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36	
3/	ABSIKAUI
20 20	Aim
39 40	
41	Marine reef habitats are typically defined subjectively. We provide the first continental-scale
42	assessment of dominant reef habitats through analysis of macroalgae and sessile animal taxa at 1299
43	sites distributed around Australia. Relationships between reef habitats and environmental and
44	anthropogenic factors are assessed, and potential changes in the future distribution and persistence of
45	habitats are considered.
46	
47	Location
48	
49	Shallow rocky and coral reefs around the Australian coast and offshore islands and shoals.
50	
51	Methods
52	
53	Cover of 38 sessile plant and animal functional groups was recorded in diver-based surveys using
54	quadrats at 906 Reef Life Survey and 393 Long-term Marine Protected Area monitoring sites.
55	Classification analyses based on the functional groups were used to identify an unambiguous set of
56	'biogenic habitat types'. Random forest and distance-based linear modelling were used to investigate
57	correlations between these habitats and environmental and anthropogenic variables.
58	
59	
60	Results
61	
62	Cluster analyses revealed distinct tropical and temperate 'realms' in benthic substratum composition,
63	each with finer scale habitats: four for the temperate realm (Canopy Algae, Barren, Epiphytic Algae-
64 65	Calcified Algae Corel and Foliose Algae). Habitate correlated with different sets of environmental and
66	calchieu Algae-Colai and Follose Algae). Habitais collelated with different sets of environmental and
67	antiropogenie conditions.
68	
69	Main conclusions
70	
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#### **PRE-REVIEW**

71 Quantitative delineation of inshore reef habitats at a continental scale identifies many of the same 72 habitat types traditionally recognized through subjective methods. Importantly, many biogenic reef 73 habitats were closely related to environmental parameters and anthropogenic stressors that are 74 predicted to change. Consequently, habitats have differing likelihood of persistence. Structurally 75 complex habitats in the temperate realm are at higher risk than more 'two-dimensional' habitats with lower biodiversity (e.g. canopy forming macroalgae versus turfing algae). In the tropical realm, 76 77 offshore and coastal habitats differed greatly in benthic composition, highlighting the importance of 78 large-scale oceanic conditions in shaping biogenic structure.

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# 81 INTRODUCTION

82

83 Shallow marine reefs house a multifarious array of habitats, supporting diverse ecologically- and 84 economically-important marine communities (Cracknell, 1999; Spalding et al., 2007). Quantitative 85 descriptions of biogenic habitat types within these reef systems have been limited, with most 86 classifications largely subjective or relying on easily measured environmental surrogates. In part for 87 this reason, the impacts of changing climate, shifting oceanic boundaries, and other stressors on 88 benthic habitats are not well defined (Commonwealth of Australia, 2006; Post, 2008). Providing 89 quantitative descriptions is useful because it provides a basis to detect change and allow management 90 to better target conservation of vulnerable habitats and associated communities. Better quantification 91 of both the habitats themselves and the environmental factors that correlate with patterns in habitat 92 distribution are required to make informed hypotheses about the future of reef communities, thereby 93 facilitating improved management.

94

95 A recurrent methodological issue when dealing with threats to ecosystems has been the scaling of 96 response and driver variables; for example, should observations be made of species, taxonomic 97 groups, or habitats? Research at the habitat level has been limited, with the focus of investigations to 98 date favoring individual species (Roff & Evans, 2002; McArthur et al., 2010; Mellin et al., 2011). 99 Regardless, opinions on how best to approach marine environmental management and conservation, 100 whilst remaining somewhat controversial, are changing, expanding from species-specific approaches 101 to include biodiversity and macroecology, and to embrace ecosystem-based approaches (Douvere, 102 2008; Costello et al., 2010).

103

Ecosystem approaches to management and conservation acknowledge the critical importance of
 habitat in supporting naturally functioning biotic communities. This approach also recognises a need

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to protect representative biodiversity – the ordinary as well as the rare or charismatic – because
'common' species or habitats uphold some of the most important ecological functions. To achieve
this, the identification of distinct habitat types, and recognition of their distribution and associated
environmental controls over local to global scales, are key requirements (Ray & McCormick-Ray,
1992; Halpern *et al.*, 2008; McArthur *et al.*, 2010).

111

112 To the present, knowledge of biological habitat elements of marine benthic communities has been 113 limited at macroecological scales by a near absence of detailed datasets that include both biotic and 114 environmental components obtained using standardised methods over large scales. Additionally, 115 spatially complex or gradational habitat assemblages make boundaries more difficult (or impossible) to quantify without fine-scale data (McArthur et al., 2010). Thus, studies and conclusions in ecology 116 have mostly been based on small-scale manipulative experiments  $(10^{0}-10^{3} \text{ m})$  that rarely offer 117 generality over large scales (Lawton, 1996; Underwood et al., 2000). This is particularly the case for 118 119 benthic marine systems, where collecting data over large spatial scales at a fine resolution is 120 logistically challenging.

121

122 Improvements in technology and increased capacity through the broader engagement of 'citizen 123 scientists' in data collection means there is now much better access to marine benthic data, providing 124 the opportunity for accelerated evolution of biogeographic classification and mapping (Diaz et al., 125 2004). Here we take advantage of a citizen science initiative which has allowed for fine resolution 126 data to be collected on macro-ecological scales. In the third largest Exclusive Economic Zone, the 127 shallow reefs off Australia's coasts extend from the tropics to the cool temperate and encompass some 128 of the richest marine ecosystems on the planet (Williams et al., 2009; Huang et al., 2012), thereby 129 providing an ideal study context for investigating factors contributing to the development and 130 persistence of habitat types.

131

We aim to provide the first continental-scale classification of habitat types on shallow coral and rocky reefs through analysis of two large-scale datasets of systematically-collected data on the percentage cover of benthic sessile plant and animal functional groups at ~1300 shallow reef sites surrounding Australia. Furthermore, relationships between habitat types and environmental and anthropogenic factors are assessed, as this knowledge is key to understanding the prevalence of one habitat over

137	http://onlinelibrary.wiley.com/doi/10.1111/geb.12620/fullPRE-REVIEWanother and to form hypotheses about likely habitat transformation associated with changing climate						
138	and increasing anthropogenic stressors.						
139							
140	We provide a quantitative approach to habitat classification in combination with random forest and						
141	distance-based linear models to investigate relationships between the distribution of biogenic reef						
142	habitats and key environmental variables in a novel approach to a field previously approached using						
143	environmental surrogates or subjective descriptions.						
144							
145							
146	METHODS						
147							
148	Study location						
149							
150	The study region encompasses shallow (<20 m) marine reefs surrounding the Australian continent and						
151	associated offshore islands and shoals. Data were drawn from two standardized quantitative surveys						
152	of reef communities that have been, and continue to be, generated in temperate Australia by the Long-						
153	term Marine Protected Area (LTMPA) monitoring program (Barrett et al., 2009) and globally by the						
154	Reef Life Survey Program (RLS; www.reeflifesurvey.com).						
155							
156	The LTMPA data used in this study encompass 857 surveys at 393 sites distributed across a 4,000 km						
157	span of temperate Australian coasts from Jervis Bay (NSW) to Jurien Bay (WA), including Tasmania						
158	(Fig. 1). A subset of 1679 surveys at 906 sites encircling Australia was selected from the global RLS						
159	dataset.						
160							
161	Survey methods and data amalgamation						
162							
163	Both the RLS and LTMPA surveys targeted sites characterised by hard substrata (i.e. rocky or coral						
164	reef) in depths <20 m. The LTMPA surveys quantified macroalgae and sessile invertebrate species in						
165	20 equidistant 0.5 x 0.5 m quadrats along a 200 m transect line. Each quadrat was divided into a 7 x 7						
166	grid giving 50 points (including one corner), under each of which the identity of the species present						
167	was recorded, to the lowest possible taxonomic level, usually to species or genus. The cover of over-						
168	story/canopy species was recorded first, and then these were moved aside to expose the understory for						
169	examination, meaning that greater than 100% cover was possible (Barrett et al., 2007; Barrett et al.,						
170	2009).						
171							
	https://www.pospmaring.adu.au/document/translating.local heathic community structure						

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172 The RLS surveys collect twenty digital photoquadrats (PQs), each covering ~ 0.3 x 0.3 m along a 50 m transect line (see http://reeflifesurvey.com/files/2008/09/rils-reef-monitoring-procedures.pdf). 173 174 Further details on the survey methods, including diver training, data quality assurance and control, and 175 data management are covered by Edgar and Stuart-Smith (2009); Stuart-Smith et al. (2013); Edgar 176 and Stuart-Smith (2014). Photoquadrats were analysed using a five point grid superimposed as a 177 quincunx over each image, under which the uppermost layer of substratum biota was scored to give an 178 estimate of percentage cover of 38 a priori defined substratum functional groups. These groups are 179 listed in Appendix S1 in Supporting Information, and are aligned with the standardized CATAMI 180 categories used throughout Australia, as described by Althaus et al. (2015). 181 182 In order to combine the RLS PQ data with the higher resolution in situ LTMPA quadrat data, taxa

from the *in situ* quadrats were mapped to the RLS substratum biota categories. The percentage cover was then adjusted to account for scoring of over- and understory cover in LTMPA quadrats and only over-story in RLS photoquadrats. This was done by an ordered prioritisation of the 50 points for canopy-formers and then understory. Permutational analysis of variance of data from sites at which both RLS and LTMPA surveys had been conducted confirmed that data from the two survey types were comparable (P=0.067; see Appendix S2).

189

Surveys from either dataset that included patchy areas of non-reef habitat were either standardized by removing the cover of soft sediment (if <50% sand/silt/seagrass) or excluded (if >50% sand/ seagrass). Both datasets were restricted to surveys conducted since 2006 to reduce the influence of potential long-term trends. Temporal variation over the survey time period was assumed to be insignificant compared with the continental-scale spatial variation of interest in the present study.

195

# 196 Classification of Biogenic Reef Habitats

197

198 Initially sites within 1° x 1° lat-long grid cells were grouped and the mean cover of substratum biota 199 was considered at sites within these cells to minimize the effect of local scale variation on continental 200 scale pattern. Hierarchical cluster analysis was used to group cells that were most similar to each 201 other. Initial clustering (Appendix S3) revealed a clear dichotomy between tropical and temperate 202 reefs. Tropical and temperate 'realms' were demarcated by considering the geography of the two 203 dominant large groups in the primary analysis with small and outlying groups merged with the larger 204 groups according to latitudinal proximity. PCO confirmed the clear separation of the two dominating 205 tropical/temperate clusters, with 60.6% of the total variation captured (Appendix S3). Subsequent 206 analyses were conducted separately for these two realms at a site resolution.

- 207 208 For the tropical analysis, macroalgal categories were binned due to low cover of macroalgae, whereas 209 in the temperate realm, macroalgae dominated the patterns of diversity and abundance, so individual 210 macroalgal categories were maintained. Stony corals were grouped together (Appendix S1). 211 212 The similarity profiles (Appendix S4) of the hierarchical cluster analyses of the tropical and temperate 213 realms were examined to delineate the dominating clusters based on a percentage similarity cut-off 214 that was chosen subjectively to yield a workable number of clusters at a point where small changes in 215 the cut-off point did not drastically change the number of clusters. The temperate dendrogram was 216 split at a similarity of 35% while the tropical dendrogram was split at a similarity of 48%. Clusters 217 with less than seven sites were examined individually and allocated to whichever of the larger clusters 218 groups had greatest centroid similarity. The resulting clusters of sites were deemed to be distinct 219 'Biogenic Reef Habitats' (BRHs) of Australia's shallow reef environment. 220 221 PCO was used to visualize the separation of the BRHs and confirm that the resulting groups aligned in 222 ordination space. Vector overlays were then used to explore which of the ordinal functional groups 223 were increasing or decreasing across the PCO diagram. The overlay was restricted to include only 224 variables with a spearman correlation >0.4 (Daniel, 1990). 225
  - All clustering and coordinate analyses were conducted in PRIMERv6 based on Bray-Curtis (Clarke &
    Warwick, 2001) matrices of square-root transformed data using a group average sorting strategy (Clarke
    & Gorley, 2006).
  - 229

# 230 Environmental and anthropogenic covariates

231

Nine physical, chemical and anthropogenic variables were used to better understand spatial
relationships between prevalence and distribution of the BRHs (Appendix S5). Physical and chemical
environmental data were sourced from CSIRO and Geoscience Australia (see Huang, 2011). Some
potential variables were not considered due to known inaccuracy near the coast or inadequate
resolution. Each site was assigned the environmental characteristics of the closest node on a 0.5
degree lat-long grid.

238

239 The variables considered for analyses included mean and standard deviation of sea surface

temperature, known to play important roles in structuring marine benthic communities (McArthur et

241 *al.*, 2010), spatial predictors of distance to coast and distance into estuaries, and physical and chemical

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variables: wave exposure, cyclone stress, average site depth, nitrate and phosphate. The estuarine 242 index was only relevant for temperate sites, of which ~19% were >5km within an estuary. Nitrate and 243 phosphate were both initially considered as proxies for nutrient levels but were found to be highly 244 245 correlated (r>0.65), so only mean nitrate was used in models. A wave exposure index was calculated 246 from wave height and period available from the AusWAM 11-year hindcast model (WAMDI Group, 247 1988) for the temperate sites. These data were not available for tropical sites. For the tropics, a 248 variable describing cyclone stress was calculated as the maximum wind speed of any cyclone 249 occurring within 150 km of each site in the prior decade, using data from the NOAA IBTrACTS data 250 set (https://www.ncdc.noaa.gov/ibtracs/).

251

Anthropogenic variables were also included to allow the impacts of human stressors to be considered
relative to environmental variables. A variable describing human population from the Gridded
Population of the World, Version 4 (GPWv4) population density (2010) was included as an index,
equating to an estimate of people per area (CIESIN, 2014). The marine protected status of each site
was also scored as 'no take', 'restrictions on fishing gear type', or 'no restrictions on fishing'.

257

# 258 Covariate analysis

259

Distance-based linear modelling (DISTLM) (Anderson et al., 2008) was used to examine the 260 261 performance of each environmental variable in explaining the variation in substratum cover between 262 different sites and between different BRHs. Draughtsman's plots of the individual covariates were used to detect extreme bivariate correlations ( $r \ge 0.65$ ) and to determine whether distributions were 263 264 skewed (a natural logarithm transformation was employed to correct skewness where necessary). 265 DISTLM was performed on separate Bray-Curtis similarity matrices for temperate and tropical realms 266 after data had been square root transformed. DISTLM was run using the PERMANOVA+ package in PRIMERv6 (Anderson et al., 2008), with 'Akaike Information Criterion' (AIC) and the stepwise 267 268 selection procedure with 9999 permutations. Distance-based redundancy analysis (dbRDA) was then 269 used to test how well the environmental and anthropogenic variables could represent the site data. 270 Vector overlays (r>0.4) were used to illustrate the importance and magnitude of each individual 271 physical variable in explaining variability in the data cloud.

272

273 Random forest (RF) models were then used to assess which environmental and anthropogenic

274 variables were most closely associated with each BRH. A RF approach deals with non-linear

relationships and interactions among predictors, as often occurs with environmental variables. 2500

trees were generated for each analysis. Variable importance plots were used to assess the importance

277	http://onlinelibrary.wiley.com/doi/10.1111/geb.12620/full PRE-REVIEW of each predictor variable in the temperate and tropical models and for each BRH in isolation. Partial
278	dependence plots (Cutler <i>et al.</i> , 2007) were used to provide graphical representation of the marginal
279	effect of the predictor variables on the probability of each BRH. All random forest modelling was
280	conducted using the <i>randomForest</i> function in the <i>randomForest</i> package (Liaw & Wiener, 2002) in
281	R (R Core Team, 2014).
282	
283	
284	
285	RESULTS
286	
287	Biogenic Reef Habitats
288	
289	The geographic distribution of clusters showed a strong biogeographic dichotomy between tropical
290	and temperate latitudes (Fig. 2). Hierarchical cluster analysis of sites within the temperate realm
291	yielded four large clusters (each >28 sites), while for the tropical realm five large clusters were
292	formed (each >33 sites) (Appendix S4). PCO showed some overlap of clusters but overall the four
293	temperate and five tropical clusters were distinguishable on ordination (Fig. 3). The first two PCO
294	axes for the temperate sites explained 47.2% of the total variation, while for the tropical sites it was
295	45.2%, indicating that the two-dimensional projections capture nearly half of the salient patterns in the
296	full data clouds. Clusters were each characterised by distinct combinations of the mean cover of
297	substratum groups and were named as separate 'Biogenic Reef Habitats (BRHs)' accordingly (Table
298	1).
299	
300	In the temperate realm the most widespread and prevalent BRH was Canopy Algae, occurring in all
301	regions surveyed (Fig. 4a). Sites in the Barren BRH were highly concentrated on the New South
302	Wales coast, together with a few sites on the Victorian and eastern Tasmanian coasts (Fig. 4b).
303	Epiphytic Algae/ Understory BRH occurred in a patchy range of locations in southern Australia and
304	Tasmania (Fig. 4c) while the Turf BRH occurred at six distinct locations on the Australian coast (Fig.
305	4d).
306	
307	Tropical BRHs showed a greater mosaic in geographic distribution compared to the temperate BRHs
308	(Fig. 4e-1). As well, the tropical BKHs were less clearly defined by particular substratum groups, with
309 210	an drns except the Ponose Algae BRH containing a mix of coral categories (Table 1).
210	

The 'Coral' BRH occurred in nearly all regions around tropical Australia, although it was 311 312 concentrated on the inshore Oueensland coast, inside the Great Barrier Reef. The 'Turf-Coral' BRH 313 occurred at most survey locations. 'Coral-Bacterial Mat' occurred in patchy distribution across the 314 tropical realm. The 'Calcified Algae-Coral' BRH occurred at the most sites and dominated the 315 offshore locations (the Coral Sea and the North West Shelf). 'Foliose Algae' was confined to the 316 southern part of the tropical region in North East Australia, while on the west coast this habitat was 317 evident as far north as the Kimberleys. The Turf BRH did not occur at sites surveyed around most of 318 northern Australia and the Great Barrier Reef.

319

## 320 Environmental and anthropogenic variables and variation in habitat

321

322 DISTLM marginal tests for the temperate sites identified all covariates to have a significant

323 relationship with the multivariate data cloud derived from the substratum cover of sites. Mean sea

surface temperature (henceforth SST), when considered alone, explained the most variation (7.6%,

325 P<0.001), while the human population index also explained a large amount of variation, 6.1%

326 (P<0.001). The best model for the temperate realm included all variables and explained 23.5% of total</li>
327 variation. However, sequential tests showed mean SST, mean nitrate, estuarine index, and SST
328 standard deviation (henceforth SST SD) to cumulatively explain a major proportion, 19.1%, of total

329

variation.

330

The DISTLM marginal tests for the tropical sites showed SST SD explained 7.3% (P<0.001) of the variation in the data cloud. Distance to coast and mean SST explained similar proportions: 7.2% (P<0.001) and 5.9% (P<0.001), respectively. All variables improved the model fit for the tropical realm, together explaining 23.4% of the variation in the data cloud. SST SD, mean SST and distance to coast cumulatively accounted for 14.9% of variation in the stepwise model (Appendix 7).

336

The first and second axes of the temperate dbRDA captured 83.9% of the fitted model but only 19.3% of the total variation of the substratum biota (Fig. 5a). Comparison of the dbRDA ordination to the corresponding PCO based on temperate data (Fig. 3a), indicated the DISTLM model has distorted patterns in the data primarily along the first axis. The vector overlay indicted that the Turf BRH aligned with an increase in estuarine index and a decrease in exposure, the Epiphytic Algae/ Understory and Canopy Algae BRHs with high exposure and low human population indices and the Barren BRH with increasing site depth, nitrate levels, human population and mean SST.

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345 The first two axes of the tropical dbRDA ordination explained 78.0% and 18.3% of the fitted and total variation respectively (Fig. 5b). As for the temperate case, comparison of the dbRDA plot with the 346 347 corresponding PCO plot (Fig. 3b) showed distortion between the model representation and the true 348 ordination. The Calcified Algae-Coral BRH sites were densely clustered and loosely aligned with 349 increasing distance from the coast, decreasing human population index, and increasing mean SST and 350 site depth. Both the Turf-Coral and the Foliose Algae group appeared to align with increased SST SD 351 and decreasing mean SST. Coral-Bacterial Mat aligned loosely with increasing human population 352 indices. The Coral BRH was comparably scattered and alignment with no obvious alignment with 353 variables in the dbRDA model.

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# 357 Environmental and anthropogenic relationships with habitat

358

Tropical and temperate random forest (RF) models gave adequate predictions of the BRHs with an overall error rate of 15.3% for the temperate model and 24.6% for the tropical model (% of sites classified incorrectly). The RF variable importance plots (Fig. 6) for the temperate and tropical models showed mean SST to be the most important predictor for both realms. Human population, wave exposure, and mean nitrate were also ranked highly. In the tropical model, distance to coast, mean nitrate, SST SD, human population and cyclone stress were of similar importance.

365

Depending on the BRH, different variables were more important for prediction and therefore more
highly correlated with a particular BRH (Fig. 7). Partial dependence plots (Appendix S8) showed the
marginal effect of a given variable on the categorical BRH outcome. Where clear monotonic
relationships were evident between covariates and the partial dependence on a BRH, the nature of the
relationship (positive (+) or negative (-)) is shown on the variable importance plots (Fig. 7).

371

Nitrate was the most important predictor variable for the Canopy Algae BRH, though mean SST and estuarine index, human population and exposure had similar ranked importance. The probability of classifying a site into the Canopy Algae BRH increased with higher mean nitrate and lower mean SSTs and estuarine index according to partial dependence plots (Fig. 7a, Appendix S8). The Barren BRH was best predicted by mean SST, with partial dependence plots indicating this habitat was more likely with greater mean SSTs as well as increases in human population index and mean nitrate (Fig. 7b). RF models found Epiphytic Algae/ Understory BRH was best predicted by exposure, with mean

http://onlinelibrary.wiley.com/doi/10.1111/geb.12620/fullPRE-REVIEW379SST and human population also highly ranked. Partial plots did not show a clear relationship for380exposure, this BRH was encountered at sites with both low and high exposure values, with lower381frequency between. Exposure and SST mean and SD were the most important predictors for the Turf382BRH. As both exposure and SST SD increased, the probability of Turf decreased while a clear383relationship with mean SST was not evident.

384

385 The tropical BRHs also showed variability in the most highly ranked predictor variables (Fig.7e-i). Coral-Bacterial Mat BRH was most closely associated with the variables SD and mean SST with 386 387 partial dependence plots showing that this habitat was unlikely at SST SD <1.5°C, and likelihood 388 increased at high SD values. As mean SST increased from 22°C to 24°C the likelihood of this habitat 389 increased but at higher temperatures the relationship became variable and noisy (Appendix S8). The 390 Coral BRH was most closely associated with distance to coast and SST SD. There was no clear 391 relationship for distance to coast while for SST Coral was more likely at mean SST >27°C and at low 392 SDs.

393

Other than site depth and MPA status, which were relatively low ranked, variables had similar
importance in correctly predicting Turf-Coral. Partial plots indicated a higher likelihood of Turf-Coral
with increasing mean SSTs and increasing distance to coast. Calcified Algae-Coral, was best predicted
by distance to coast, being most probable farther from shore, at low SST SDs and high mean SST.
The Foliose Algae BRH was most closely associated with human population, distance to coast and
mean SST. The relationship to distance to coast was not obvious but partial dependence plots shows
higher likelihood at high human population indices, and as mean SST decreased.

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### 403 **DISCUSSION**

404

# 405 Biogenic reef habitats

406

On the basis of quantitative analyses, the current study identified nine distinct broad-scale habitats,
termed 'Biogenic Reef Habitats (BRHs),' on shallow reefs surrounding Australia. These fit within
Level 6 of the 10-level nested hierarchical framework for classifying marine biodiversity of Last *et al.*(2010) (*i.e.* as "biological facies", or "map-able units characterised by groups of particular species of
coral, sponges, algae and other macro-biotic groups"). Last *et al.* (2010) considered that, while species
are the fundamental units of biodiversity, biological facies comprise the smallest practical unit for
conservation management at regional scales.

415 The major demarcation between tropical and temperate realms, when assessed at the coarse spatial

416 resolution of 1°x1° lat-long grid cells, corresponds with the strong temperature-related divide in

417 species distributions (Stuart-Smith *et al.*, 2015). Despite a very different approach used for derivation,

- realms delineated in this study closely match the realms identified by Spalding *et al.* (2007): the
- 419 Central Indo-Pacific and the Temperate Australasian.
- 420

421 Four BRHs were defined in the temperate realm and five in the tropical realm, each distinguished by a 422 particular makeup of substratum biota. However, distinctions were subtler than expected, particularly 423 in the tropical realm. Most BRHs contained a mixture of substratum functional groups that co-424 occurred in different proportions, rather than pure stands of a particular functional group (e.g. corals 425 were conspicuous elements of four of the five tropical BRHs). Inshore reef habitats appear to be 426 considerably more complex than generally recognised in subjective habitat classifications where 427 dominant functional groups are recognized (e.g. kelp, turf). Thus, at the 200-m span of sites examined, 428 functional groups such as branching coral did not consistently occur as monotypic entities, but were 429 interspersed with soft corals, dead coral, turf, and a variety of other coral forms (including massive 430 and encrusting corals).

431

# 432 *Temperate habitats*

433

434 The dominant habitat identified in temperate Australia is characterised by large brown canopyforming macroalgae (Fucales and Laminariales). A similar habitat is present in most of the world's 435 436 temperate oceans, with indications that this habitat is amongst the most threatened of marine habitat 437 types (Dayton, 1985). Globally, altered environmental regimes, some as a direct result of anthropogenic stressors such as pollution or fishing, and others more indirect such as broad-scale 438 439 climate change, are leading to widespread loss of structurally complex habitats that support diverse 440 communities (Steneck et al., 2002; Connell et al., 2008; Johnson et al., 2011). Airoldi et al. (2008) 441 describe this change as a 'flattening' of the marine environment, with replacement of structurally-442 complex habitats by more two-dimensional counterparts. Canopy Algae and Epiphytic Algae-443 Understory BRHs in the present study represent architecturally complex habitats that are juxtaposed 444 with the Barren BRH, characterised by bare rock and crustose coralline algae, and Turf BRH, 445 characterised by low lying mats of turfing algae.

446

447 Mean SST was found to be the most important correlate of tropical and temperate BRHs. Increased
448 SST was positively correlated with the 'flat' habitats – the Barren and the Turf BRH – and negatively

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correlated with the structurally complex Canopy Algae and Epiphytic Algae-Understory BRHs. This 449 450 is a concern given increasing ocean temperatures observed and predicted, suggesting long-term 451 warming could contribute to the 'flattening' of marine habitats. Furthermore, human population was 452 the second most important predictor variable for the temperate RF model, and was positively 453 correlated with Barren BRH and negatively correlated with Canopy Algae and Epiphytic Algae-454 Understory. Thus, our results consistently suggest that increasing sea temperature and human 455 population growth both represent key threats to reef biodiversity, supporting findings of (Mora et al., 456 2011). Here, the threat is via impacts to structurally-complex habitats that support high diversity reef 457 associated communities. For future studies, examining structural complexity more quantitatively at the 458 site level would be beneficial, however this metric was not available for all sites in this study 459 (Alexander et al., 2009).

460

461 A link between the Turf BRH and anthropogenic stressors was evident in the locations of this habitat. 462 While human population did not emerge as a key correlate of this habitat, Turf sites were adjacent to 463 metropolitan coasts (viz. Hobart, Melbourne, Sydney, Perth), albeit with additional sites located near 464 Albany (WA) and upper Spencer Gulf (South Australia), the latter a reverse estuary with extreme 465 natural disturbance associated with variability in SST and salinity (Seddon et al., 2000). The presence 466 of Turf around four of five temperate Australian capital cities implies a link to anthropogenic 467 pressures, as do prior studies near Adelaide, the fifth capital city, where displacement of canopy-468 forming algae by turf mats has been documented (Gorgula & Connell, 2004; Connell et al., 2008). 469 Ecological theory suggests that 'weedy' plants – fast recruitment, growth and reproduction – such as 470 turfing algae, are favored in environments that are frequently disturbed (such as by human activities), 471 while slower-growing, more structurally-complex species, such as those of the Canopy Algae BRH, 472 are disadvantaged due to their life history strategies (Tilman & Lehman, 2001).

473

High human population indices were also associated with the Barren BRH. Speculatively, this may
relate to fishing pressure for key predators of these urchins, such as the southern rock-lobster, blue
groper and pink snapper (Pederson & Johnson, 2006; Ling *et al.*, 2009). Canopy Algae and Barren
BRHs had strong opposing relationships with mean SST and human population, exemplifying
concerns over human-driven shifts from structurally complex to flatter habitats with the Barren BRH
representing the lowest diversity habitat (Ling, 2008).

480

481 Tropical habitats

482

# **PRE-REVIEW**

Tropical coral reefs support some of the most diverse marine ecosystems on earth (Jackson & Sala,
2001; Sala & Knowlton, 2006; Green *et al.*, 2009), but vary substantially both in the amount of live
coral cover and their structural complexity. Five distinctive tropical BRHs were identified here: Coral,
Coral-Bacterial Mat, Calcified Algae-Coral, Turf-Coral and Foliose Algae. These were complexly
arranged, both in composition and also in spatial distribution.

488

489 As for the temperate realm, the major correlate of BRHs in the tropical realm was mean SST 490 according to both DISTLM and RF results. Variation in SST was a stronger correlate in the tropical 491 realm than the temperate, perhaps reflecting low tolerance of corals and other sessile biotic groups to 492 variation in temperature anomalies (Jokiel & Coles, 1977; Coles & Brown, 2003). The Coral BRH 493 was characterised by a diverse array of different coral elements - the genera Pocillopora and 494 Acropora, bleached and dead coral, branching, massive, encrusting and soft corals – and possessed a 495 strong negative relationship with SST variability. This, in combination with the Coral BRH occurring 496 frequently at some of the warmest Australian locations (greater than 27°C mean SST), indicates 497 vulnerability to bleaching with continued ocean warming.

498

Turfing algae is a common feature on most coral reefs and supports a diverse array of herbivores (Green *et al.*, 2009), which utilise production generated by fast growth and high turnover regardless of low standing biomass. The Turf-Coral BRH had approximately 40% mean cover of turfing algae, and was associated with high mean SST and increasing distance offshore. It was present at 158 of 509 tropical survey sites in almost all surveyed regions. While the Coral BRH better fits common perceptions of a diverse coral reef, the degree to which the Turf-Coral habitat is 'natural' or partially affected by anthropogenic stressors is a key question.

506

507 A turfing algae dominated state has been proposed to occur as an alternative stable state to coral in 508 tropical ecosystems (Green et al., 2009; Norström et al., 2009). As well as herbivorous fishes, nutrient 509 and light levels are considered important variables in transitions, with high nutrients and low light 510 levels providing turfing algae with a competitive advantage over corals, particularly after disturbances 511 such as cyclones (Hughes et al., 2007; Green et al., 2009). In the present study, the probability of the 512 Turf-Coral BRH increased with increasing mean nitrate concentrations, whereas the probability of 513 Coral BRH decreased with nitrate concentrations, supporting nutrient levels as providing a potential 514 competitive advantage.

515

Turf mats with heavy loads of cyanobacterial slime are generally viewed as an undesirable or
unhealthy reef state (Green *et al.*, 2009). In contrast to the Coral BRH, the Coral-Bacterial Mat BRH

## PRE-REVIEW

was most prevalent in areas of high variation in SST. The geographic distribution of the CoralBacterial Mat BRH did not give a clear indication of oceanic parameters that may be associated with
this habitat. Turbidity may play an important role as good water quality is a key factor affecting the
survival of coral, whereas cyanobacteria can proliferate as water quality declines (Wittenberg &
Hunte, 1992; Fabricius *et al.*, 2005). Coral- Bacterial Mat occurred in locations with high amounts of
suspended sediment in the water column due to large tidal movement in northwestern Australia and in
the Gulf of Carpentaria (Somers & Long, 1994; Stoddart & Anstee, 2004; Burford *et al.*, 2008).

525

Foliose Algae, with distribution on the east coast localised near the Queensland-NSW border, and on the west coast extending northwards along the coast from the Abrolhos Islands, was associated with high human population, low mean SST relative to other tropical locations, and high variability in SST. The association with human population index may signify that more frequent anthropogenic disturbance is decreasing coral resilience and allowing macroalgae to expand, though given this habitat occurred most frequently in the temperate-tropical realm transition, competition between tropical and temperate species is perhaps a more likely driver.

533

534 The Calcified Algae-Coral BRH occurred almost exclusively offshore (>200km), dominating the 535 Coral Sea and North West Shelf. Sites classified into this group had a high cover of crustose coralline 536 algae, green calcified algae (Halimeda spp.), and small contributions from a variety of coral functional 537 groups. The offshore geography of this BRH supports the findings of Drew (1983), that average 538 biomass of Halimeda spp. increased with increasing distance from the GBR to the Coral Sea. 539 Different oceanic conditions at these offshore sites are likely to be a key driver (Andrews & Clegg, 540 1989) with high mean SSTs and low SST variability found as key correlates of this habitat, similar to 541 those for the Coral BRH. Calcified Algae likely represents an alternative to the Coral BRH that is 542 maintained by frequent physical disturbance from storm and cyclone activity (Calcified Algae-Coral 543 was positively correlated with cyclone index).

544

The DISTLM models captured only a small proportion of total variation in the tropical models,
suggesting additional unassessed factors probably play important roles in shaping the broad-scale
distribution of BRHs. For example, light reaching reef benthos in tropical environments can be
affected by turbidity, which was not assessed in the current study but will clearly contribute to
whether a diverse range of corals or algal turfs prevail. Moreover, much of the variability in habitat
types may occur at local scales <1 km, whereas this variability could not be considered in models due</li>
to the coarse grain of available covariate data (typically ~5 km, Appendix S5).

552

553 *Co* 554

555 This is the first study to our knowledge to examine pattern associated with reef habitat types over a 556 continental scale using field survey data, and includes inference about process at the habitat level. 557 Nine BRHs were delineated, four in the temperate realm, and five in the tropical realm, all 558 characterised by unique functional sets of algae, sessile invertebrates and corals. Relationships 559 identified between the objectively-defined BRHs and environmental variables allowed formulation of 560 conceptual models associated with potential threats to coastal systems (such as increasing mean SST 561 will lead to decline in canopy algae and increase in barrens and turf-coral BRHs). These models will 562 be tested and refined as time series data become available by using the current distribution of habitats 563 as an irreplaceable baseline for assessing future change. The models can provide guidance to 564 management efforts as they indicate likely influences of local as well as global stressors. 565

566 In particular, the association of many BRHs with temperature and human population provides a clear

567 warning in the context of changing climate and increasing anthropogenic stress to global marine

568 systems. The future of particular habitats, including some previously considered common and

resilient, such as canopy forming algae and coral communities, should be questioned.

- 570
- 571

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573

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# 583 List of brief titles of supporting information

584585 Appendix S1 Substratum categories used for hierarchical clustering

586
587 Appendix S2 Statistical comparison of two survey types: Reef Life Survey, RLS, and Long-term
588 Marine Protected Area, LTMPA
589

- 590 Appendix S3 Environmental and anthropogenic covariates and sources591
- 592 Appendix S4 Dendrogram of hierarchical cluster analyses of 1x1° lat-long grid cells.

- 594 Appendix S5 Dendrograms of hierarchical clustering of sites within tropical and temperate realms
- 596 Appendix S6 Mean percentage cover of substratum categories in Biogenic Reef Habitats597
- 598 Appendix S7 Distance-based linear modelling (DISTLM) results for temperate and tropical analyses 599
- Appendix S8 Partial dependence plots random forest models601
- 602 **Biosketch**

595

- 603 The authors' research focusses on broad-scale trends in rocky and coral reef biodiversity related to
- 604 pressures such as fishing, ocean warming, invasive species and pollution. The availability of data
- 605 collected using standardised methods from the Reef Life Survey program, which covers not just coral
- reefs, but also rocky reefs from the Antarctic to the Arctic, allows their research to tackle uniquely
- broad questions. Their ultimate goals are to improve the way marine biodiversity is monitored,
- 608 reported, managed and protected, through contributing to more ecologically-informed policy at larger
- scales, and by providing guidance to local management.
- 610

# 611 **References**

- Natural Resource Management Ministerial Council 2010. Australia's Biodiversity Conservation
   Strategy 2010-2030. Australian Government, Department of Sustainability, Environment,
- 614 Water, Population and Communities. Canberra.
- 615 <u>http://www.environment.gov.au/biodiversity/publications/strategy-2010-</u>
   616 30/pubs/biodiversity-strategy-2010.pdf.
- Airoldi, L., Balata, D. & Beck, M.W. (2008) The Gray Zone: Relationships between habitat loss and
  marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology*, 366, 8-15.
- Alexander, T.J., Barrett, N., Haddon, M. & Edgar, G. (2009) Relationships between mobile
   macroinvertebrates and reef structure in a temperate marine reserve. *Marine Ecology Progress Series*, 389, 31-44.
- Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C.H., Stuart-Smith, R.,
  Barrett, N., Edgar, G. & Colquhoun, J. (2015) A standardised vocabulary for identifying
  benthic biota and substrata from underwater imagery: the CATAMI classification scheme. *PloS one*, **10**, e0141039.
- Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008) *PERMANOVA+ for PRIMER: Guide to software and statistical methods.* PRIMER-E, Plymouth, UK.
- Andrews, J.C. & Clegg, S. (1989) Coral Sea circulation and transport deduced from modal
   information models. *Deep Sea Research Part A. Oceanographic Research Papers*, 36, 957 974.
- Barrett, N.S., Buxton, C.D. & Edgar, G.J. (2009) Changes in invertebrate and macroalgal
   populations in Tasmanian marine reserves in the decade following protection. *Journal of Experimental Marine Biology and Ecology*, **370**, 104-119.
- Barrett, N.S., Edgar, G.J., Buxton, C.D. & Haddon, M. (2007) Changes in fish assemblages following
  10 years of protection in Tasmanian marine protected areas. *Journal of Experimental Marine Biology and Ecology*, 345, 141-157.

	http://onlinelibrary.wiley.com/doi/10.1111/geb.12620/full	PRE-REVIEW					
638	Burford, M.A., Alongi, D.M., McKinnon, A.D. & Trott, L.A. (2008) Pr	rimary production and					
639	nutrients in a tropical macrotidal estuary. Darwin Harbour, Australia, Estuarine Coastal						
640	and Shelf Science, <b>79</b> , 440-448.						
641	CIESIN (2014) Gridded Population of the World. Version 4 (GPWv4) 2010. In. Center for						
642	International Earth Science Information Network. Columbia University.						
643	Clarke, K. & Warwick, R. (2001) An approach to statistical analysis and interpretation. <i>Change in</i>						
644	Marine Communities, <b>2</b>						
645	Clarke, K. & Gorley, R. (2006) User manual/tutorial. PRIMER-E Lt	d., Plymouth, 93.					
646	Coles, S. & Brown, B.E. (2003) Coral bleaching—capacity for accli	matization and adaptation.					
647	Advances in marine biology, <b>46</b> , 183-223.						
648	Commonwealth of Australia (2006) A guide to the Integrated man	rine and Coastal					
649	Regionalisation of Australia Version 4.0. In. Department of	f the Environment and					
650	Heritage, Canberra, Australia.						
651	Connell, S., Russell, B., Turner, D., Shepherd, A., Kildea, T., Miller, I	D., Airoldi, L. & Cheshire, A.					
652	(2008) Recovering a lost baseline: missing kelp forests fro	om a metropolitan coast. <i>Marine</i>					
653	Ecology-Progress Series, <b>360</b> , 63-72.						
654	Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H. & Milos	slavich, P. (2010) A Census of					
655	Marine Biodiversity Knowledge, Resources, and Future Ch	allenges. <i>PLoS ONE</i> , <b>5</b> , e12110.					
656	Cracknell, A.P. (1999) Remote sensing techniques in estuaries an	d coastal zones an update.					
657	International Journal of Remote Sensing, <b>20</b> , 485-496.						
658	Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibso	on, J. & Lawler, J.J. (2007)					
659	Random forests for classification in ecology. <i>Ecology</i> , <b>88</b> , 2	2/83-2/92.					
660	Daniel, W.W. (1990) Applied nonparametric statistics (2nd ed.). He	oughton Mifflin, Boston.					
661	Dayton, P.K. (1985) Ecology of Kelp communities. Annual Review	of Ecology and Systematics, <b>16</b> ,					
662	215-245. Diaz D.L. Salan M. & Valanta D.M. (2004) A review of approaches	a fan alagaifring hanthig					
003 664	babitate and evaluating babitate quality. <i>Journal of Environ</i>	s for classifying bentfille					
665	191	mental management, <b>73</b> , 105-					
666	Douvere F (2008) The importance of marine spatial planning in	advancing ecosystem-based					
667	sea use management <i>Marine Policy</i> <b>32</b> , 762-771	advallenig ceosystem based					
668	Drew, E. (1983) Halimeda biomass, growth rates and sediment g	eneration on reefs in the					
669	central great barrier reef province. <i>Coral Reefs.</i> <b>2</b> , 101-110	).					
670	Edgar, G.I. & Stuart-Smith. R.D. (2009) Ecological effects of marin	e protected areas on rocky reef					
671	communities: a continental-scale analysis. <i>Marine Ecology</i>	Progress Series, <b>388</b> , 51-62.					
672	Edgar, G.J. & Stuart-Smith, R.D. (2014) Systematic global assessm	ent of reef fish communities by					
673	the Reef Life Survey program. <i>Scientific Data</i> , <b>1</b>	2					
674	Fabricius, K., De'ath, G., McCook, L., Turak, E. & Williams, D.M. (20	005) Changes in algal, coral and					
675	fish assemblages along water quality gradients on the insh	nore Great Barrier Reef. Marine					
676	<i>Pollution Bulletin</i> , <b>51</b> , 384-398.						
677	Gorgula, S. & Connell, S. (2004) Expansive covers of turf-forming	algae on human-dominated					
678	coast: the relative effects of increasing nutrient and sedim	ent loads. <i>Marine Biology</i> , <b>145</b> ,					
679	613-619.						
680	Green, A.L., Bellwood, D.R. & Choat, H. (2009) Monitoring function	nal groups of herbivorous reef					
681	fishes as indicators of coral reef resilience. A practical guid	de for coral reef managers in the					
682	Asia Pacific Region. IUCN, Gland, Switzerland. Available onl	ine at: <u>http://cmsdata</u> . iucn.					
683	org/downloads/resilience_herbivorous_monitoring.pdf,						
684	Halpern, B.S., McLeod, K.L., Rosenberg, A.A. & Crowder, L.B. (2008	B) Managing for cumulative					
685	impacts in ecosystem-based management through ocean z	zoning. Ucean and Coastal					
080	management, <b>51</b> , 203-211.						

- Huang, S., Stephens, P. & Gittleman, J. (2012) Traits, trees and taxa: global dimensions of
  biodiversity in mammals. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 279, 4997-5003.
- Huang, Z., Brooke, B.P., Whitta, N., Potter, A., Fuller, M., Dunn, J., Pitcher, R. (2011) Australian
  Marine Physical Environmental Data Descriptions and Metadata. In: *Geoscience Australia Recored 2010* (ed. G. Australia), Canberra.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L.,
  Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. & Willis, B. (2007) Phase shifts,
  herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360-365.
- Jackson, J.B.C. & Sala, E. (2001) Unnatural Oceans. *Scientia Marina*, **65**, 273-281.
- Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D.,
  Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R.,
  Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R.,
  Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A., Swadling,
  K.M. & Nyan Taw (2011) Climate change cascades: shifts in oceanography, species'
  ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology*, 400, 17-32.
- Jokiel, P. & Coles, S. (1977) Effects of temperature on the mortality and growth of Hawaiian reef
   corals. *Marine Biology*, 43, 201-208.
- Last, P.R., Lyne, V.D., Williams, A., Davies, C.R., Butler, A.J. & Yearsley, G.K. (2010) A hierarchical
   framework for classifying seabed biodiversity with application to planning and managing
   Australia's marine biological resources. *Biological Conservation*, 143, 1675-1686.
- T10 Lawton, J.H. (1996) Patterns in Ecology. In, p. 145. Munksgaard International Publishers, Ltd.
- T11 Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. *R news*, **2**, 18-22.
- Ling, S.D. (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic
   diversity: a new and impoverished reef state. *Oecologia*, **156**, 883-894.
- Ling, S.D., Johnson, C.R., Frusher, S.D. & Ridgway, K.R. (2009) Overfishing reduces resilience of
   kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 22341-22345.
- McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W.,
  Mellin, C., Cresswell, I.D. & Radke, L.C. (2010) On the use of abiotic surrogates to describe
  marine benthic biodiversity. *Estuarine, Coastal and Shelf Science*, 88, 21-32.
- Mellin, C., Delean, S., Caley, M.J., Edgar, G.J., Meekan, M.G., Pitcher, C.R., Przeslawski, R. &
   Williams, A. (2011) Effectiveness of biological surrogates for predicting patterns of
   marine biodiversity. *PLoS One*, in press.
- Mora, C., Aburto-Oropeza, O., Bocos, A.A., Ayotte, P.M., Banks, S., Bauman, A.G., Beger, M.,
  Bessudo, S., Booth, D.J. & Brokovich, E. (2011) Global human footprint on the linkage
  between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol*, 9, e1000606.
- Norström, A.V., Nyström, M., Lokrantz, J. & Folke, C. (2009) Alternative states on coral reefs:
  beyond coral-macroalgal phase shifts. *Mar Ecol Prog Ser*, **376**, 295-306.
- Pederson, H.G. & Johnson, C.R. (2006) Predation of the sea urchin *Heliocidaris erythrogramma*by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. *Journal of Experimental Marine Biology and Ecology*, **336**, 120-134.
- Post, A.L. (2008) The application of physical surrogates to predict the distribution of marine
  benthic organisms. *Ocean & Coastal Management*, **51**, 161-179.
- R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for statistical computing, Vienna, Austria.
- Ray, G.C. & McCormick-Ray, M.G. (1992) Marine and estuarine protected areas: a strategy for a national representative system within Australian coastal and marine environments.
  Australian National Parks and Wildlife Service, Canberra, Australia.

	http://onlinelibrary.wiley.com/doi/10.1111/geb.12620/full PRE-REVIEW						
738	Roff, I.C. & Evans, S.M.I. (2002) Frameworks for marine conservation — non-hierarchical						
739	annroaches and distinctive babitats <i>Aquatic Conservation</i> : Marine and Freshwater						
740	Ecosystems 12, 635-648						
741	Sala E & Knowlton N (2006) Global marine biodiversity trends. In: Annual Review of						
742	Sala, E. & KIIOWITOII, N. (2000) GIODAI IIIATIIE DIOUIVEISILY LIEIIUS. III: ANNUAL REVIEW OF Environment and Pasources pp. 02-122						
743	Seddon S Connolly R M & Edwane K S (2000) Large-scale seagrass dieback in northern						
743	Security, S., Connolly, K.M. & Euyvalle, K.S. (2000) Large-Scale Seagrass aleback in northern						
745	Somers I & Long B (1994) Note on the sediments and hydrology of the Culf of Carpentaria						
745	Somers, I. & Long, B. (1994) Note on the seaments and hydrology of the Gulf of Carpentaria,						
740	Australia. Murine unu rresnwater Kesearch, 45, 283-291. Spolding M.D. Foy, H.F. Allon, C.D. N.D. Fordoño, 7.A. Einleyson, M. Holnorr, D.C. Joyes, M.A.						
747	Spaining, M.D., Fox, H.E., Allell, G.K., N. D., Ferdana, Z.A., Finiayson, M., Halpern, B.S., Jorge, M.A.,						
740	Lombana, A., Lourie, S.A., Martin, K.D., McManus, K.D., Molnar, J., Kecchia, C.A. &						
749	Robertson, J. ( $2007$ ) Marine ecoregions of the world: a bioregionalization of coastal and						
750	Sheh areas. Bioscience, 57, 573-583.						
/51	Steneck, R.S., Granam, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J.						
/52	(2002) Kelp forest ecosystems: biodiversity, stability, resilience and future.						
/53	Environmental Conservation [Environ. Conserv.]. <b>29</b> , 436-459.						
754	Stoddart, J. & Anstee, S. (2004) Water quality, plume modelling and tracking before and during						
755	dredging in Mermaid Sound, Dampier, Western Australia. Corals of the Dampier Harbour:						
756	their survival and reproduction during the dredging programs of 2004, pp. 13-33.						
757	MScience Pty Ltd, University of Western Australia, Western Australia.						
758	Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J. & Bates, A.E. (2015) Thermal biases						
759	and vulnerability to warming in the world's marine fauna. <i>Nature</i> , <b>528</b> , 88-92.						
760	Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith,						
761	J.F., Hill, N.A., Kininmonth, S.J., Airoldi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P.,						
762	Navarrete, S.A., Soler, G.A., Strain, E.M.A., Willis, T.J. & Edgar, G.J. (2013) Integrating						
763	abundance and functional traits reveals new global hotspots of fish diversity. <i>Nature,</i>						
764	<b>501</b> , 539-542.						
765	Tilman, D. & Lehman, C. (2001) Human-caused environmental change: Impacts on plant						
766	diversity and evolution. Proceedings of the National Academy of Sciences of the United						
767	<i>States of America</i> , <b>98</b> , 5433-5440.						
768	Underwood, A.J., Chapman, M.G. & Connell, S.D. (2000) Observations in ecology: you can't make						
769	progress on processes without understanding the patterns. Journal of Experimental						
770	Marine Biology and Ecology, <b>250</b> , 97-115.						
771	WAMDI Group (1988) The WAM model-a third generation ocean wave prediction model. Journal						
772	of Physical Oceanography, <b>18</b> , 1775-1810.						
773	Williams, A., Bax, N.J., Kloser, R.J., Althaus, F., Barker, B. & Keith, G. (2009) Australia's deep-water						
774	reserve network: implications of false homogeneity for classifying abiotic surrogates of						
775	biodiversity. ICES Journal of Marine Science 66, 214-224.						
776	Wittenberg, M. & Hunte, W. (1992) Effects of eutrophication and sedimentation on juvenile						
777	corals. <i>Marine Biology</i> , <b>112</b> , 131-138.						
778							
770	Tables						
115	Tables						
780							
781	Table 1. Nine clusters classified from analyses of sites in the tropical and temperate realms with the						
782	mean percentage cover of each of the RLS Substratum Biota Categories. Percentage cover has been						
783	rounded to zero decimal places. RLS Substratum Biota Categories with less than 5% cover in any						
784	BRH are not shown here. The full table is available for reference in Appendix S6 in Supporting						
785	Information.						
	Temperate Tropical						

ttp://onlinelibrary.wiley.com/doi/10.1111/geb.12620/full PRE-REVIEW									
Biogenic Reef Habitat (BRH)	Canopy Algae	Turf	Epiphytic Algae - Caulerpa	Barren	Foliose Algae	Turf Coral	Calcified Algae-Coral	Coral- Bacterial Mat	Coral
Sessile taxa categories									
Bare Rock	2	6	0	23	1	3	10	9	1
Foliose brown algae	5	1	6	3	31	3	0	4	2
Hard branching corals	0	0	0	1	1	2	3	4	9
Branching Acropora	0	0	0	0	0	1	6	11	15
Caulerpa	1	3	15	0	1	1	0	0	0
Crustose coralline algae	4	0	0	30	1	7	21	4	1
Dead Coral	0	0	0	1	0	5	1	1	10
Encrusting corals	0	2	0	2	2	8	12	8	6
Filamentous Epiphytic Algae	1	0	38	0	0	0	0	0	3
Filamentous rock-attached algae	1	14	0	0	0	1	0	0	1
Large brown fucoid kelps	42	5	11	1	10	0	0	1	0
Green Calcified Algae	0	0	0	0	0	2	12	0	0
Laminarian kelps	24	0	3	3	0	0	0	0	0
Massive corals	0	0	0	0	1	3	5	8	6
Pebbles/Coral rubble	1	0	1	3	5	4	6	4	5
Foliose red algae	6	6	13	0	11	2	0	0	0
Bacterial slime on bare rock	1	0	0	9	4	4	1	26	3
Soft corals and gorgonians	0	1	0	0	1	4	5	7	8
Turfing algae	4	52	8	8	18	40	8	3	15
Number of sites in cluster	612	29	44	101	34	158	199	62	56

# 787 Figure Legends

Figure 1. Locations of Australian field surveys included in analyses. Reef Life Survey, RLS, sites are
shown by red crosses and Long-term Marine Protected Area, LTMPA, monitoring sites by blue
circles.

Figure 2. Geographic distribution of seven clusters formed from hierarchical clustering of 1° x1° latlong grid cells. Two clusters dominated the analysis, one shown in red, populating the low latitudes
and the other shown in blue, populating the high latitudes. The small clusters are shown in orange at
Shark Bay (WA), grey at Geographe Bay (WA), green in Upper Spencer Gulf (SA) and Port Phillip
Bay (VIC), pink at Eden (NSW) and aqua in southern Queensland.

Figure 3. Principal coordinates ordination plot of a) temperate sites and b) tropical sites based on the
estimated cover of substratum biota. The colours/shapes show, in a) the four and in b) the five
Biogenic Reef Habitats (BRH) formed from hierarchical cluster analysis. Vector overlays show the
substratum biota most highly correlated (Spearman correlation coefficient >0.4) in the data cloud. The
length of lines in the vector overlay indicated the magnitude of the Spearman correlation coefficient.

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- **Figure 4.** Geographic distribution of the nine Biogenic Reef Habitats, BRHs, defined through
- hierarchical cluster analyses. a)- d) show Australia with south facing triangles indicating the
- 806 distribution of the four temperate BRHs: a) Canopy Algae, b) Barren, c) Epiphytic Algae/ Understory 807 and d) Turf. e) - f) show the five tropical BRHs with north facing triangles: e) Coral–Bacterial Mat, f)
- 808 Coral, g) Turf–Coral, h) Calcified Algae–Coral and i) Foliose Algae respectively.
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	http://onlinelibrary.wiley.com/doi/10.1111/geb.12620/full PRE-REVIEW
810 811 812 813 814	<b>Figure 5.</b> dbRDA ordinations of a) temperate sites and b) tropical sites identifying the greatest variation between sites based on the cover of substratum functional groups. The vector overlays shows the most strongly correlated environmental variables calculated from the multiple partial correlations ( $r > 0.4$ ).
815 816 817 818 819 820	<b>Figure 6.</b> Random forest variable importance plots showing the relative importance of the a) 9 and b) 8 covariates used in the temperate and tropical models respectively. The percentage change in accuracy for a given predictor variable is measured by the change between models that include or do not include that predictor variable. Errors associated with temperate and tropical models were 15.3% and 24.6% respectively. Models were based on 2500 trees.
821 822 823 824 825 826 827 828 829 830	<b>Figure 7.</b> Results of random forest analyses showing the relative importance of the a)-d) 9 and e)-i) 8 covariates used in the temperate and tropical models respectively. The first four plots (a-d) show the relative importance of the predictors for each temperate BRH and the last five (e-i) show the relative importance of each predictor for the tropical BRHs. The percentage change in accuracy for a given predictor variable is measured by the change between models that include or do not include that predictor variable. The errors associated with temperate and tropical models were 15.3% and 24.6% respectively. The models were based on 2500 trees. Where clear relationships were evident between covariates and the partial dependence on a BRH the nature of the relationship (positive (+) or negative (-)) is shown on the bar plots.
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Figure 1. Locations of Australian field surveys included in analyses. Reef Life Survey, RLS, 845 sites are shown by red crosses and Long-term Marine Protected Area, LTMPA, monitoring 846 sites by blue circles. 847

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853 Figure 2. Geographic distribution of seven clusters formed from hierarchical clustering of 1°

x1° lat-long grid cells. Two clusters dominated the analysis, one shown in red, populating the low latitudes and the other shown in blue, populating the high latitudes. The small clusters

are shown in orange at Shark Bay (WA), grey at Geographe Bay (WA), green in Upper Spencer Gulf (SA) and Port Phillip Bay (VIC), pink at Eden (NSW) and agua in southern

- 858 Queensland.
- Uueensian
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- 860

a) Temperate



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Figure 3. Principal coordinates ordination plot of a) temperate sites and b) tropical sites
based on the estimated cover of substratum biota. The colours/shapes show, in a) the four
and in b) the five Biogenic Reef Habitats (BRH) formed from hierarchical cluster analysis.

866 Vector overlays show the substratum biota most highly correlated (Spearman correlation

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coefficient >0.4) in the data cloud. The length of lines in the vector overlay indicated the 867 868 magnitude of the Spearman correlation coefficient.

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871 872 Figure 4. Geographic distribution of the nine Biogenic Reef Habitats, BRHs, defined through hierarchical cluster analyses. a)- d) show Australia with south facing triangles indicating the 873 distribution of the four temperate BRHs: a) Canopy Algae, b) Barren, c) Epiphytic Algae/ 874 875 Understory and d) Turf. e) - f) show the five tropical BRHs with north facing triangles: e) Coral-Bacterial Mat, f) Coral, g) Turf-Coral, h) Calcified Algae-Coral and i) Foliose Algae 876 877 respectively.

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Figure 5. dbRDA ordinations of a) temperate sites and b) tropical sites identifying the greatest variation between sites based on the cover of sessile taxa functional groups. The vector overlays shows the most strongly correlated environmental variables calculated from the multiple partial correlations (r > 0.4).

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Figure 6. Random forest variable importance plots showing the relative importance of the a)

890 9 and b) 8 covariates used in the temperate and tropical models respectively. The

891 percentage change in accuracy for a given predictor variable is measured by the change

between models that include or do not include that predictor variable. Errors associated with temperate and tropical models were 15.3% and 24.6% respectively. Models were based on

- 894 2500 trees.
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907 Figure 7. Results of random forest analyses showing the relative importance of the a)-d) 9 908 and e)-i) 8 covariates used in the temperate and tropical models respectively. The first four plots (a-d) show the relative importance of the predictors for each temperate BRH and the 909 910 last five (e-i) show the relative importance of each predictor for the tropical BRHs. The percentage change in accuracy for a given predictor variable is measured by the change 911 between models that include or do not include that predictor variable. The errors associated 912 913 with temperate and tropical models were 15.3% and 24.6% respectively. The models were 914 based on 2500 trees. Where clear relationships were evident between covariates and the partial dependence on a BRH the nature of the relationship (positive (+) or negative (-)) is 915 916 shown on the bar plots.

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