0.10	-0.06
Latitude	0.07	0.04	-0.10	1.00	0.30
Longitude	0.03	-0.18	-0.06	0.30	1.00
OverallClimateScore	0.16	-0.11	0.11	-0.20	0.05
ConnectivityScore	0.15	-0.01	0.13	-0.11	0.24
CycloneScore	-0.16	-0.21	0.04	-0.36	-0.23
HistoricHeatStress	0.24	-0.04	0.07	0.20	0.09
MarketGravity	0.03	0.08	0.08	0.14	-0.02
SedimentationScore	-0.06	-0.04	-0.18	0.16	-0.26
NutrientScore	-0.02	-0.06	-0.04	0.05	-0.13
Ports	-0.06	0.07	0.02	0.13	-0.02
TourismValue	0.19	0.00	-0.05	0.11	-0.09
CumulativeHumanImpacts	0.02	-0.01	-0.06	0.27	-0.19

	OverallClimateScore	ConnectivityScore	CycloneScore	HistoricHeatStress	MarketGravity
aspect	-0.06	-0.10	-0.03	-0.04	-0.05
WWE	-0.11	0.02	-0.10	-0.12	-0.17
NDVI	0.03	0.15	-0.09	-0.13	-0.30
MeanChlaSurveyYear	0.15	0.09	0.10	0.05	0.20
Population50km	0.13	0.02	-0.05	0.19	0.34
Population20km	0.15	0.03	0.08	0.16	0.26
MeanChlaAllYears	0.15	0.10	0.09	0.04	0.21
ChlaSD	0.14	0.10	0.09	0.06	0.20
ChlaKurtosis	0.05	0.05	0.14	0.02	0.13
ChlaCV	-0.20	-0.05	-0.09	-0.23	-0.09
HII100km	0.25	0.21	-0.11	0.23	0.52
HII75km	0.25	0.17	-0.07	0.23	0.53
HII50km	0.21	0.11	-0.09	0.23	0.52
HII25km	0.10	0.06	-0.16	0.17	0.48
HII10km	0.03	-0.07	-0.24	0.16	0.40
LandArea15km	0.02	-0.05	-0.07	0.08	0.34
LandArea50km	0.19	0.12	0.02	0.13	0.39
NPP_max	0.22	0.08	0.17	0.13	0.44
NPP_mean	0.18	0.06	0.15	0.07	0.36
NPP_min	0.17	0.06	0.18	0.04	0.32
NPP_sd	0.22	0.03	0.15	0.17	0.44
ReefArea15km	0.06	0.23	0.03	-0.03	-0.08
ReefArea200km	0.36	0.60	0.08	0.07	0.05
MeanWaveEnergy	-0.05	-0.29	0.06	-0.07	-0.12
MMM	0.16	0.11	0.09	0.21	0.12
sdSST	0.04	0.19	-0.42	-0.07	0.15
cvSST	0.03	0.18	-0.42	-0.07	0.14
kurtSST	-0.16	-0.17	0.38	-0.03	-0.04

	OverallClimateScore	ConnectivityScore	CycloneScore	HistoricHeatStress	MarketGravity
MeanNumAnnualStorms	-0.14	-0.09	-0.83	0.06	-0.17
NumStorms5Yrs_TropPlus	-0.07	-0.09	-0.63	0.07	-0.12
NumStorms5Yrs_Cat3Plus	0.06	0.16	-0.56	0.18	0.17
NumStorms10Yrs_TropPlus	-0.07	-0.08	-0.68	0.06	-0.08
NumStorms10Yrs_Cat3Plus	0.07	0.21	-0.58	0.16	0.16
maxDHW	-0.78	-0.26	0.04	-0.82	-0.46
AnnualMeanMaxDHW	-0.67	-0.10	0.06	-0.91	-0.23
DHW_over_4	-0.66	-0.16	0.10	-0.85	-0.21
DHW_over_8	-0.78	-0.23	0.11	-0.84	-0.20
MeanSST_surveymonth	-0.02	0.08	0.00	0.04	-0.03
RankMonth_SST	0.16	0.15	-0.16	0.24	0.03
Depth	-0.11	-0.01	-0.21	-0.04	0.08
MeanPARSurveyMonth	0.11	0.13	0.04	0.07	0.08
Latitude	-0.20	-0.11	-0.36	0.20	0.14
Longitude	0.05	0.24	-0.23	0.09	-0.02
OverallClimateScore	1.00	0.60	0.13	0.81	0.38
ConnectivityScore	0.60	1.00	0.03	0.22	0.30
CycloneScore	0.13	0.03	1.00	-0.14	0.02
HistoricHeatStress	0.81	0.22	-0.14	1.00	0.35
MarketGravity	0.38	0.30	0.02	0.35	1.00
SedimentationScore	0.14	0.09	-0.05	0.14	0.34
NutrientScore	0.31	0.24	0.01	0.23	0.49
Ports	-0.01	-0.14	0.02	0.07	0.21
TourismValue	0.29	0.15	-0.24	0.33	0.45
CumulativeHumanImpacts	0.29	0.12	-0.06	0.36	0.73

	SedimentationScore	NutrientScore	Ports	TourismValue	CumulativeHumanImpacts
aspect	0.02	-0.01	-0.04	0.01	-0.03
WWE	-0.12	-0.25	-0.09	-0.06	-0.19
NDVI	-0.35	-0.30	-0.17	-0.30	-0.49
MeanChlaSurveyYear	0.18	0.37	0.02	0.10	0.22
Population50km	0.24	0.43	0.05	0.18	0.35
Population20km	0.18	0.32	0.07	0.11	0.28
MeanChlaAllYears	0.17	0.37	0.01	0.10	0.21
ChlaSD	0.17	0.30	0.00	0.11	0.21
ChlaKurtosis	0.20	0.19	-0.01	0.03	0.17
ChlaCV	0.05	-0.05	0.02	0.03	-0.01
HII100km	0.46	0.71	-0.04	0.37	0.58
HII75km	0.48	0.72	-0.02	0.38	0.60
HII50km	0.51	0.69	0.00	0.38	0.62
HII25km	0.55	0.62	0.02	0.35	0.62
HII10km	0.53	0.45	0.11	0.40	0.61
LandArea15km	0.51	0.47	0.05	0.32	0.53
LandArea50km	0.47	0.61	-0.03	0.32	0.51
NPP_max	0.28	0.54	0.05	0.20	0.41
NPP_mean	0.25	0.51	0.02	0.16	0.34
NPP_min	0.22	0.47	0.00	0.12	0.29
NPP_sd	0.24	0.47	0.09	0.21	0.41
ReefArea15km	-0.17	-0.17	-0.07	-0.15	-0.21
ReefArea200km	-0.12	0.03	-0.13	-0.04	-0.16
MeanWaveEnergy	-0.03	-0.12	0.10	-0.07	-0.08
MMM	0.05	-0.01	0.12	-0.04	0.13
sdSST	-0.04	0.20	-0.11	0.15	0.00
cvSST	-0.02	0.21	-0.12	0.15	0.00
kurtSST	0.11	-0.05	0.09	-0.13	0.10

	SedimentationScore	NutrientScore	Ports	TourismValue	CumulativeHumanImpacts
MeanNumAnnualStorms	-0.08	-0.09	-0.06	0.08	-0.12
NumStorms5Yrs_TropPlus	-0.01	-0.06	0.02	0.11	-0.04
NumStorms5Yrs_Cat3Plus	0.16	0.16	-0.05	0.27	0.20
NumStorms10Yrs_TropPlus	-0.04	-0.04	0.00	0.12	-0.05
NumStorms10Yrs_Cat3Plus	0.08	0.10	-0.06	0.24	0.12
maxDHW	-0.23	-0.34	-0.01	-0.31	-0.40
AnnualMeanMaxDHW	-0.18	-0.19	-0.08	-0.28	-0.33
DHW_over_4	-0.20	-0.23	-0.07	-0.27	-0.31
DHW_over_8	-0.16	-0.19	-0.02	-0.24	-0.23
MeanSST_surveymonth	-0.05	-0.06	0.06	-0.03	-0.02
RankMonth_SST	-0.06	-0.02	-0.06	0.19	0.02
Depth	-0.04	-0.06	0.07	0.00	-0.01
MeanPARSurveyMonth	-0.18	-0.04	0.02	-0.05	-0.06
Latitude	0.16	0.05	0.13	0.11	0.27
Longitude	-0.26	-0.13	-0.02	-0.09	-0.19
OverallClimateScore	0.14	0.31	-0.01	0.29	0.29
ConnectivityScore	0.09	0.24	-0.14	0.15	0.12
CycloneScore	-0.05	0.01	0.02	-0.24	-0.06
HistoricHeatStress	0.14	0.23	0.07	0.33	0.36
MarketGravity	0.34	0.49	0.21	0.45	0.73
SedimentationScore	1.00	0.67	0.05	0.45	0.76
NutrientScore	0.67	1.00	-0.04	0.31	0.67
Ports	0.05	-0.04	1.00	0.14	0.36
TourismValue	0.45	0.31	0.14	1.00	0.73
CumulativeHumanImpacts	0.76	0.67	0.36	0.73	1.00

887 **Supplementary Table 3.** Variable inflation scores used to select variables included in the
888 PERMANOVAs, for variables selected by the CCA. We excluded those with VIF > 10 (shaded).
889 For categorical variables with multiple levels (e.g. Contributor, Habitat, Management, Month by
890 SST, and Methods), we show the maximum VIF. The descriptions of each variable are in
891 Supplementary Table 1.
892
893

All Sites	
Variable	VIF
Contributor	305.18
Latitude	22.64
Month (ranked by SST)	4.98
Storms within 5 years (Type 3 Plus)	3.95
maxDHW	8.44
Cumulative human impact	8.71
Habitat	4.15
Nutrients (agriculture)	5.00
Mean wave energy	4.31
Longitude	10.93
Cyclone score	11.51
NPP _{SD}	7.16
Climate score	16.54
SST _{SD}	7.16
Market gravity	13.34
MMM	2.15
Depth	2.65
Reef area (200 km)	3.29
SST (kurtosis)	67.29
Connectivity score	11.86
Management	6.77
NDVI	1.96
Mean PAR (survey month)	5.00
WWE	457.30
Aspect	3.12
Chl _a (kurtosis)	1.87

894

Realm 9. Mid-tropical North Pacific	
Variable	VIF
Month (ranked by SST)	39.86
sdSST	1399.22
Mean PAR (survey month)	17.98
Cyclone score	27.09
Mean wave energy	53.88
MMM	87.97
Connectivity score	12.84
Contributor	2243.78
Latitude	12401.24
SST (kurtosis)	948.99
Storms within 5 years (type 3 plus)	2.97
Nutrients (agriculture)	7.98

895
896

Realm 13. Indo-Pacific seas & Indian Ocean	
Variable	VIF
Contributor	323.15
SST _{SD}	57.29
Month (ranked by SST)	13.86
Longitude	414.91
Cumulative human impacts	12.36
Chl _a (kurtosis)	2.12
Latitude	89.97
Reef area (200 km)	7.31
Depth	1.98
Market gravity	20.75
Management	10.20
NPP _{SD}	14.22
NDVI	1.49
Mean SST (month of survey)	2.09
Reef area (15km)	3.61
Nutrients (agriculture)	11.63
SST (kurtosis)	44.96
Mean wave energy	3.31
Climate score (overall)	41.52
Connectivity score	15.41

897
898

Realm 16. Coral Sea	
Variable	VIF
Contributor (max)	19113.93
Human population (20 km)	1535.29
MaxDHW	11.29
Nutrients (agriculture)	4.79
NDVI	4.42
Connectivity score	38.02
Climate score (overall)	35.05
Latitude	50.24
Chla (kurtosis)	5.67
Mean wave energy	4.42
Storms within 5 years (Type 3 plus)	1.49
Mean PAR (survey month)	15.71
Month (ranked by SST)	553.32
Mean SST (survey month)	104.94
Reef area (200 km)	13.76
Management	10.09
Cyclone score	16.87
NPP _{SD}	1.99

899
900

Realm 17. Mid South Tropical Pacific	
Variable	VIF
Contributor (max)	19113.93
Cyclone score	109.21
Management	3.79
Aspect	1.26
Depth	1.40
Market Gravity	14.57
NDVI	1.65
Mean PAR (survey month)	3.83
Latitude	1356.94
MaxDHW	99.48

901
902

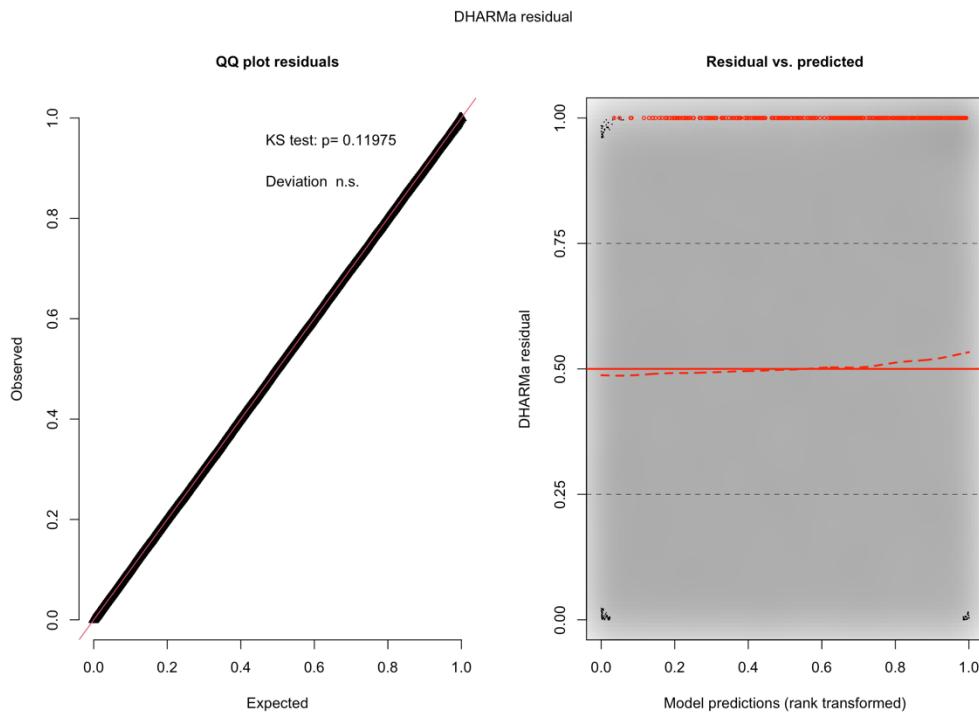
Realm 20. Offshore West Pacific	
Variable	VIF
Contributor	662.17
Month (ranked by SST)	6177.86
Longitude	513.55
MaxDHW	86.85
Mean SST (survey month)	3401.77
Reef area (200 km)	901.62
Connectivity score	163.17
NDVI	5.86
WWE	5.34
Aspect	5.39
Market gravity	357.29
Mean wave energy	3.62
Storms within 5 years (Type 3 Plus)	161.77
SST _{SD}	1443.77
MMM	116.86
Latitude	8939.16
SST (kurtosis)	5442.84
Cumulative human impacts	46.51
Habitat	11.85
Human population (20 km)	22.96
Mean PAR (survey month)	39.86
Cyclone score	1808.99
Climate score (overall)	1476.10

903
904

Realm 29. NW Pacific	
Variable	VIF
Contributor	60.62
Depth	10.38
Chla (kurtosis)	4.38
Connectivity score	11.38
Nutrients (agriculture)	3.27
Management	8.51
WWE	1.91
Reef area (15 km)	17.82

905
906

907 **Supplementary Materials 4. Diagnostic plots for beta-distributed zero-inflated GLMMS**
908
909 All Macroalgae.
910 **a. Residual Plots**

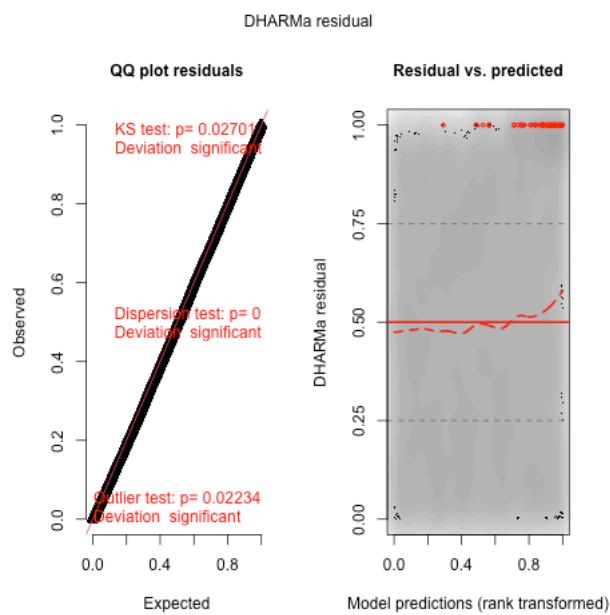


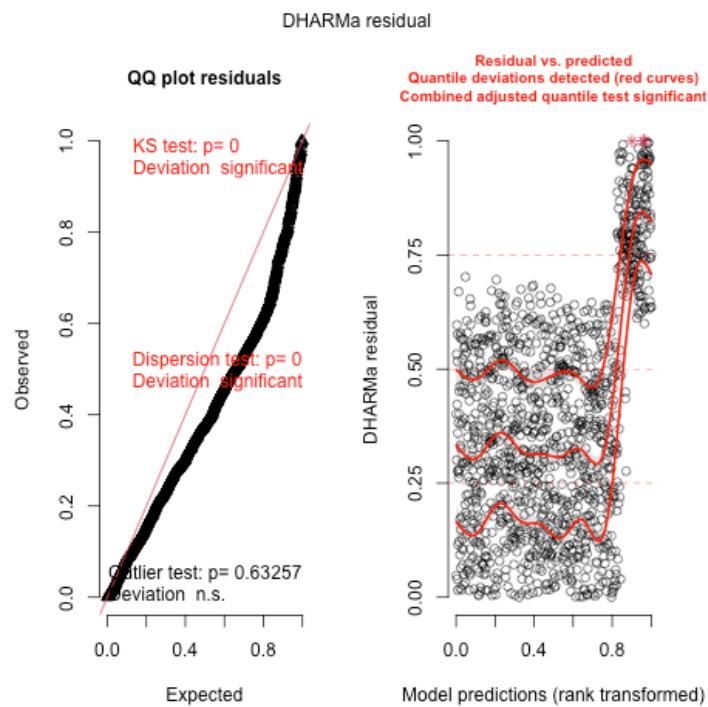
911
912 **b. Moran's Test**
913 Moran I statistic standard deviate = -0.27834, p-value = 0.6096
914 alternative hypothesis: greater
915 sample estimates:
916 Moran I statistic Expectation Variance
917 -8.623524e-04 -9.254718e-06 9.394231e-06

920 All Brown Macroalgae.

921 a. Residual Plots

922



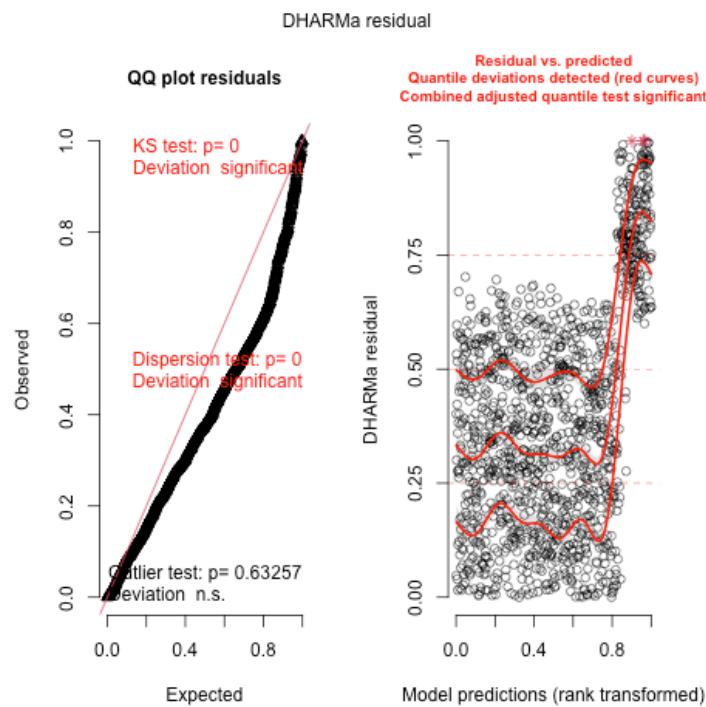


b. Moran's Test

Moran I statistic standard deviate = 2.511, p-value = 0.006019
 alternative hypothesis: greater
 sample estimates:

Moran I statistic	Expectation	Variance
0.0897219292	-0.0008058018	0.0012997689

949 *Dictyopteris*.
950 a. Residual plots

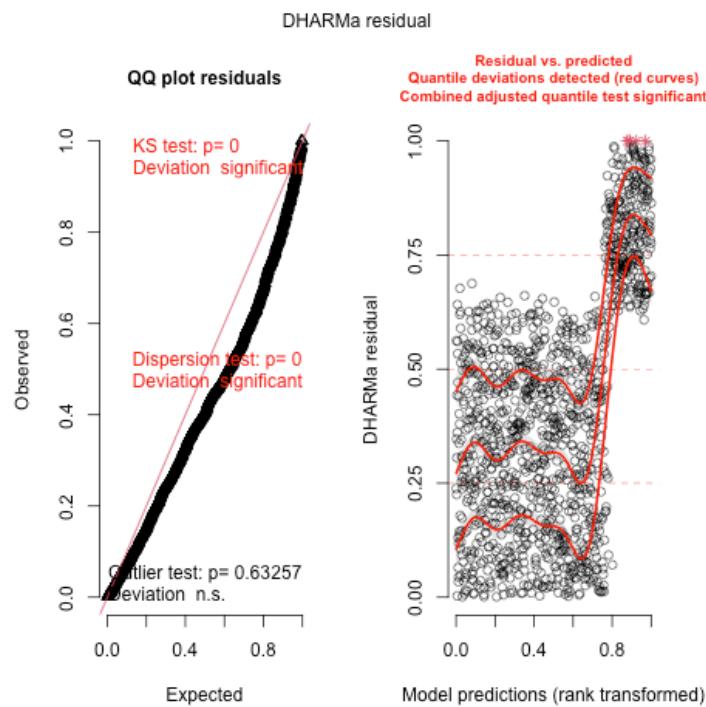


951 b. Moran's test

952
953
954
955 Moran I statistic standard deviate = 2.511, p-value = 0.006019
956 alternative hypothesis: greater
957 sample estimates:
958 Moran I statistic Expectation Variance
959 0.0897219292 -0.0008058018 0.0012997689
960
961
962
963

964 *Lobophora*.

965 a. Residual Plots



966

967

b. Moran's Test

968

969 Moran I statistic standard deviate = 2.4397, p-value = 0.007349

970 alternative hypothesis: greater

971 sample estimates:

972 Moran I statistic Expectation Variance
973 0.0804870752 -0.0008058018 0.0011102454

974

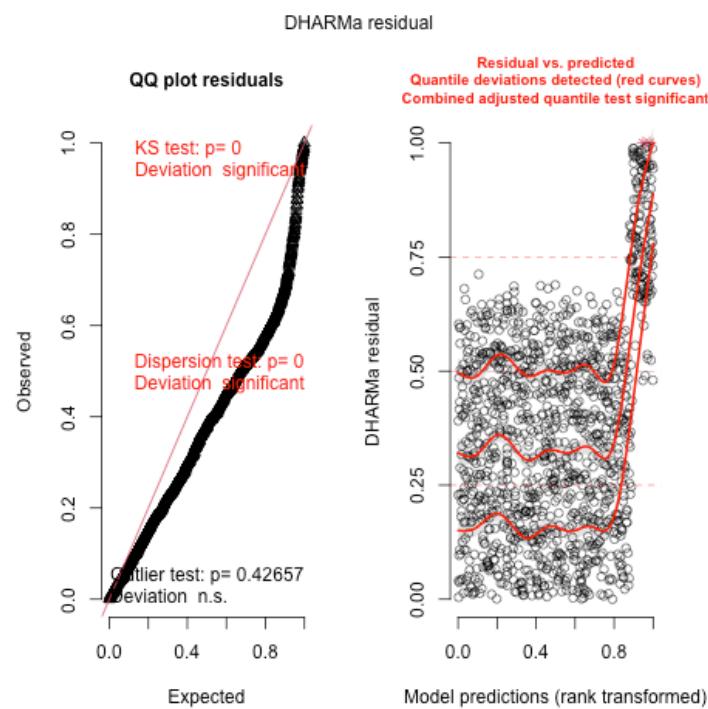
975

976

977

Padina.

978

a. Residual Plots

979

980

b. Moran's Test

981

982 Moran I statistic standard deviate = 6.3323, p-value = 1.208e-10

983 alternative hypothesis: greater

984 sample estimates:

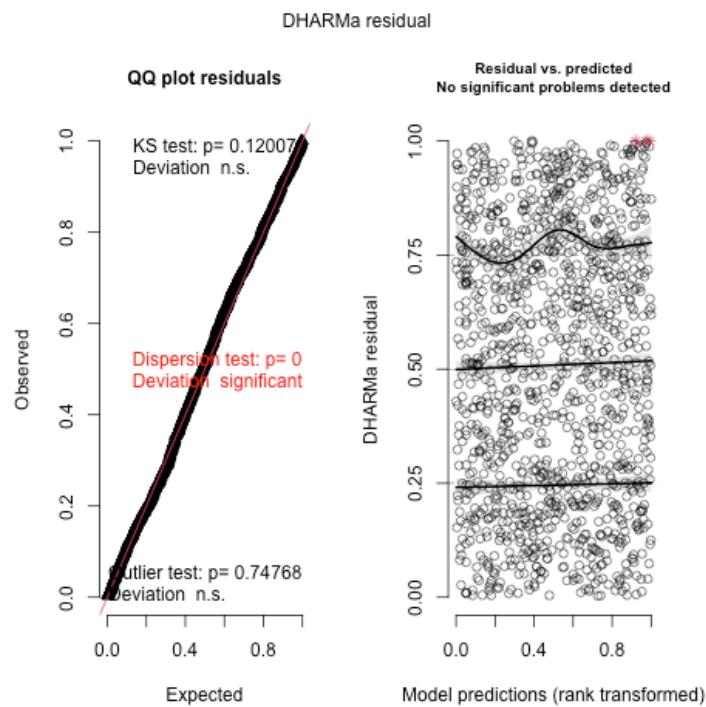
985 Moran I statistic Expectation Variance
986 0.2277455693 -0.0008058018 0.0013026996

987

988

989

990 *Spatoglossum*.
991 a. Residual Plots



992

993 b. Moran's Test

994

995 Moran I statistic standard deviate = -2.332, p-value = 0.9901

996 alternative hypothesis: greater

997 sample estimates:

998 Moran I statistic Expectation Variance
999 -0.0433821098 -0.0008058018 0.0003333396

1000

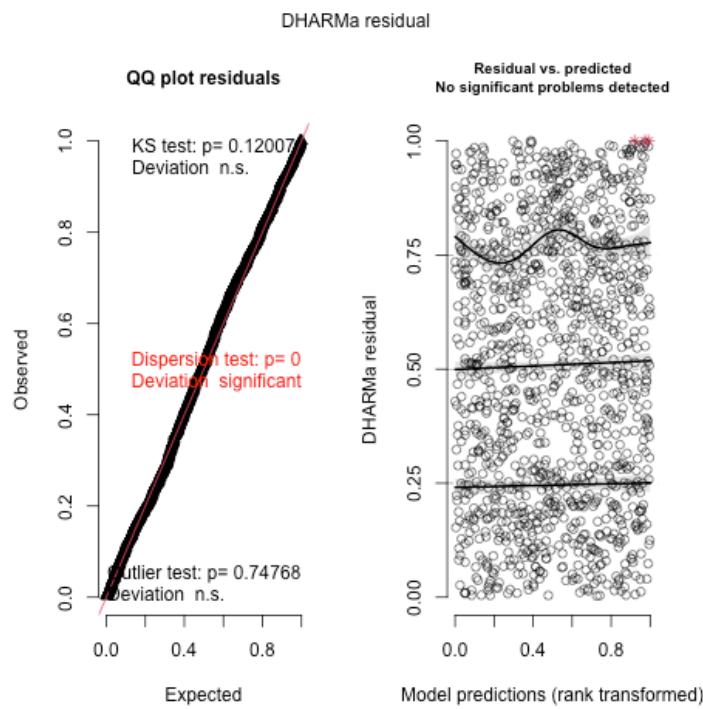
1001

1002

1003

1004 *Sargassum*.

1005 a. Residual Plots



1006 b. Moran's Test

1007 Moran I statistic standard deviate = 3.7477, p-value = 8.923e-05

1008 alternative hypothesis: greater

1009 sample estimates:

1010 Moran I statistic Expectation Variance

1011 0.1339887139 -0.0008058018 0.0012936429

1012

1013

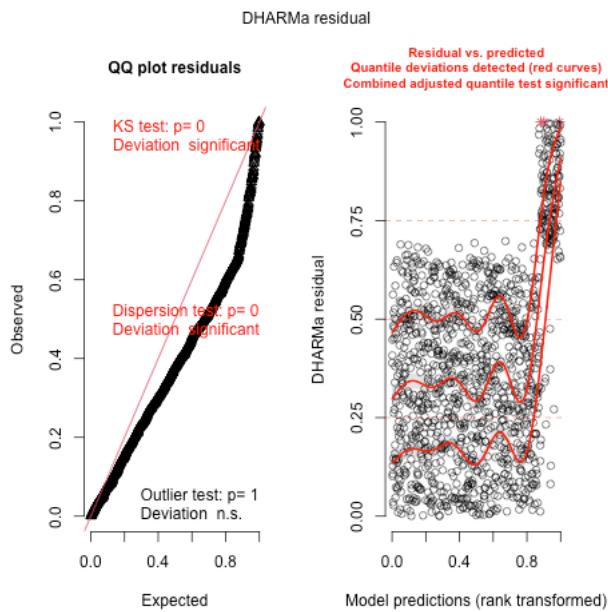
1014

1015

1016
1017

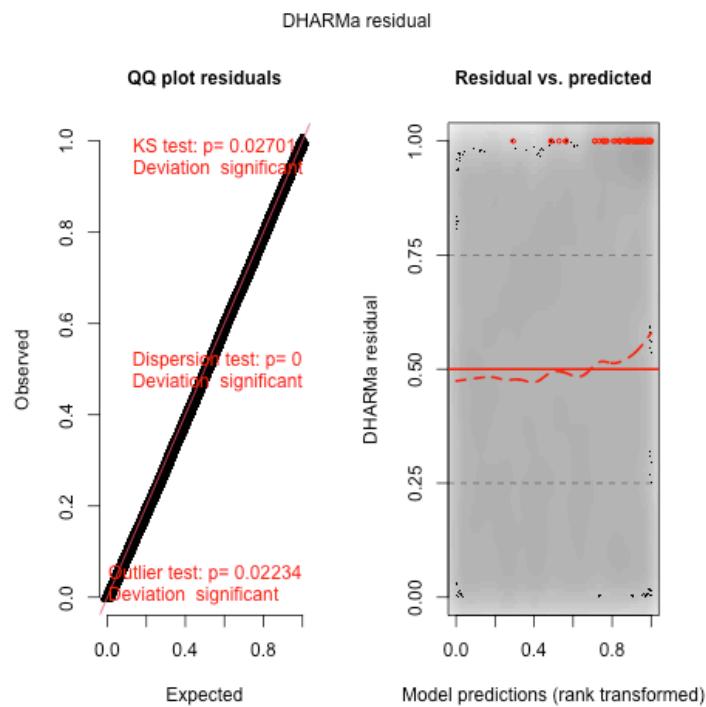
Turbinaria.

a. Residual Plots



1018
1019
1020 Moran I statistic standard deviate = -29.869, p-value = 1
1021 alternative hypothesis: greater
1022 sample estimates:
1023 Moran I statistic Expectation Variance
1024 -0.9648241706 -0.0008058018 0.0010416729
1025
1026
1027
1028
1029

1030 All Green Macroalgae.
1031 a. Residual Plots

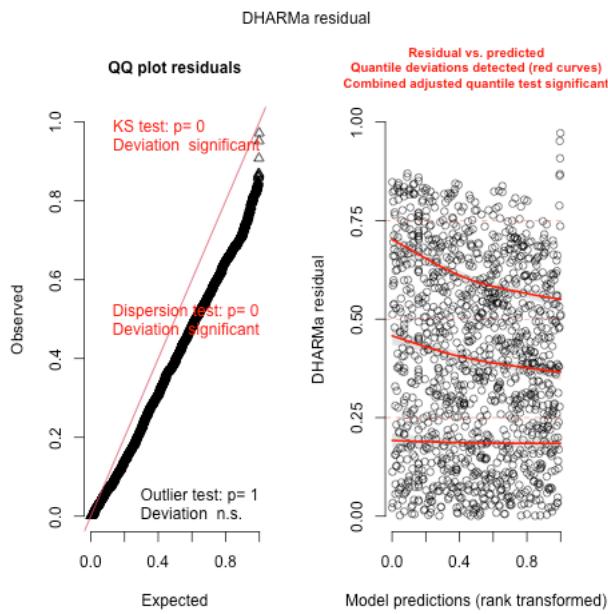


1032
1033 b. Moran's Test
1034

1035 Moran I statistic standard deviate = 0.2079, p-value = 0.4177
1036 alternative hypothesis: greater
1037 sample estimates:
1038 Moran I statistic Expectation Variance
1039 1.297462e-03 -3.834209e-05 4.128299e-05

1040
1041
1042

1043 *Bryopsis*.
1044 a. Residual Plots

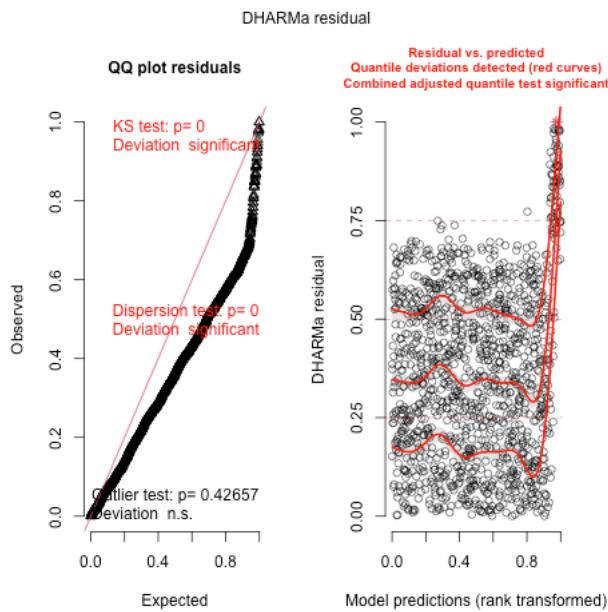


1045
1046 b. Moran's Test
1047 Moran I statistic standard deviate = -6.5094, p-value = 1
1048 alternative hypothesis: greater
1049 sample estimates:
1050 Moran I statistic Expectation Variance
1051 -0.1960915596 -0.0008058018 0.0009000443
1052
1053

1054
1055

Chlorodesmis.

a. Residual Plots



1056
1057
1058
1059
1060
1061
1062
1063
1064

b. Moran's Tests

Moran I statistic standard deviate = -19.767, p-value = 1

alternative hypothesis: greater

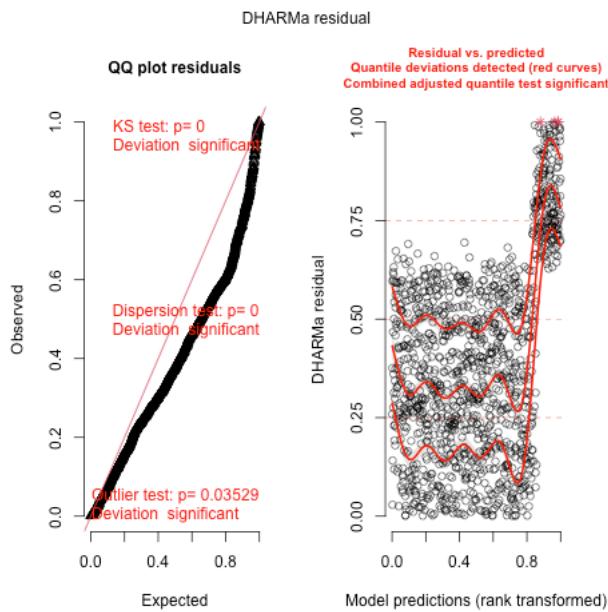
sample estimates:

Moran I statistic	Expectation	Variance
-0.7246005841	-0.0008058018	0.0013407505

1065
1066

Caulerpa.

a. Residual Plots



1067
1068
1069
1070
1071
1072
1073
1074
1075
1076

b. Moran's Test

Moran I statistic standard deviate = 8.4404, p-value < 2.2e-16

alternative hypothesis: greater

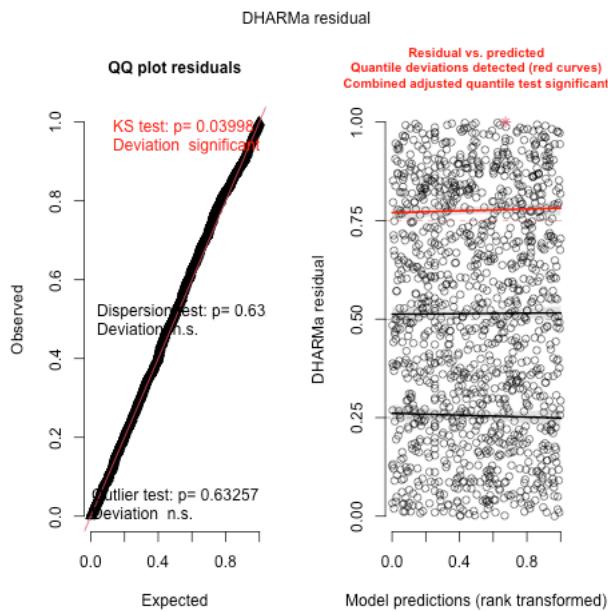
sample estimates:

Moran I statistic	Expectation	Variance
0.2959883933	-0.0008058018	0.0012364874

1077
1078

Cladophoropsis.

a. Residual Plots



1079
1080
1081
1082
1083
1084
1085
1086
1087
1088

b. Moran's Test

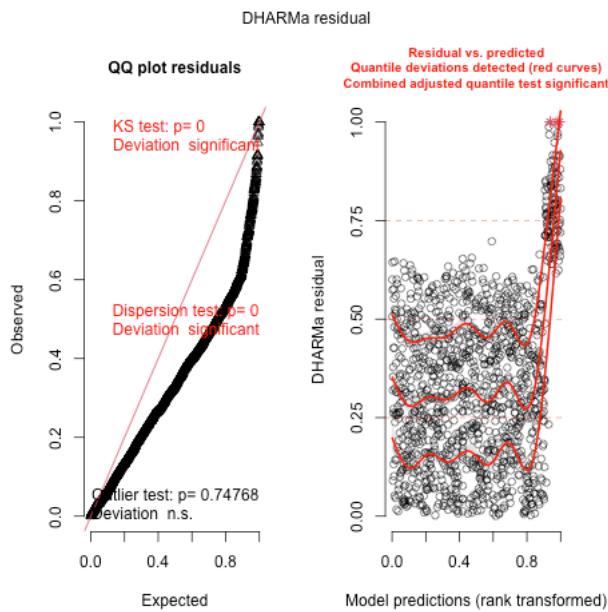
Moran I statistic standard deviate = 13.674, p-value < 2.2e-16

alternative hypothesis: greater

sample estimates:

Moran I statistic	Expectation	Variance
0.4489339689	-0.0008058018	0.0010817439

1089 *Dictyosphaeria*.
1090 a. Residual Plots



1091
1092 b. Moran's Test
1093

1094 Moran I statistic standard deviate = 1.5434, p-value = 0.06137

1095 alternative hypothesis: greater

1096 sample estimates:

1097 Moran I statistic Expectation Variance
1098 0.0514275036 -0.0008058018 0.0011453833

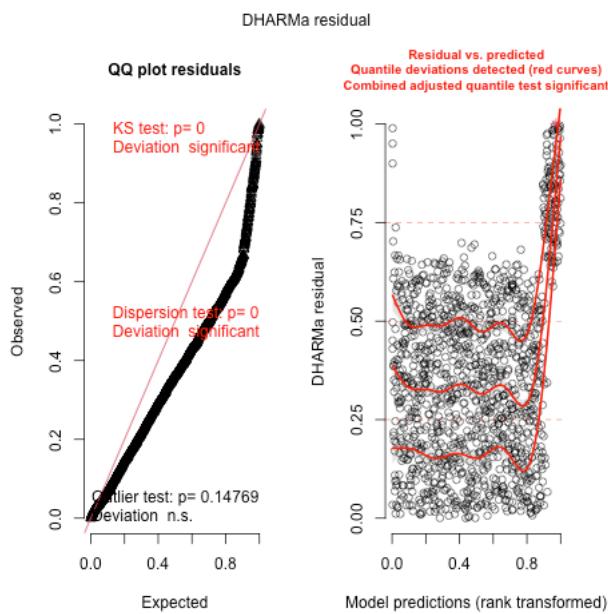
1099
1100
1101

1102 ***Halimeda***.
1103 a. Residual Plots
1104
1105 b. Moran's Test
1106
1107 Moran I statistic standard deviate = 5.1213, p-value = 1.517e-07
1108 alternative hypothesis: greater
1109 sample estimates:
1110 Moran I statistic Expectation Variance
1111 0.273599174 -0.001680672 0.002889309
1112
1113

1114
1115

Microdictyon.

a. Residual Plots



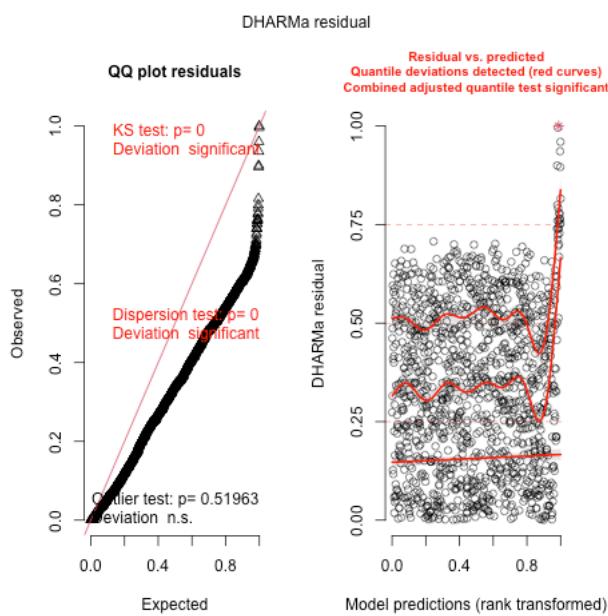
1116
1117
1118
1119
1120
1121
1122
1123
1124
1125

b. Moran's Test

Moran I statistic standard deviate = -0.52639, p-value = 0.7007
alternative hypothesis: greater
sample estimates:
Moran I statistic Expectation Variance
-0.0199539804 -0.0008058018 0.0013232546

1126 *Neomeris*.

1127 **a. Residual Plots**



1128

1129 **b. Moran's Test**

1130

1131 Moran I statistic standard deviate = 14.933, p-value < 2.2e-16

1132 alternative hypothesis: greater

1133 sample estimates:

1134 Moran I statistic Expectation Variance
1135 0.3849908498 -0.0008058018 0.0006674577

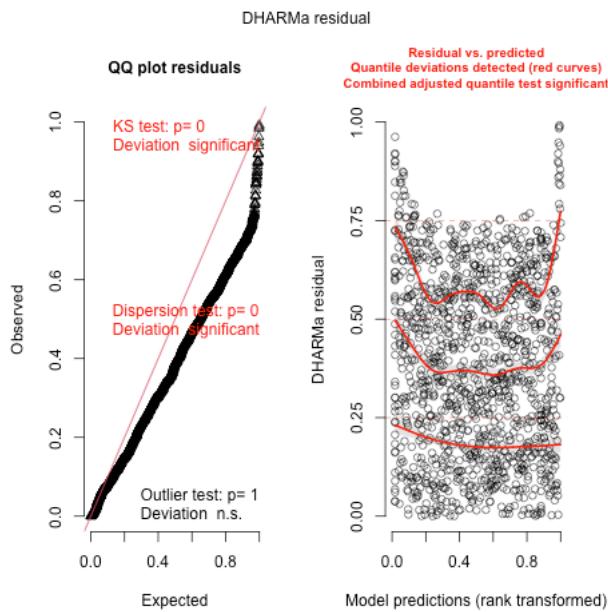
1136

1137

1138
1139

Udotea.

a. Residual Plots



1140
1141
1142
1143
1144
1145
1146
1147
1148
1149

b. Moran's Test

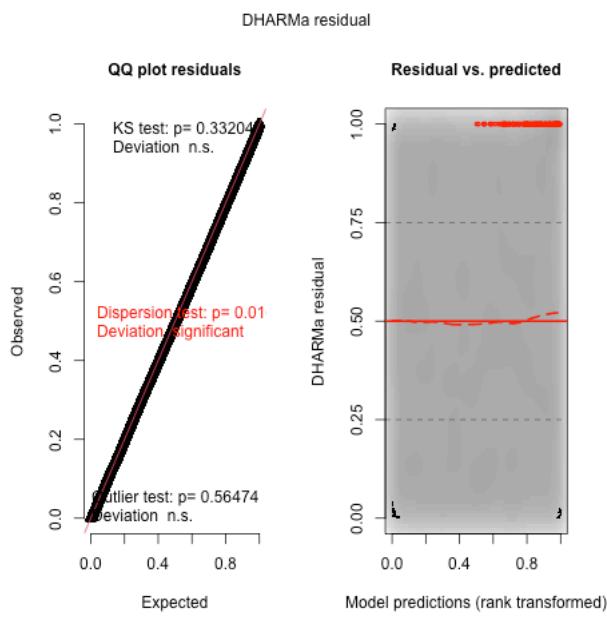
Moran I statistic standard deviate = -31.969, p-value = 1

alternative hypothesis: greater

sample estimates:

Moran I statistic	Expectation	Variance
-0.9915109931	-0.0008058018	0.0009603581

1150 *All Red Macroalgae*.
1151 a. Residual Plots



1152 b. Moran's Test

1153
1154
1155 Moran I statistic standard deviate = -0.28934, p-value = 0.6138
1156 alternative hypothesis: greater
1157 sample estimates:
1158 Moran I statistic Expectation Variance
1159 -1.185480e-03 -1.677430e-05 1.631486e-05

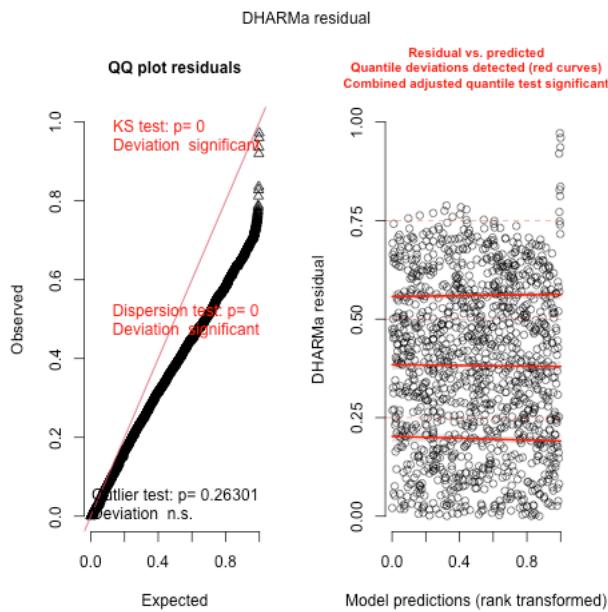
1160
1161

1162

Amansia.

1163

a. Residual Plots



1164

b. Moran's Test

1165

1166

1167

1168

Moran I statistic standard deviate = 4.8454, p-value = 6.319e-07

1169

alternative hypothesis: greater

1170

sample estimates:

1171

Moran I statistic	Expectation	Variance
0.1566480591	-0.0008058018	0.0010559787

1172

1173

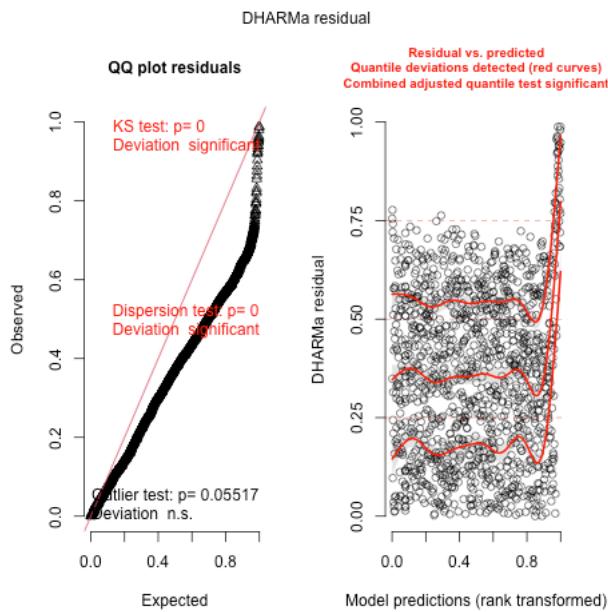
1174

1175

Asparagopsis.

1176

a. Residual Plots



1177

b. Moran's Test

1178

1179

Moran I statistic standard deviate = 5.1317, p-value = 1.436e-07

1180

alternative hypothesis: greater

1181

sample estimates:

1182

Moran I statistic	Expectation	Variance
0.1789781895	-0.0008058018	0.0012274012

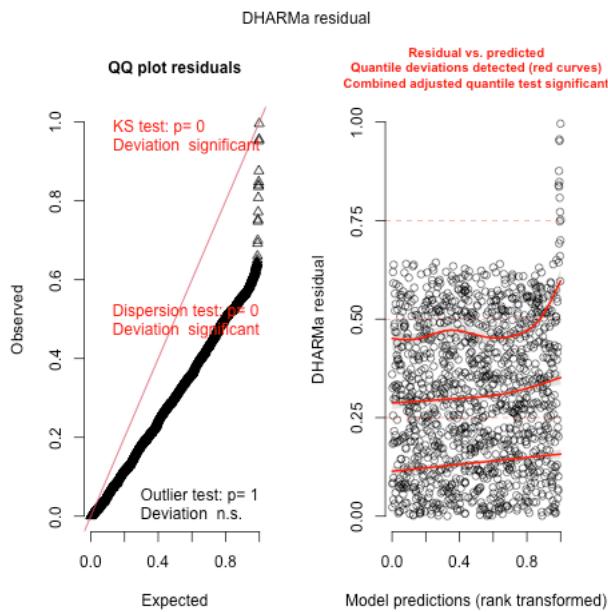
1183

1184

1185

1186

1187 *Ceratodictyon*.
1188 a. Residual Plots

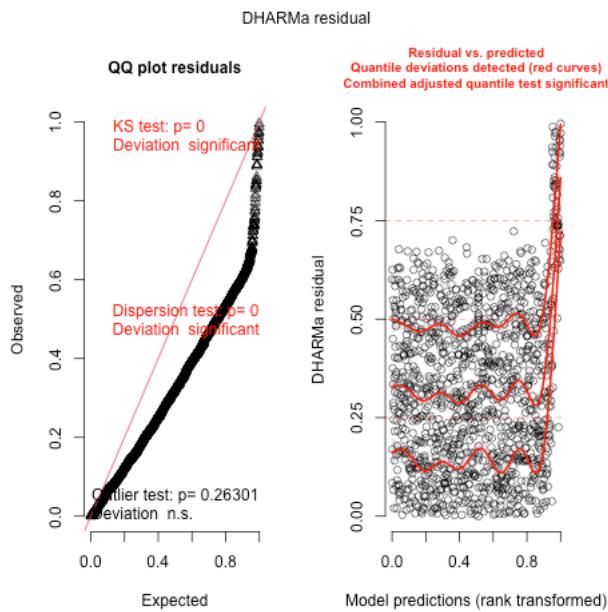


1189
1190 b. Moran's Test
1191
1192 Moran I statistic standard deviate = -15.611, p-value = 1
1193 alternative hypothesis: greater
1194 sample estimates:
1195 Moran I statistic Expectation Variance
1196 -0.5042586961 -0.0008058018 0.0010400224

1199
1200

Galaxaura.

a. Residual Plots



1201
1202
1203
1204
1205
1206
1207
1208
1209
1210

b. Moran's Test

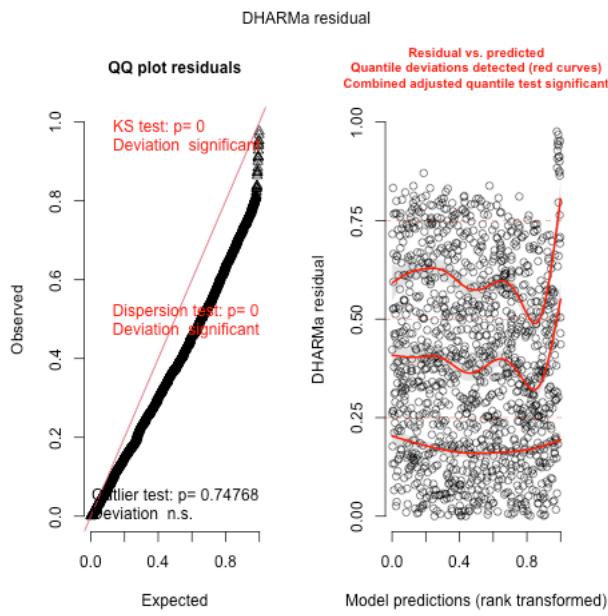
Moran I statistic standard deviate = 19.188, p-value < 2.2e-16

alternative hypothesis: greater

sample estimates:

Moran I statistic	Expectation	Variance
0.4802926162	-0.0008058018	0.0006286597

1211 *Halymenia*.
1212 a. Residual Plots

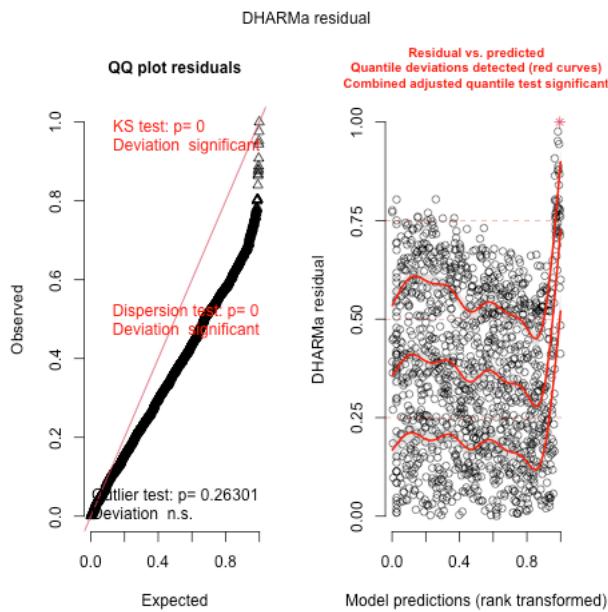


1213
1214
1215 b. Moran's I
1216
1217 Moran I statistic standard deviate = -13.839, p-value = 1
1218 alternative hypothesis: greater
1219 sample estimates:
1220 Moran I statistic Expectation Variance
1221 -0.4858614635 -0.0008058018 0.0012284550
1222
1223

1224
1225

Hypnea.

a. Residual Plots



1226
1227
1228
1229
1230
1231
1232
1233
1234
1235

b. Moran's I

Moran I statistic standard deviate = -4.0611, p-value = 1

alternative hypothesis: greater

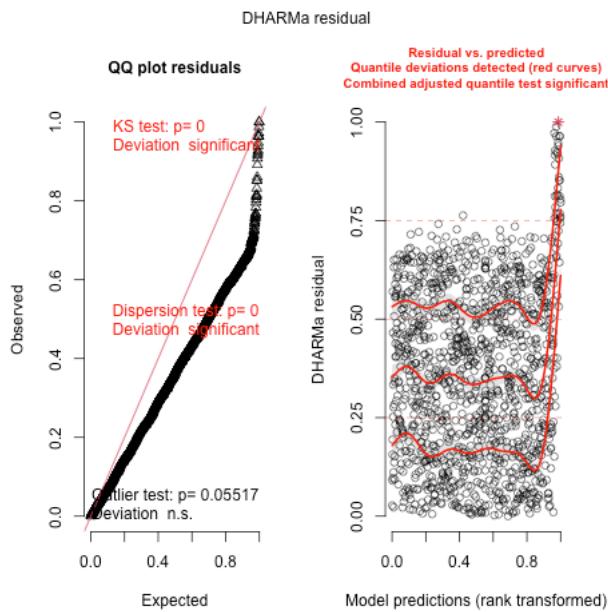
sample estimates:

Moran I statistic	Expectation	Variance
-0.0774534269	-0.0008058018	0.0003562212

1236
1237

Laurencia.

a. Residual Plots



1238
1239
1240
1241
1242
1243
1244
1245
1246
1247

b. Moran's Test

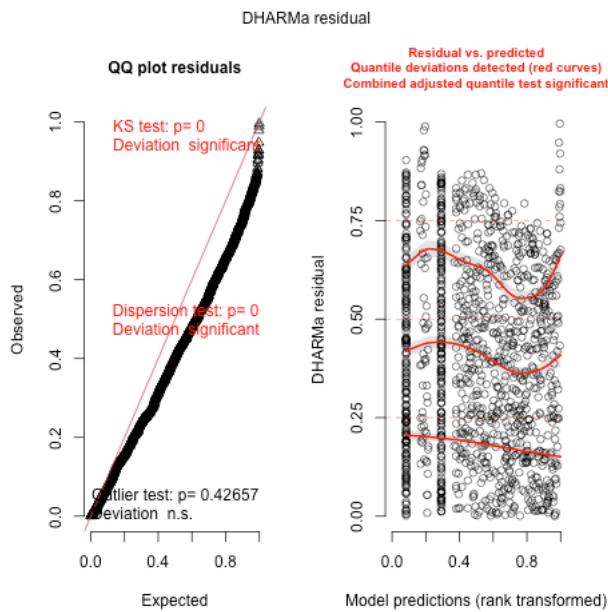
Moran I statistic standard deviate = -33.023, p-value = 1

alternative hypothesis: greater

sample estimates:

Moran I statistic	Expectation	Variance
-0.9841853743	-0.0008058018	0.0008867521

1248 *Neurymenia*.
1249 a. Residual Plots



1250
1251 b. Moran's Test
1252
1253 Moran I statistic standard deviate = -32.351, p-value = 1
1254 alternative hypothesis: greater
1255 sample estimates:
1256 Moran I statistic Expectation Variance
1257 -0.9150749293 -0.0008058018 0.000798700
1258
1259

1260
1261
1262
1263

Supplementary Table 5. Ten most common macroalgae taxa by average value, across all sites and within biogeographic realms.

All Sites (1205 Total)				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	12.80	88.20	6.79
<i>Sargassum</i>	Brown	13.00	62.00	6.25
<i>Microdictyon</i>	Green	12.00	69.70	5.00
<i>Halimeda</i>	Green	8.02	77.30	4.44
<i>Amansia</i>	Red	6.34	13.50	4.96
<i>Cladophoropsis</i>	Green	4.76	9.30	4.51
<i>Dictyopteris</i>	Brown	4.60	14.60	4.00
<i>Ceratodictyon</i>	Red	4.44	20.00	1.23
<i>Lobophora</i>	Brown	3.89	82.70	1.31
<i>Padina</i>	Brown	3.21	24.40	2.08
<i>Spatoglossum</i>	Brown	3.17	12.20	0.53

1264

9. Mid-tropical North Pacific (101)				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	6.83	24.40	5.13
<i>Padina</i>	Brown	5.41	11.60	4.82
<i>Halimeda</i>	Green	5.16	21.60	4.39
<i>Microdictyon</i>	Green	3.98	12.60	2.43
<i>Asparagopsis</i>	Red	3.09	3.33	3.09
<i>Neomeris</i>	Green	3.08	3.35	3.08
<i>Lobophora</i>	Brown	2.24	9.30	1.99
<i>Liagora</i>	Red	1.68	1.68	1.68
<i>Turbinaria</i>	Brown	1.53	3.33	0.93
<i>Dictyota</i>	Brown	1.27	5.83	0.31
<i>Caulerpa</i>	Green	0.22	0.51	0.17

1265
1266

13. Indo-Pacific seas & Indian Ocean				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	18.40	88.20	14.80
<i>Microdictyon</i>	Green	12.80	69.70	3.66
<i>Sargassum</i>	Brown	10.10	62.00	4.92
<i>Halimeda</i>	Green	8.16	77.30	4.94
<i>Cystoseiria</i>	Brown	7.12	26.40	3.53
<i>Lobophora</i>	Brown	4.50	82.67	0.68
<i>Cladophoropsis</i>	Green	4.12	6.23	4.10
<i>Jania</i>	Red	3.56	6.54	3.66
<i>Turbinaria</i>	Brown	3.00	29.50	1.07
<i>Padina</i>	Brown	2.91	12.40	1.64
<i>Spyridia</i>	Red	2.46	2.46	2.46

1267

1268

16. Coral Sea [324]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	15.60	78.50	9.74
<i>Galaxaura</i>	Red	26.10	35.20	26.10
<i>Sargassum</i>	Brown	22.40	59.10	19.70
<i>Halimeda</i>	Green	14.10	44.60	11.20
<i>Sargassopsis</i>	Brown	8.20	37.20	4.25
<i>Hydroclathrus</i>	Brown	5.59	13.60	5.75
<i>Dictosphaeria</i>	Green	5.04	14.10	0.76
<i>Dictyopteris</i>	Brown	4.75	10.20	4.25
<i>Caulerpa</i>	Green	4.50	30.00	1.43
<i>Lobophora</i>	Brown	3.07	23.60	0.69
<i>Laurencia</i>	Brown	3.05	13.70	1.67

1269

17. Mid South Tropical Pacific [166]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	11.40	37.90	9.07
<i>Microdictyon</i>	Green	9.11	12.30	9.31
<i>Lobophora</i>	Brown	6.33	28.50	4.52
<i>Turbinaria</i>	Brown	5.67	26.10	4.50
<i>Padina</i>	Brown	4.73	6.00	5.00
<i>Chlorodesmis</i>	Green	4.58	8.33	4.17
<i>Halimeda</i>	Green	4.26	22.80	2.38
<i>Sargassum</i>	Brown	3.83	6.00	4.00
<i>Asparagopsis</i>	Red	3.81	8.00	3.33
<i>Galaxaura</i>	Red	3.58	7.48	4.45
<i>Dictyota</i>	Brown	3.31	15.30	1.71

1270
1271

20. Offshore West Pacific [114]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	12.70	85.40	4.70
<i>Eckloniopsis</i>	Brown	31.50	40.80	31.50
<i>Ptilophora</i>	Red	25.00	37.90	25.00
<i>Microdictyon</i>	Green	16.10	43.90	15.40
<i>Ventricaria</i>	Green	15.70	15.70	15.70
<i>Vanvoorstia</i>	Red	12.80	12.80	12.80
<i>Corallina</i>	Red	11.80	20.50	11.80
<i>Ceratodictyon</i>	Red	11.50	20.00	10.50
<i>Prionitis</i>	Red	11.40	11.40	11.40
<i>Cladophoropsis</i>	Green	9.30	9.30	9.30
<i>Amansia</i>	Red	9.06	13.50	9.12

1272
1273

1274

29. NW Pacific [57]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	5.70	22.10	2.66
<i>Padina</i>	Brown	8.54	17.00	8.54
<i>Caulerpa</i>	Green	5.40	5.40	5.40
<i>Amansia</i>	Red	3.63	11.60	1.45
<i>Spatoglossum</i>	Brown	3.17	12.20	0.53
<i>Neomeris</i>	Green	2.93	11.50	1.45
<i>Gracilaria</i>	Red	2.41	2.41	2.41
<i>Lobophora</i>	Brown	1.97	8.53	0.99
<i>Actinotrichia</i>	Red	1.68	1.68	1.68
<i>Halimeda</i>	Green	1.43	11.00	0.27
<i>Dudresnaya</i>	Red	1.20	1.20	1.20

1275

1276 **Supplementary Table 6. SIMPER results.**

1277

Realm 16 vs Realm 13

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.428	0.314	1.365	8.928	7.092	0.536	0.001	***
MIC	0.066	0.188	0.352	0.131	3.078	0.619	0.833	
SRG	0.060	0.168	0.354	2.139	1.031	0.694	0.001	***
LPA	0.060	0.151	0.393	0.751	1.055	0.768	1.000	
CLP	0.038	0.114	0.331	0.953	0.317	0.815	0.264	
PAD	0.034	0.107	0.319	0.261	0.447	0.858	0.998	
TRB	0.020	0.079	0.257	0.026	0.543	0.883	1.000	
CHL	0.017	0.077	0.217	0.191	0.029	0.904	0.152	
DIC	0.015	0.061	0.248	0.146	0.237	0.923	1.000	
DCT	0.012	0.048	0.245	0.062	0.238	0.938	0.843	
GLA	0.009	0.074	0.127	0.213	0.043	0.950	0.811	
ASP	0.008	0.058	0.145	0.018	0.131	0.961	0.971	
HYP	0.007	0.048	0.153	0.053	0.173	0.970	0.218	
LAU	0.007	0.031	0.221	0.287	0.006	0.978	0.006	**
UDO	0.005	0.035	0.132	0.162	0.000	0.984	0.001	***
DPT	0.003	0.018	0.152	0.155	0.000	0.988	0.997	
HLA	0.003	0.020	0.134	0.011	0.047	0.991	0.721	
CLS	0.002	0.016	0.123	0.000	0.071	0.994	0.549	
CER	0.002	0.013	0.148	0.000	0.062	0.996	0.998	
VAL	0.001	0.019	0.071	0.000	0.010	0.998	0.838	
NEO	0.001	0.014	0.070	0.000	0.010	0.999	0.994	
BRY	0.001	0.008	0.107	0.000	0.027	1.000	0.827	

Contrast: 16_9

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
HA	0.454	0.310	1.464	8.928	3.736	0.564	0.001 ***
PAD	0.078	0.204	0.384	0.261	0.833	0.661	0.002 **
LPA	0.074	0.157	0.474	0.751	0.600	0.753	0.774
SRG	0.043	0.148	0.288	2.139	0.000	0.806	0.451
MIC	0.036	0.128	0.281	0.131	0.612	0.851	0.994
CLP	0.033	0.109	0.302	0.953	0.027	0.891	0.567
DIC	0.026	0.097	0.264	0.146	0.258	0.923	0.754
CHL	0.017	0.073	0.229	0.191	0.000	0.944	0.328
TRB	0.008	0.042	0.196	0.026	0.071	0.954	1.000
LAU	0.008	0.034	0.223	0.287	0.000	0.963	0.106
GLA	0.006	0.070	0.090	0.213	0.000	0.971	0.843
NEO	0.006	0.036	0.154	0.000	0.095	0.978	0.113
ASP	0.005	0.031	0.171	0.018	0.095	0.984	0.940
UDO	0.005	0.037	0.142	0.162	0.000	0.991	0.090 .
DPT	0.003	0.020	0.155	0.155	0.000	0.995	0.875
DCT	0.002	0.022	0.083	0.062	0.000	0.997	1.000
HYP	0.002	0.009	0.163	0.053	0.000	0.999	0.986
HLA	0.001	0.014	0.071	0.011	0.000	1.000	0.949

Contrast: 16_17

Column1	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.403	0.312	1.290	8.928	3.721	0.477	0.005	**
LPA	0.107	0.187	0.570	0.751	2.115	0.604	0.005	**
TRB	0.056	0.136	0.407	0.026	1.202	0.669	0.001	***
DIC	0.054	0.141	0.386	0.146	1.080	0.734	0.001	***
SRG	0.045	0.144	0.316	2.139	0.153	0.787	0.346	
MIC	0.041	0.157	0.257	0.131	0.607	0.835	0.999	
CLP	0.039	0.119	0.329	0.953	0.129	0.882	0.257	
CHL	0.023	0.097	0.242	0.191	0.122	0.909	0.003	**
PAD	0.023	0.093	0.242	0.261	0.158	0.936	1.000	
ASP	0.019	0.094	0.198	0.018	0.229	0.958	0.053	.
GLA	0.015	0.082	0.187	0.213	0.243	0.976	0.135	
LAU	0.007	0.032	0.219	0.287	0.000	0.985	0.059	.
UDO	0.005	0.037	0.132	0.162	0.000	0.991	0.038	*
DPT	0.003	0.019	0.153	0.155	0.000	0.994	0.967	
DCT	0.003	0.024	0.108	0.062	0.021	0.997	1.000	
HYP	0.001	0.008	0.160	0.053	0.000	0.999	0.999	
HLA	0.001	0.017	0.060	0.011	0.000	1.000	0.993	

Contrast: 16_20

Column1	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.372	0.330	1.127	8.928	1.528	0.415	0.448	
LPA	0.073	0.180	0.406	0.751	0.679	0.496	0.855	
CLP	0.070	0.145	0.481	0.953	1.437	0.574	0.001	***
PAD	0.066	0.150	0.440	0.261	1.780	0.647	0.006	**
SRG	0.056	0.166	0.338	2.139	0.344	0.710	0.065	.
MIC	0.047	0.159	0.298	0.131	1.548	0.762	0.973	
CHL	0.032	0.096	0.332	0.191	0.583	0.798	0.001	***
CER	0.028	0.116	0.243	0.000	0.996	0.829	0.001	***
TRB	0.027	0.082	0.325	0.026	0.301	0.859	0.898	
DPT	0.026	0.088	0.292	0.155	1.232	0.888	0.001	***
DCT	0.023	0.061	0.374	0.062	0.989	0.913	0.008	**
AMA	0.015	0.070	0.210	0.000	0.876	0.929	0.001	***
DIC	0.013	0.064	0.208	0.146	0.213	0.944	1.000	
GLA	0.009	0.079	0.118	0.213	0.019	0.955	0.647	
LAU	0.008	0.035	0.225	0.287	0.004	0.963	0.031	*
HLA	0.006	0.030	0.215	0.011	0.098	0.971	0.007	**
NEO	0.006	0.033	0.196	0.000	0.370	0.978	0.016	*
UDO	0.005	0.040	0.126	0.162	0.000	0.983	0.088	.
VAL	0.004	0.025	0.166	0.000	0.333	0.988	0.036	*
VEN	0.003	0.023	0.123	0.000	0.212	0.991	0.009	**
BRY	0.002	0.019	0.130	0.000	0.130	0.994	0.040	*
CLS	0.002	0.016	0.134	0.000	0.159	0.996	0.449	
HYP	0.002	0.011	0.166	0.053	0.001	0.998	0.984	
ASP	0.002	0.009	0.183	0.018	0.029	1.000	0.999	

Contrast: 16_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.413	0.376	1.100	8.928	0.633	0.439	0.035	*
LPA	0.160	0.233	0.686	0.751	2.017	0.609	0.001	***
NRM	0.055	0.135	0.410	0.000	0.933	0.668	0.001	***
CLP	0.046	0.148	0.308	0.953	0.129	0.716	0.151	
SRG	0.046	0.155	0.294	2.139	0.005	0.764	0.378	
PAD	0.043	0.158	0.270	0.261	0.408	0.809	0.499	
GLA	0.032	0.100	0.319	0.213	0.179	0.843	0.010	**
SPT	0.029	0.098	0.293	0.000	0.582	0.874	0.001	***
CHL	0.025	0.116	0.220	0.191	0.002	0.901	0.066	.
LAU	0.021	0.060	0.349	0.287	0.141	0.923	0.001	***
AMA	0.019	0.075	0.248	0.000	0.401	0.943	0.008	**
TRB	0.011	0.075	0.143	0.026	0.001	0.954	1.000	
DPT	0.009	0.056	0.167	0.155	0.045	0.964	0.199	
MIC	0.009	0.079	0.112	0.131	0.000	0.973	1.000	
DIC	0.007	0.032	0.223	0.146	0.038	0.981	1.000	
HYP	0.007	0.033	0.211	0.053	0.057	0.989	0.294	
UDO	0.006	0.047	0.129	0.162	0.003	0.995	0.072	.
DCT	0.002	0.023	0.085	0.062	0.000	0.997	1.000	
HLA	0.002	0.024	0.062	0.011	0.000	0.999	0.786	
VAL	0.001	0.005	0.116	0.000	0.004	0.999	0.831	
ASP	0.001	0.006	0.095	0.018	0.000	1.000	1.000	
NEO	0.000	0.001	0.220	0.000	0.003	1.000	0.989	

Contrast: 13_9

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
HA	0.365	0.272	1.340	7.092	3.736	0.486	0.670
MIC	0.092	0.211	0.435	3.078	0.612	0.608	0.117
PAD	0.077	0.185	0.413	0.447	0.833	0.710	0.002 **
LPA	0.073	0.160	0.455	1.055	0.600	0.807	0.841
DIC	0.032	0.097	0.330	0.237	0.258	0.850	0.428
SRG	0.025	0.116	0.217	1.031	0.000	0.883	0.960
TRB	0.021	0.074	0.277	0.543	0.071	0.911	0.979
CLP	0.014	0.062	0.226	0.317	0.027	0.930	1.000
ASP	0.013	0.062	0.212	0.131	0.095	0.947	0.432
DCT	0.011	0.045	0.254	0.238	0.000	0.962	0.641
HYP	0.007	0.049	0.134	0.173	0.000	0.971	0.317
NEO	0.006	0.036	0.175	0.010	0.095	0.980	0.041 *
GLA	0.004	0.037	0.111	0.043	0.000	0.985	0.979
CHL	0.002	0.019	0.124	0.029	0.000	0.988	1.000
CLS	0.002	0.018	0.129	0.071	0.000	0.991	0.408
CER	0.002	0.014	0.157	0.062	0.000	0.994	0.972
HLA	0.002	0.013	0.151	0.047	0.000	0.997	0.768
VAL	0.001	0.013	0.091	0.010	0.000	0.998	0.701
BRY	0.001	0.009	0.112	0.027	0.000	1.000	0.498
LAU	0.000	0.004	0.056	0.006	0.000	1.000	1.000

Contrast: 13_17

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
HA	0.337	0.279	1.210	7.092	3.721	0.422	0.999
LPA	0.102	0.183	0.555	1.055	2.115	0.549	0.015 *
MIC	0.092	0.220	0.421	3.078	0.607	0.664	0.017 *
TRB	0.062	0.135	0.459	0.543	1.202	0.742	0.001 ***
DIC	0.059	0.138	0.430	0.237	1.080	0.816	0.001 ***
SRG	0.028	0.114	0.250	1.031	0.153	0.852	0.980
PAD	0.024	0.080	0.306	0.447	0.158	0.882	1.000
ASP	0.024	0.100	0.244	0.131	0.229	0.913	0.001 ***
CLP	0.020	0.081	0.248	0.317	0.129	0.938	0.999
GLA	0.013	0.060	0.218	0.043	0.243	0.954	0.273
DCT	0.012	0.046	0.253	0.238	0.021	0.969	0.811
CHL	0.009	0.055	0.163	0.029	0.122	0.980	0.989
HYP	0.006	0.049	0.132	0.173	0.000	0.988	0.393
CLS	0.002	0.017	0.126	0.071	0.000	0.991	0.455
CER	0.002	0.014	0.153	0.062	0.000	0.993	0.996
HLA	0.002	0.013	0.142	0.047	0.000	0.996	0.926
VAL	0.001	0.019	0.073	0.010	0.001	0.997	0.745
NEO	0.001	0.014	0.073	0.010	0.000	0.999	0.962
BRY	0.001	0.008	0.110	0.027	0.000	1.000	0.701
LAU	0.000	0.004	0.055	0.006	0.000	1.000	1.000

Contrast: 13_20

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.321	0.292	1.102	7.092	1.528	0.370	1.000	
MIC	0.098	0.221	0.443	3.078	1.548	0.483	0.020	*
LPA	0.067	0.173	0.388	1.055	0.679	0.560	0.973	
PAD	0.065	0.134	0.481	0.447	1.780	0.635	0.006	**
CLP	0.053	0.116	0.456	0.317	1.437	0.696	0.009	**
SRG	0.039	0.139	0.278	1.031	0.344	0.741	0.641	
TRB	0.034	0.088	0.385	0.543	0.301	0.780	0.502	
DCT	0.030	0.069	0.433	0.238	0.989	0.814	0.001	***
CER	0.029	0.111	0.264	0.062	0.996	0.848	0.001	***
DPT	0.023	0.086	0.268	0.000	1.232	0.875	0.001	***
DIC	0.023	0.085	0.267	0.237	0.213	0.901	0.943	
CHL	0.017	0.048	0.358	0.029	0.583	0.921	0.225	
AMA	0.015	0.068	0.212	0.000	0.876	0.937	0.001	***
ASP	0.010	0.060	0.159	0.131	0.029	0.948	0.793	
NEO	0.007	0.036	0.207	0.010	0.370	0.957	0.002	**
GLA	0.007	0.054	0.132	0.043	0.019	0.965	0.883	
HLA	0.007	0.025	0.272	0.047	0.098	0.973	0.001	***
HYP	0.007	0.050	0.136	0.173	0.001	0.981	0.306	
VAL	0.006	0.032	0.173	0.010	0.333	0.987	0.003	**
CLS	0.004	0.023	0.183	0.071	0.159	0.992	0.038	*
BRY	0.003	0.018	0.168	0.027	0.130	0.996	0.004	**
VEN	0.003	0.023	0.123	0.000	0.212	0.999	0.019	*
LAU	0.001	0.012	0.083	0.006	0.004	1.000	1.000	

Contrast: 13_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.399	0.329	1.214	7.092	0.633	0.424	0.111	
LPA	0.145	0.218	0.667	1.055	2.017	0.578	0.001	***
MIC	0.070	0.202	0.349	3.078	0.000	0.653	0.506	
NRM	0.052	0.126	0.413	0.000	0.933	0.708	0.001	***
PAD	0.041	0.137	0.299	0.447	0.408	0.751	0.569	
SRG	0.027	0.123	0.222	1.031	0.005	0.780	0.846	
SPT	0.027	0.094	0.289	0.000	0.582	0.809	0.001	***
GLA	0.026	0.074	0.349	0.043	0.179	0.836	0.038	*
CLP	0.025	0.106	0.238	0.317	0.129	0.863	0.845	
DIC	0.020	0.078	0.257	0.237	0.038	0.885	0.909	
TRB	0.020	0.082	0.243	0.543	0.001	0.906	0.967	
AMA	0.018	0.072	0.248	0.000	0.401	0.925	0.012	*
DCT	0.013	0.055	0.246	0.238	0.000	0.939	0.450	
HYP	0.013	0.063	0.202	0.173	0.057	0.953	0.060	.
LAU	0.012	0.044	0.271	0.006	0.141	0.965	0.022	*
ASP	0.011	0.072	0.150	0.131	0.000	0.977	0.538	
DPT	0.006	0.045	0.122	0.000	0.045	0.983	0.465	
CHL	0.004	0.038	0.104	0.029	0.002	0.987	0.999	
VAL	0.003	0.029	0.093	0.010	0.004	0.990	0.196	
CER	0.002	0.016	0.155	0.062	0.000	0.992	0.914	
CLS	0.002	0.019	0.128	0.071	0.000	0.995	0.311	
HLA	0.002	0.016	0.141	0.047	0.000	0.997	0.596	
NEO	0.002	0.018	0.087	0.010	0.003	0.999	0.646	
BRY	0.001	0.009	0.110	0.027	0.000	1.000	0.368	
UDO	0.000	0.001	0.178	0.000	0.003	1.000	0.997	

Contrast: 9_17

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.316	0.264	1.195	3.736	3.721	0.406	0.999	
LPA	0.124	0.193	0.644	0.600	2.115	0.565	0.008	**
DIC	0.076	0.159	0.480	0.258	1.080	0.663	0.001	***
PAD	0.069	0.192	0.363	0.833	0.158	0.752	0.009	**
MIC	0.066	0.181	0.367	0.612	0.607	0.838	0.636	
TRB	0.060	0.136	0.440	0.071	1.202	0.914	0.003	**
ASP	0.025	0.095	0.258	0.095	0.229	0.946	0.035	*
GLA	0.011	0.053	0.206	0.000	0.243	0.960	0.462	
CLP	0.011	0.055	0.192	0.027	0.129	0.974	1.000	
CHL	0.008	0.055	0.144	0.000	0.122	0.984	0.925	
SRG	0.006	0.031	0.189	0.000	0.153	0.991	1.000	
NEO	0.006	0.036	0.161	0.095	0.000	0.999	0.086	.
DCT	0.001	0.013	0.080	0.000	0.021	1.000	1.000	

Signif. codes: 0 , \ddot{A} 0.001 , \ddot{A} 0.001 , \ddot{A} 0.01 , \ddot{A} 0.05 , \ddot{A} 0.1 , \ddot{A} 1

Contrast: 9_20

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.289	0.279	1.035	3.736	1.528	0.340	1.000	
PAD	0.113	0.221	0.513	0.833	1.780	0.474	0.001	***
LPA	0.087	0.184	0.472	0.600	0.679	0.576	0.424	
MIC	0.073	0.186	0.394	0.612	1.548	0.662	0.488	
CLP	0.051	0.110	0.466	0.027	1.437	0.723	0.068	.
DIC	0.035	0.118	0.298	0.258	0.213	0.764	0.309	
CER	0.032	0.122	0.259	0.000	0.996	0.801	0.001	***
DPT	0.026	0.095	0.274	0.000	1.232	0.832	0.001	***
TRB	0.026	0.065	0.399	0.071	0.301	0.862	0.814	
DCT	0.023	0.060	0.389	0.000	0.989	0.890	0.026	*
SRG	0.019	0.097	0.192	0.000	0.344	0.912	0.967	
CHL	0.017	0.043	0.390	0.000	0.583	0.932	0.340	
AMA	0.016	0.075	0.216	0.000	0.876	0.951	0.005	**
NEO	0.013	0.050	0.252	0.095	0.370	0.966	0.003	**
ASP	0.006	0.032	0.197	0.095	0.029	0.973	0.825	
HLA	0.006	0.024	0.252	0.000	0.098	0.980	0.051	.
VAL	0.005	0.027	0.172	0.000	0.333	0.986	0.084	.
GLA	0.003	0.035	0.096	0.000	0.019	0.990	0.918	
VEN	0.003	0.025	0.124	0.000	0.212	0.993	0.074	.
CLS	0.002	0.017	0.135	0.000	0.159	0.996	0.429	
BRY	0.002	0.016	0.144	0.000	0.130	0.999	0.127	
LAU	0.001	0.010	0.083	0.000	0.004	1.000	0.979	
HYP	0.000	0.003	0.077	0.000	0.001	1.000	1.000	

Contrast: 9_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.378	0.333	1.136	3.736	0.633	0.410	0.426	
LPA	0.172	0.224	0.767	0.600	2.017	0.596	0.001	***
PAD	0.103	0.258	0.398	0.833	0.408	0.707	0.003	**
NRM	0.062	0.138	0.449	0.000	0.933	0.774	0.001	***
MIC	0.037	0.132	0.276	0.612	0.000	0.814	0.939	
DIC	0.036	0.125	0.288	0.258	0.038	0.853	0.324	
SPT	0.032	0.103	0.305	0.000	0.582	0.887	0.001	***
GLA	0.024	0.054	0.442	0.000	0.179	0.912	0.096	.
AMA	0.021	0.079	0.265	0.000	0.401	0.935	0.013	*
CLP	0.015	0.085	0.175	0.027	0.129	0.951	0.974	
LAU	0.013	0.046	0.291	0.000	0.141	0.966	0.022	*
NEO	0.007	0.043	0.169	0.095	0.003	0.974	0.064	.
DPT	0.006	0.046	0.141	0.000	0.045	0.981	0.421	
ASP	0.006	0.036	0.167	0.095	0.000	0.987	0.775	
HYP	0.006	0.030	0.194	0.000	0.057	0.993	0.420	
TRB	0.004	0.028	0.158	0.071	0.001	0.998	1.000	
SRG	0.001	0.005	0.138	0.000	0.005	0.999	0.999	
VAL	0.001	0.004	0.138	0.000	0.004	1.000	0.702	
CHL	0.000	0.002	0.138	0.000	0.002	1.000	1.000	
UDO	0.000	0.001	0.191	0.000	0.003	1.000	0.797	

Contrast: 17_20

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.244	0.255	0.957	3.721	1.528	0.278	1.000	
LPA	0.115	0.205	0.560	2.115	0.679	0.409	0.006	**
MIC	0.076	0.204	0.373	0.607	1.548	0.496	0.375	
TRB	0.069	0.140	0.497	1.202	0.301	0.575	0.001	***
DIC	0.064	0.155	0.413	1.080	0.213	0.648	0.001	***
CLP	0.056	0.122	0.463	0.129	1.437	0.712	0.006	**
PAD	0.055	0.127	0.433	0.158	1.780	0.775	0.092	.
CER	0.029	0.117	0.251	0.000	0.996	0.809	0.001	***
DPT	0.024	0.090	0.272	0.000	1.232	0.837	0.001	***
DCT	0.023	0.060	0.384	0.021	0.989	0.863	0.008	**
SRG	0.023	0.098	0.231	0.153	0.344	0.889	0.969	
CHL	0.022	0.066	0.340	0.122	0.583	0.914	0.048	*
ASP	0.021	0.098	0.210	0.229	0.029	0.938	0.076	.
AMA	0.015	0.072	0.214	0.000	0.876	0.955	0.001	***
GLA	0.013	0.065	0.206	0.243	0.019	0.971	0.281	
NEO	0.007	0.034	0.198	0.000	0.370	0.978	0.020	*
HLA	0.006	0.023	0.240	0.000	0.098	0.985	0.035	*
VAL	0.004	0.026	0.169	0.001	0.333	0.990	0.040	*
VEN	0.003	0.024	0.124	0.000	0.212	0.993	0.002	**
BRY	0.003	0.022	0.118	0.000	0.130	0.996	0.050	*
CLS	0.002	0.017	0.135	0.000	0.159	0.999	0.435	
LAU	0.001	0.013	0.069	0.000	0.004	1.000	0.994	

Contrast: 17_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.289	0.290	0.997	3.721	0.633	0.310	1.000	
LPA	0.203	0.239	0.849	2.115	2.017	0.528	0.001	***
DIC	0.070	0.170	0.414	1.080	0.038	0.604	0.002	**
TRB	0.063	0.153	0.414	1.202	0.001	0.672	0.008	**
NRM	0.057	0.134	0.427	0.000	0.933	0.733	0.001	***
MIC	0.044	0.175	0.250	0.607	0.000	0.780	0.909	
GLA	0.036	0.086	0.417	0.243	0.179	0.819	0.003	**
SPT	0.030	0.101	0.299	0.000	0.582	0.851	0.001	***
CLP	0.028	0.116	0.244	0.129	0.129	0.882	0.722	
ASP	0.025	0.116	0.212	0.229	0.000	0.908	0.063	.
PAD	0.022	0.113	0.196	0.158	0.408	0.932	0.977	
AMA	0.019	0.076	0.256	0.000	0.401	0.953	0.007	**
LAU	0.014	0.052	0.267	0.000	0.141	0.968	0.009	**
CHL	0.009	0.062	0.147	0.122	0.002	0.978	0.823	
SRG	0.007	0.034	0.203	0.153	0.005	0.985	0.999	
DPT	0.006	0.050	0.125	0.000	0.045	0.992	0.466	
HYP	0.006	0.031	0.182	0.000	0.057	0.998	0.449	
DCT	0.001	0.014	0.079	0.021	0.000	0.999	1.000	
VAL	0.001	0.005	0.125	0.001	0.004	1.000	0.790	
NEO	0.000	0.001	0.232	0.000	0.003	1.000	0.929	
UDO	0.000	0.001	0.183	0.000	0.003	1.000	0.899	

Contrast: 20_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.184	0.251	0.733	1.528	0.633	0.195	1.000	
LPA	0.177	0.252	0.701	0.679	2.017	0.382	0.001	***
PAD	0.077	0.180	0.426	1.780	0.408	0.463	0.009	**
CLP	0.068	0.156	0.433	1.437	0.129	0.534	0.007	**
NRM	0.059	0.140	0.419	0.000	0.933	0.596	0.001	***
MIC	0.048	0.167	0.291	1.548	0.000	0.647	0.868	
AMA	0.036	0.107	0.333	0.876	0.401	0.685	0.001	***
CER	0.034	0.135	0.253	0.996	0.000	0.721	0.002	**
DPT	0.033	0.112	0.300	1.232	0.045	0.757	0.001	***
GLA	0.032	0.090	0.354	0.019	0.179	0.790	0.021	*
SPT	0.031	0.102	0.298	0.000	0.582	0.823	0.001	***
TRB	0.029	0.084	0.343	0.301	0.001	0.853	0.681	
DCT	0.026	0.066	0.388	0.989	0.000	0.880	0.023	*
SRG	0.023	0.115	0.203	0.344	0.005	0.905	0.891	
CHL	0.018	0.048	0.385	0.583	0.002	0.924	0.249	
DIC	0.018	0.081	0.227	0.213	0.038	0.944	0.890	
LAU	0.016	0.055	0.286	0.004	0.141	0.960	0.003	**
NEO	0.008	0.036	0.210	0.370	0.003	0.968	0.072	.
HLA	0.007	0.028	0.245	0.098	0.000	0.976	0.040	*
HYP	0.007	0.035	0.192	0.001	0.057	0.983	0.318	
VAL	0.005	0.028	0.196	0.333	0.004	0.989	0.066	.
BRY	0.004	0.032	0.114	0.130	0.000	0.992	0.035	*
VEN	0.003	0.026	0.124	0.212	0.000	0.996	0.057	.
CLS	0.002	0.017	0.135	0.159	0.000	0.998	0.370	
ASP	0.001	0.009	0.167	0.029	0.000	1.000	0.976	
UDO	0.000	0.001	0.177	0.000	0.003	1.000	0.851	

1286 **Supplementary Table 7. PERMANOVA results.**1287 Variables significant at $\alpha = 0.05$ are bolded and those significant at $\alpha =$ are italicized.

All sites.					
	Sum of Squares	R ²	Pseudo-F	p-value	
Model	29.08	0.10	2.62		< 0.01
Residual	266.23	0.90			
Total	295.30	1.00			
Variables					
Month (ranked by SST)	9.26	0.03	2.16		< 0.01
Storms within 5 years (Type 3+)	0.79	0.00	2.21		0.02
MaxDHW	0.99	0.00	2.79		< 0.01
Cumulative human impacts	1.72	0.01	4.81		< 0.01
Habitat	5.52	0.02	5.14		< 0.01
Nutrients (agriculture)	0.37	0.00	1.02		0.42
Mean wave energy	0.72	0.00	1.99		0.03
NPP _{SD}	0.43	0.00	1.19		0.28
Reef area (200km)	1.46	0.00	4.06		< 0.01
Management	3.27	0.01	4.56		< 0.01
NDVI	0.90	0.00	2.51		< 0.01
Mean PAR (survey month)	0.79	0.00	2.22		0.02
Aspect	0.23	0.00	0.65		0.81
Ch _a (kurtosis)	0.67	0.00	1.87		0.05
Residual	424.38	0.96			
Total	443.18	1.00			

b. Mid-tropical North Pacific

Formula = percent ~ Storms within 5 years (Type 3+) + nutrients (agriculture)

	Sum of Squares	R ²	Pseudo-F	p-value
Model	9.97	0.05	1.63	0.08
Residual	19.30	0.94		
Total	19.27	1.00		
Variables				
Population (20 km)	0.38	0.02	3.94	< 0.01
Depth	0.59	0.01	2.21	0.03
Residual	18.30	0.94		
Total	19.27	1.00		

1288

Indo-Pacific seas & Indian Ocean

Formula = percent ~ Chl_a (kurt) + reef area (200 km) + depth + NDVI + mean SST (survey month) + reef area (15 km) + mean wave energy

	Sum of Squares	R ²	Pseudo-F	p-value
Model	23.54	0.18	7.60	< 0.01
Residual	110.02	0.82		
Total	133.56	1.00		
Variables				
Reef area (200 km)	1.56	0.01	5.55	< 0.01
Mean wave energy	1.14	0.01	4.06	< 0.01
Depth	2.89	0.02	10.27	< 0.01
Mean SST (survey month)	1.29	0.01	4.59	< 0.01
Chl _a (kurtosis)	1.26	0.01	4.49	< 0.01
Reef area (15 km)	4.58	0.03	16.27	0.04
Mean PAR (survey month)	1.94	0.01	6.88	
Cumulative Human Impact	4.92	0.04	17.50	
Aspect	0.66	0.01	2.35	0.02
Residual	110.02	0.82		
Total	133.56	1.00		

Coral Sea.				
<i>Formula = percent ~ nutrients (agriculture) + NDVI + chl_a (kurtosis) + mean wave energy + storms within 5 years (type 3+) + NPP_{SD}</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	16.28	0.21	9.88	< 0.01
Residual	60.13	0.79		
Total	76.41	1.00		
Variables				
Nutrients (agriculture)	4.58	0.06	16.66	< 0.01
NDVI	3.05	0.04	11.12	< 0.01
Chl_a (kurtosis)	1.26	0.02	4.59	< 0.01
Mean wave energy	2.97	0.04	10.81	< 0.01
Storms within 5 years (Type 3+)	0.92	0.01	3.36	< 0.01
NPP_{SD}	3.50	0.05	12.76	< 0.01
Residual	60.13	0.79		
Total	76.41	1.00		

Mid South Tropical Pacific					
<i>Formula = percent ~ management + aspect + depth + NDVI + mean PAR (survey month)</i>					
	Sum of Squares	R ²	Pseudo-F	p-value	
Model	10.76	0.18	5.80	< 0.01	
Residual	48.26	0.82			
Total	59.02	1.00			
Variables					
Management	5.00	0.08	8.08	< 0.01	
Aspect	0.17	0.02	0.54	0.83	
Depth	2.57	0.04	8.29	< 0.01	
NDVI	0.89	0.02	2.87	< 0.01	
Mean PAR (survey month)	2.14	0.04	6.91	< 0.01	
Residual	48.26	0.82			
Total	59.02	1.00			

1290

Offshore West Pacific					
<i>Formula = percent ~ NDVI + WWE + aspect + mean wave energy</i>					
	Sum of Squares	R ²	Pseudo-F	p-value	
Model	3.28	0.07	1.99	< 0.01	
Residual	46.62	0.93			
Total	49.90	1.00			
Variables					
NDVI	1.31	0.03	3.16	< 0.01	
WWE	0.49	0.01	1.19	0.26	
Aspect	0.42	0.01	1.01	0.42	
Mean wave energy	1.06	0.02	2.58	< 0.01	
Residual	46.62	0.93			
Total	49.90	1.00			

1291

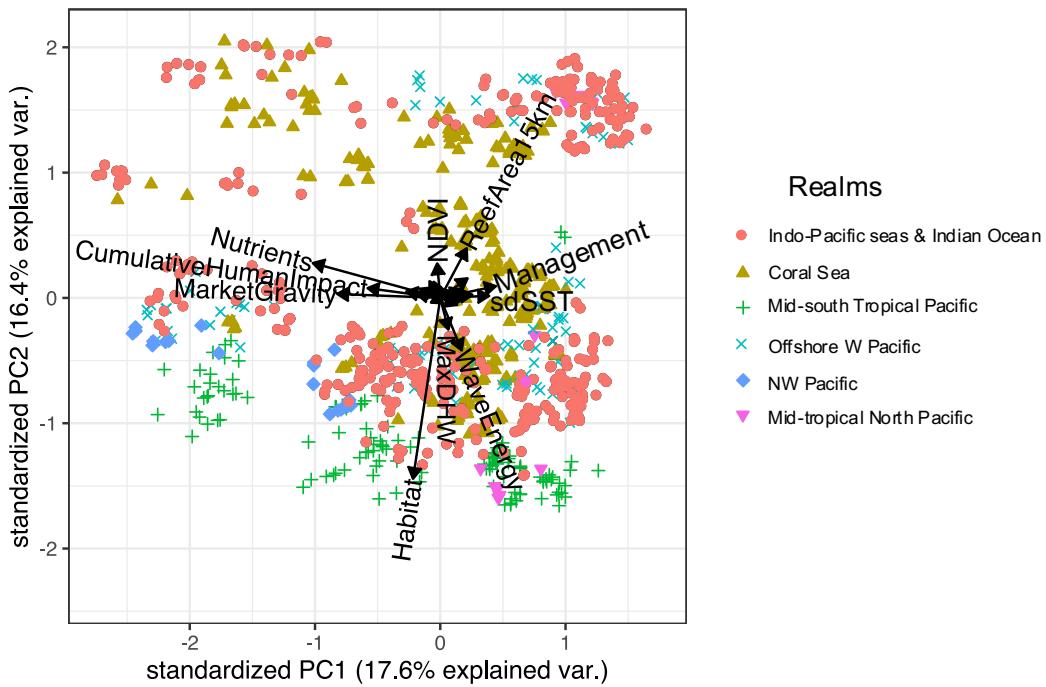
NW Pacific					
<i>Formula = percent ~ chl_a (kurtosis) + nutrients + management + WWE</i>					
	Sum of Squares	R ²	Pseudo-F	p-value	
Model	0.54	0.02	1.36	< 0.01	
Residual	19.74	0.84			
Total	23.57	1.00			
Variables					
Chl _a (kurtosis)	0.54	0.02	1.36	0.12	
Nutrients (agriculture)	0.85	0.04	2.16	< 0.01	
Management	2.09	0.09	2.65	< 0.01	
WWE	0.35	0.01	0.88	0.62	
Residual	19.74	0.86			
Total	23.57	1.00			

1293 **SuppMaterials 8. Principle Component Analysis of environmental variables as**
1294 **(a) a biplot and (b) scree plot.**

1295

1296 **a. Biplot of Principal Component Analysis.**

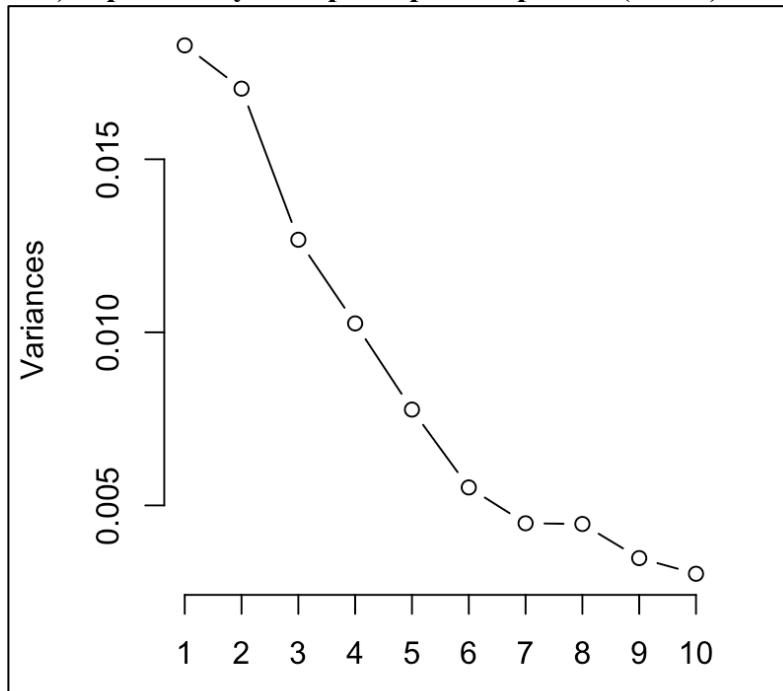
1297



1298

1299

1300 **b. Scree plot of Principal Component Analysis, showing the amount of variation (y-**
1301 **axis) explained by each principal component (x-axis).**



1302

1303
1304
1305
1306
1307

Supplementary Table 9. Full results for the Zero-Inflated Generalized Linear Mixed Effects Models. For ease of interpretation, we multiplied the estimates for NDVI by -1 because the variables have inverse relationships with disturbance. In the table below, positive values indicate that macroalgae percent cover increases as disturbance increases, and negative values indicate that the percent cover decreases as disturbance increases.

Genus / Category	R ²		Cumulative Human Impacts		Log (Population 20km)		Market Gravity		NDVI		Nutrients	
	Marg	Cond	Est	p	Est	p	Est	p	Est	p	Est	p
All Macroalgae	0.01	0.13	0.96	0.85	0.09	<0.01	1.59	<0.01	1.57	<0.01	0.51	<0.01
All Brown Macroalgae	0.07	0.10	1.91	0.14	0.05	<0.01	0.92	0.74	2.14	<0.01	0.30	<0.01
<i>Dictyota</i>	0.13	NA	2.21	0.79	0.05	0.54	1.07	0.97	1.76	0.66	0.17	0.27
<i>Dictyopteris</i>	0.84	NA	2.72	0.93	2.67	0.97	7.13	0.76	3.29	0.43	0.29	0.84
<i>Lobophora</i>	0.06	NA	11.60	0.38	0.01	0.51	0.43	0.62	2.02	0.55	0.28	0.41
<i>Padina</i>	0.17	0.34	1.43	0.93	0.00	<0.01	5.65	0.46	6.29	0.31	0.13	0.34
<i>Spatoglossum</i>	0.99	NA	4.95	0.94	0.03	0.87	0.00	0.71	15.86	0.86	1.78	0.95
<i>Sargassum</i>	0.35	NA	0.08	0.62	0.00	<0.01	1.10	0.98	7.88	0.55	4.78	0.56
<i>Turbinaria</i>	0.19	0.93	0.21	0.62	0.00	0.54	1.67	0.79	0.57	0.71	0.63	0.79
All Green Macroalgae	0.06	NA	1.24	0.03	0.27	<0.01	1.31	0.07	1.98	<0.01	0.57	<0.01
<i>Bryopsis</i>	0.94	1.00	0.29	1.00	0.26	1.00	0.00	0.05	1.27	1.00	0.12	0.00
<i>Chlorodesmis</i>	0.24	0.91	0.31	0.60	0.03	0.99	0.12	0.50	0.36	0.64	0.09	0.38
<i>Caulerpa</i>	0.03	NA	4.53	0.64	0.38	0.87	3.82	0.50	1.98	0.59	0.13	0.25
<i>Cladophoropsis</i>	0.07	1.00	0.15	0.11	0.00	0.99	0.11	0.64	0.36	0.47	0.42	0.91
<i>Dictosphaeria</i>	0.22	NA	0.69	0.92	0.19	0.87	1.91	0.81	3.33	0.49	3.63	0.64
<i>Halimeda</i>	0.01	NA	10.11	<0.01	1.54	0.83	0.22	<0.01	0.90	0.76	0.29	<0.01
<i>Microdictyon</i>	0.95	NA	1.21	0.29	0.84	0.82	0.19	0.54	5.47	0.28	0.87	0.96
<i>Neomeris</i>	0.11	NA	17.66	0.77	5.94	0.90	0.24	0.79	2.66	0.80	0.06	0.57
<i>Udotea</i>	0.94	1.00	0.08	0.72	0.04	0.42	1.72	0.91	0.62	0.89	0.58	0.89
All Red Macroalgae	0	--	--	--	--	--	--	--	--	--	--	--
<i>Amansia</i>	0.93	NA	2.94	0.94	5.07	0.91	0.19	0.85	16.39	0.76	0.04	0.69
<i>Asparagopsis</i>	0.53	0.73	1.29	0.96	Inf	0.78	0.56	0.87	12.54	0.41	0.50	0.82
<i>Ceratodictyon</i>	0.88	0.95	31.89	0.81	0.00	0.41	0.35	0.90	3.84	0.83	0.06	0.72
<i>Galaxaura</i>	0.42	NA	0.21	0.76	7.32	0.88	0.26	0.68	0.57	0.83	1.20	0.95
<i>Halymenia</i>	0.27	0.58	0.10	0.84	0.00	0.01	33.76	0.53	0.08	0.57	0.00	0.43
<i>Hypnea</i>	0.71	NA	0.00	0.12	0.00	<0.01	1.29	0.97	Inf	0.08	8.26	0.53
<i>Laurencia</i>	0.69	0.99	0.33	0.85	84.81	0.83	0.92	0.98	18.89	0.42	0.65	0.88
<i>Neurymenia</i>	1.00	1.00	952.82	0.78	Inf	0.71	0.00	0.60	0.36	0.89	0.02	0.66

1308

Supplementary Materials 10. Estimated parameters for GLMM models. P-values computed using a Wald z-distribution approximation. Values significant at a $\alpha = 0.05$ are in bold, while those significant at α are in italics.

Taxa	NDVI			Log(Population)			Market Gravity			Cumulative Human Impacts			Nutrients from agriculture		
	Est	z	p	Est	z	p	Est	z	p	Est	z	p	Est	z	P
All Macroalgae	0.15	2.13	0.03	0.71	2.42	0.02	-0.09	-0.85	0.40	0.02	0.11	0.91	-0.34	-3.33	<0.01
All Brown Macroalgae	-0.31	-2.74	<0.01	0.74	2.14	0.03	-0.36	-2.07	0.04	1.55	4.86	<0.01	-0.98	-6.15	<0.01
<i>Dictyota</i>	-0.29	-1.22	0.22	0.41	0.49	0.63	-0.72	-2.22	0.03	2.33	3.77	<0.01	-0.85	-2.73	<0.01
<i>Dictyopteris</i>	4.17	1.90	0.06	-0.20	-0.04	0.97	-6.21	-2.35	0.02	8.37	2.42	0.02	-1.48	-1.34	0.18
<i>Lobophora</i>	-0.21	-1.12	0.26	0.40	0.50	0.62	-0.55	-1.70	0.09	1.22	2.06	0.04	-1.05	-3.60	<0.01
<i>Padina</i>	-0.21	-0.69	0.49	1.06	1.57	0.12	0.10	0.24	0.81	2.05	2.86	<0.01	-1.67	-4.18	<0.01
<i>Spatoglossum</i>	-18.42	-1.29	0.20	22.17	0.57	0.57	29.59	1.80	0.07	14.77	1.80	0.07	-6.56	-1.88	0.06
<i>Sargassum</i>	-1.57	-3.15	<0.01	0.53	0.72	0.47	-0.19	-0.37	0.71	1.67	1.64	0.10	-1.59	-3.60	<0.01
<i>Turbinaria</i>	0.37	0.89	0.37	-1.35	-1.20	0.23	2.12	3.00	<0.01	-0.44	0.35	0.73	-0.02	-0.03	0.98
All Green Macroalgae	0.36	4.10	<0.01	1.11	2.72	<0.01	-0.15	-1.22	0.22	-0.54	-2.42	0.02	-0.05	-0.40	0.70
<i>Bryopsis</i>	1.30	0.83	0.41	-2.19	-2.99	<0.01	3.61	1.61	0.11	-5.31	-4.21	<0.01	4.91	7.14	<0.01
<i>Chlorodesmis</i>	0.00	0.01	0.99	-12.05	-0.67	0.50	0.39	0.41	0.68	-1.26	-0.75	0.45	1.32	1.83	0.07
<i>Caulerpa</i>	0.44	1.81	0.07	1.02	0.94	0.35	0.18	0.40	0.69	-0.69	-0.99	0.32	0.34	0.47	0.48
<i>Cladophoropsis</i>	0.52	0.18	0.86	-11.47	-3.53	<0.01	2.23	0.68	0.50	-5.27	-0.97	0.33	-2.30	-0.62	0.54
<i>Dictyosphaeria</i>	0.35	1.19	0.24	0.70	0.29	0.77	-1.18	-3.68	<0.01	0.82	1.21	0.23	1.52	3.11	<0.01
<i>Halimeda</i>	-0.11	-0.30	0.76	-0.35	0.21	0.83	-1.50	-2.85	<0.01	2.31	2.60	<0.01	-1.23	-2.60	<0.01
<i>Microdictyon</i>	0.12	0.33	0.74	-71.56	-1.27	0.21	-1.41	-2.36	0.02	1.86	1.05	0.30	-0.73	-1.02	0.31
<i>Neomeris</i>	-0.33	-0.32	0.75	2.46	0.34	0.73	-0.03	-0.03	0.97	-2.20	-1.28	0.20	0.66	0.79	0.43
<i>Udotea</i>	2.51	3.71	<0.01	-58.79	-58.00	<0.01	-4.26	-6.30	<0.01	1.93	0.87	0.38	0.18	0.11	0.92
All Red Macroalgae	-0.11	-0.63	0.53	1.77	4.76	<0.01	-0.37	-1.70	0.09	0.35	1.01	0.31	-0.33	-1.70	0.09
<i>Amansia</i>	-7.52	-1.39	0.16	-11.65	-1.05	0.29	-1.00	-0.27	0.90	-1.43	-0.12	0.90	3.86	0.48	0.63
<i>Asparagopsis</i>	-2.05	-2.25	0.03	-11.51	-0.56	0.58	1.15	1.63	0.11	-0.16	-0.12	0.90	-0.42	-0.68	0.50
<i>Ceratodictyon</i>	-3.79	-1.55	0.12	1.25	0.91	0.37	-4.20	-2.49	<0.01	1.66	0.66	0.51	0.08	0.06	0.96
<i>Galaxaura</i>	1.41	2.83	<0.01	-0.52	-0.16	0.87	1.85	1.82	0.07	-4.43	-2.24	0.03	1.53	2.00	0.05
<i>Halymenia</i>	0.45	0.43	0.67	1.47	1.10	0.27	-0.64	0.33	0.74	-0.30	-0.18	0.86	1.64	1.06	0.29
<i>Hypnea</i>	-3.07	2.52	0.01	2.59	3.43	<0.01	-1.80	-2.27	0.02	5.14	2.86	0.01	-2.36	-3.70	<0.01
<i>Laurencia</i>	0.10	0.14	0.89	-14.49	-3.04	<0.01	-2.99	-2.60	0.01	-1.63	-0.74	0.46	1.18	1.45	0.15