Received: 8 September 2016 | Revised: 7 June 2017 | Accepted: 22 June 2017

DOI: 10.1111/geb.12620

RESEARCH PAPER

WILEY Global Ecology and Biogeography A Journal of Macroecology

Translating local benthic community structure to national biogenic reef habitat types

Anna K. Cresswell[1,2] | Graham J. Edgar[1] | Rick D. Stuart-Smith[1] | Russell J. Thomson[3] | Neville S. Barrett[1] | Craig R. Johnson[1]

[1]Institute for Marine and Antarctic Studies, Hobart, Tasmania, Australia

[2]Indian Ocean Marine Research Centre, The University of Western Australia, Crawley, Western Australia, Australia

[3]Centre for Research in Mathematics, Western Sydney University, Penrith, New South Wales, Australia

Correspondence
Anna K. Cresswell, Indian Ocean Marine Research Centre, The University of Western Australia, M097, 35 Stirling Highway, Crawley, WA 6009, Australia.
Email: anna.cresswell@csiro.au

Funding information
Analyses were facilitated by the Australian Research Council and the Marine Biodiversity Hub, a collaborative partnership supported through the Australian Government's National Environmental Science Programme.

Editor: Joshua Madin

Abstract

Aim: Marine reef habitats are typically defined subjectively. We provide a continental-scale assessment of dominant reef habitats through analysis of macroalgae and sessile animal taxa at sites distributed around Australia. Relationships between reef habitats and environmental and anthropogenic factors are assessed, and potential changes in the future distribution and persistence of habitats are considered.

Location: Shallow rocky and coral reefs around the Australian coast.

Methods: Cover of 38 sessile biota functional groups was recorded in diver-based surveys using quadrats at 1,299 sites. Classification analyses based on the functional groups were used to identify an unambiguous set of 'biogenic habitat types'. Random forest and distance-based linear modelling were used to investigate correlations between these habitats and environmental and anthropogenic variables.

Results: Cluster analyses revealed tropical and temperate 'realms' in benthic substratum composition, each with finer-scale habitats: four for the temperate realm (canopy algae, barren, epiphytic algae–understorey and turf) and five for the tropical realm (coral, coral–bacterial mat, turf–coral, calcified algae–coral and foliose algae). Habitats were correlated with different sets of environmental and anthropogenic conditions, with key associations in the temperate realm between mean sea temperature and canopy-forming algae (negative) and barren habitat (positive). Variation in sea temperature was also an important correlate in the tropical realm.

Main conclusions: Quantitative delineation of inshore reef habitats at a continental scale identifies many of the same habitat types traditionally recognized through subjective methods. Importantly, many biogenic reef habitats were closely related to environmental parameters and anthropogenic variables that are predicted to change. Consequently, habitats have differing likelihood of persistence. Structurally complex habitats in the temperate realm are at greater risk than more 'two-dimensional' habitats (e.g., canopy-forming versus turfing algae). In the tropical realm, offshore and coastal habitats differed greatly, highlighting the importance of large-scale oceanic conditions in shaping biogenic structure.

KEYWORDS
Australia, biogeography, climate change, habitat type, macroecology, marine management

1 | INTRODUCTION

Shallow marine reefs house a multifarious array of habitats, supporting diverse ecologically and economically important marine communities (Cracknell, 1999; Spalding et al., 2007). When it comes to characterizing reef-associated biodiversity and understanding responses to human pressures, observations can be made at a range of levels, such as species, taxonomic groups or habitats. Research at the species level has tended to be the major focus of monitoring efforts, with habitat-level studies more limited (McArthur et al., 2010; Mellin et al., 2011; Roff & Evans, 2002). Aside from a few notable examples (Connell & Irving, 2008; Irving, Connell, & Gillanders, 2004; Marzinelli et al., 2015; Wernberg et al., 2013), quantitative descriptions of biogenic habitat types within reef systems have largely been subjective or dependent on easily measured environmental surrogates and have not covered scales relevant to national policies or ecosystem-based management. Opinions on how best to approach marine environmental management and conservation, whilst remaining somewhat controversial, are changing, expanding from species-specific approaches to include biodiversity and macroecology and to embrace ecosystem-based approaches (Costello et al., 2010; Douvere, 2008).

Ecosystem approaches to management and conservation acknowledge the crucial importance of habitat in supporting naturally functioning biotic communities. This approach also recognizes a need 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 (Halpern, McLeod, Rosenberg, & Crowder, 2008; Wondolleck & Yaffee, 2017).

Until now, knowledge of biological habitat elements of marine benthic communities has been limited at macroecological scales by a near absence of detailed datasets that include both biotic and environmental components obtained using standardized methods over large scales. Additionally, spatially complex or gradational habitat assemblages make delineation of boundaries more difficult (or impossible) without fine-scale data (McArthur et al., 2010). Thus, studies and conclusions in ecology have mostly been based on small-scale manipulative experiments (10 to 10^3 m) that rarely offer generality over large scales (Borer et al., 2014; Underwood, Chapman, & Connell, 2000). This is particularly the case for benthic marine systems, where the collection of data over large spatial scales at a fine resolution is logistically challenging.

Improvements in technology and increased capacity through the broader engagement of 'citizen scientists' in data collection have greatly improved access to marine benthic data, providing the opportunity for accelerated evolution of biogeographical classification and mapping (Diaz, Solan, & Valente, 2004; Newman et al., 2012). Here, we take advantage of citizen science and scientific monitoring initiatives that have allowed for fine-resolution data to be collected on macroecological scales. In the third largest exclusive economic zone, the shallow reefs off Australia's coasts extend from the tropics to the cool temperate regions and encompass some of the richest marine ecosystems on the planet (Huang, Stephens, & Gittleman, 2012; Williams et al., 2009), thereby providing an ideal study context for the investigation of factors contributing to the development and persistence of habitat types.

We provide a 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 *c.* 1,300 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 another and to form hypotheses about likely habitat transformation associated with changing climate and increasing anthropogenic stressors.

We provide a quantitative approach to habitat classification in combination with random forest and distance-based linear models to investigate relationships between the distribution of biogenic reef habitats (BRHs) and key environmental variables in a novel approach to a field previously approached using environmental surrogates or subjective descriptions.

2 | METHODS

2.1 | Study location

The study region encompassed shallow (< 20 m) marine reefs surrounding the Australian continent and associated offshore islands and shoals. Data were drawn from standardized quantitative surveys of reef communities globally through the Reef Life Survey programme (RLS; www.reeflifesurvey.com), and also in temperate Australia through the long-term marine protected area (LTMPA) monitoring programme (Barrett, Buxton, & Edgar, 2009).

Data from 1,679 surveys at 906 sites were included in the study, representing all sites surveyed by RLS divers in Australian waters during the study period for which photoquadrat data were readily available. Additional LTMPA data used in this study encompass 857 surveys at 393 sites distributed across a 4,000 km span of temperate Australian coasts from Jervis Bay (New South Wales) to Jurien Bay (Western Australia), including Tasmania (Figure 1). Both the RLS and LTMPA programmes aim to collect spatially dispersed data nationally and across temperate Australia, respectively. With the Australian Institute of Marine Sciences Great Barrier Reef Long-Term Monitoring programme,

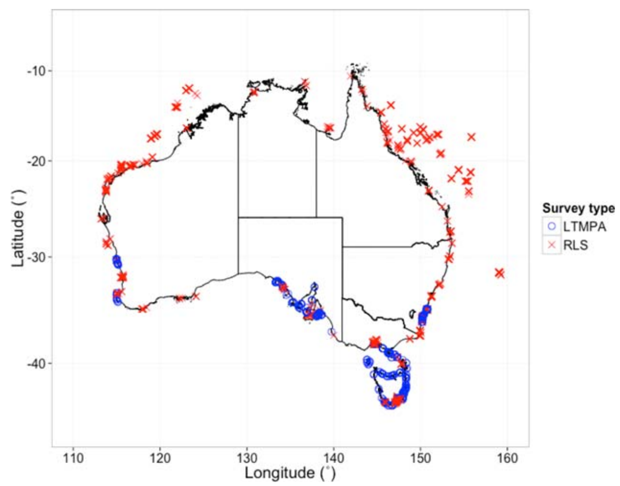

FIGURE 1 Locations of Australian field surveys included in analyses. Reef Life Survey (RLS) sites are shown by red crosses and Long-term Marine Protected Area (LTMPA) monitoring sites by blue circles

they contribute substantially to Australian State of the Marine Environment Reporting in the marine realm (Stuart-Smith et al., 2017).

2.2 | Survey methods and data amalgamation

Both the RLS and LTMPA surveys targeted sites characterized by hard substrata (i.e., rocky or coral reef) in depths < 20 m. The LTMPA surveys quantified macroalgae and sessile invertebrate species in 20 equidistant 0.5 m $\times$ 0.5 m quadrats along a 200 m transect line. Each quadrat was divided into a 7 $\times$ 7 grid giving 50 points (including one corner), under each of which the identity of the species present was recorded, to the lowest possible taxonomic level, usually to species or genus. The cover of overstorey/canopy species was recorded first, and then these were moved aside to expose the understorey for examination, meaning that $>$ 100% cover was possible (Barrett, Edgar, Buxton, & Haddon, 2007; Barrett et al., 2009).

The RLS surveys target the same reef types but collect 20 digital photoquadrats (PQs), each covering *c.* 0.3 m $\times$ 0.3 m along a 50 m transect line (see http://reeflifesurvey.com/files/2008/09/rils-reef-monitoring-procedures.pdf). Further details on the survey methods, including diver training, data quality assurance and data management, are covered by Edgar and Stuart-Smith (2009, 2014); Stuart-Smith et al. (2013). PQs were analysed using a five-point grid superimposed as a quincunx over each image, under which the uppermost layer of substrata biota was scored to give an estimate of percentage cover of 38 a priori-defined substratum functional groups. These groups are listed in Appendix S1 in Supporting Information and are aligned with the standardized Collaborative and Annotation tools for Marine Imagery and video (CATAMI) classification scheme used throughout Australia, as described by Althaus et al. (2015). CATAMI combines course-level taxonomy and morphology for the consistent classification of benthic substrates and biota in marine imagery. CATAMI classification categories relevant to Australian shallow marine reefs were chosen for the analyses here.

In order to increase the spatial coverage of data for this study and 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 understorey cover in LTMPA quadrats and only overstorey in RLS PQs. This was done by an ordered prioritization of the 50 points for canopy formers and then understorey. Permutational analysis of variance of data from sites at which both RLS and LTMPA surveys had been conducted was used to test whether the composition of substratum functional groups recorded from each of the survey types was comparable for the same sites and regions. The two survey types were found to give statistically consistent information, although marginal, on multivariate functional group structure, despite differences in survey year and some differences in depths for the replicate surveys compared from each method ($p = .067$; see Supporting Information Appendix S2).

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 between 2006 and 2013 to reduce the influence of potential long-term trends, while maintaining sufficient spatial coverage. Although transformation between habitats can occur (Ling, 2008), such phenomena are relatively rare. Consequently, 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.

2.3 | Classification of biogenic reef habitats

Initially, sites within 1° $\times$ 1° latitude–longitude grid cells were grouped, and the mean cover of substratum biota was considered for sites within these cells to minimize the effect of local-scale variation on the continental-scale pattern. Hierarchical cluster analysis was used to group cells that were most similar to each other. Initial clustering (Supporting Information Appendix S3) revealed a clear dichotomy that corresponded geographically to a tropical–temperate division (Figure 2). Tropical and temperate ‘realms’ were demarcated from this cluster analysis by considering the geography of the two dominant large groups in the primary analysis, with small and outlying groups merged with the larger groups according to latitudinal proximity. Principal coordinates analysis (PCaO) confirmed the clear separation of the two dominating tropical/temperate clusters, with 60.6% of the total variation captured (Supporting Information Appendix S3). Subsequent analyses could then be conducted separately for these two realms at a site resolution.

For the tropical analysis, macroalgal categories were binned because of low cover of macroalgae, whereas in the temperate realm

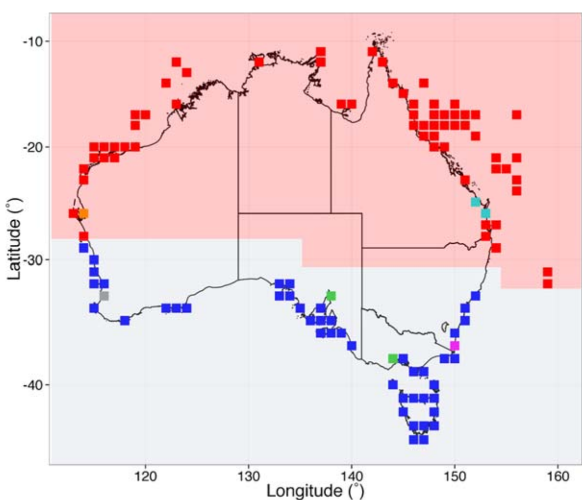

FIGURE 2 Geographical distribution of seven clusters formed from hierarchical clustering of 1° $\times$ 1° latitude–longitude grid cells. Two clusters dominated the analysis, one shown in red, populating the low latitudes, and the other shown in blue, populating the high latitudes. The small clusters are shown in orange at Shark Bay (Western Australia), grey at Geographe Bay (Western Australia), green in Upper Spencer Gulf (South Australia) and Port Phillip Bay (Victoria), pink at Eden (New South Wales) and aqua in southern Queensland

macroalgae dominated the patterns of diversity and abundance, so individual macroalgal categories were maintained. Stony corals were grouped together (Supporting Information Appendix S1).

The similarity profiles (Supporting Information Appendix S4) of the hierarchical cluster analyses of the tropical and temperate realms were examined to delineate the dominating clusters based on a percentage similarity cut-off that was chosen subjectively to yield a workable number of clusters at a point where small changes in the cut-off point did not drastically change the number of clusters. The temperate dendrogram was split at a similarity of 35%, whereas the tropical dendrogram was split at a similarity of 48%. Clusters with fewer than seven sites were examined individually and allocated to whichever of the larger clusters groups had greatest centroid similarity. The resulting clusters of sites were deemed to be distinct BRHs of Australia's shallow reef environment.

PCO was used to visualize the separation of the BRHs and confirm that the resulting groups aligned in ordination space. Vector overlays based on a Spearman correlation cut-off > 0.4 (Daniel, 1990) were then used to explore relationships between BRHs and dominant substrata.

All clustering and coordinate analyses were conducted in PRIMERv6 using Bray–Curtis matrices, square-root transformation of data and group average sorting strategy (Clarke & Gorley, 2006).

2.4 | Environmental and anthropogenic covariates

Nine physical, chemical and anthropogenic variables were used to gain a better understanding of the spatial relationships between prevalence and distribution of the BRHs (Supporting Information Appendix S5). Physical and chemical environmental data were sourced from the Commonwealth Scietific and Industrial Research Organization (CSIRO) and Geoscience Australia (see Huang et al., 2011; Ridgway, Dunn, & Wilkin, 2002). Some potential variables, such as slope and relief bathymetry, oxygen, salinity and chlorophyll, were not considered because of known inaccuracy near the coast or inadequate resolution of the available data. Each site was assigned the environmental characteristics of the closest node on a 0.5° latitude–longitude grid.

The variables included because of known important roles in structuring marine benthic communities elsewhere (McArthur et al., 2010; O'Hara & Poore, 2000; Wernberg et al., 2013) comprised sea surface temperature (mean and *SD*), spatial predictors (distance to coast and distance into estuaries for temperate sites given that *c*. 19% of temperate sites were located $<$ 5 km from or within estuaries) and physical and chemical variables (wave exposure, cyclone stress, average site depth, nitrate and phosphate). Nitrate and phosphate were both initially considered as proxies for nutrient levels but were found to be highly correlated ($r > .65$), so only mean nitrate was used in models. A wave exposure index was calculated from wave height and period available from the AusWAM 11-year hindcast model (WAMDI Group, 1988) for the temperate sites. These data were not available for tropical sites. For the tropics, a variable describing cyclone stress was calculated as the maximal wind speed of any cyclone occurring within 150 km of each site in the previous decade, using data from the NOAA International Best Track Archive for Climate Stewardship (IBTrACTS) dataset (https://www.ncdc.noaa.gov/ibtracs/).

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 protection status of each site was also scored as 'no take', 'restrictions on fishing gear type' or 'no restrictions on fishing'.

2.5 | Covariate analysis

Distance-based linear modelling (DISTLM; Anderson, Gorley, & Clarke, 2008) was used to examine the performance of each environmental variable in explaining the variation in substratum cover between different sites and between different BRHs. Draughtsman's plots of the individual covariates were used to detect extreme bivariate correlations ($r \geq .65$) and to determine whether distributions were skewed. A natural logarithm transformation was used to correct skewness where necessary. DISTLM was performed on separate Bray–Curtis similarity matrices for temperate and tropical realms 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 selection procedure with 9,999 permutations. Distance-based redundancy analysis (dbRDA) was then used to test how well environmental and anthropogenic variables explained variability in site data. Vector overlays ($r > .4$) illustrated the importance and magnitude of each individual physical variable in explaining variability in the data cloud.

Random forest (RF) models were used to assess which environmental and anthropogenic variables were most closely associated with each BRH. A RF approach deals with nonlinear relationships and interactions among predictors, as often occur with environmental variables. Two thousand five hundred trees were generated for each analysis. Variable importance plots were used to assess the importance of each predictor variable in the temperate and tropical models and for each BRH in isolation. Partial dependence plots (Cutler et al., 2007) were used to provide graphical representation of the marginal effect of the predictor variables on the probability of each BRH. All random forest modelling was conducted using the *randomForest* function in the *randomForest* package (Liaw & Wiener, 2002) in R (R Core Team, 2014).

3 | RESULTS

3.1 | Biogenic reef habitats

The geographical distribution of clusters showed a biogeographical dichotomy between tropical and temperate latitudes (Figure 2). Hierarchical cluster analysis of sites within the temperate realm yielded four large clusters (each $>$ 28 sites), whereas for the tropical realm five large clusters were formed (each $>$ 33 sites; Supporting Information Appendix S4). PCO showed some overlap of clusters, but overall the four temperate and five tropical clusters were distinguishable on ordination

(Figure 3). The first two PCO axes for the temperate sites explained 47.2% of the total variation, whereas for the tropical sites it was 45.2%, indicating that the two-dimensional projections capture nearly half of the salient patterns in the full data clouds. Clusters were each characterized by distinct combinations of the mean cover of substratum groups and were named as separate BRHs accordingly (Table 1).

In the temperate realm, the most widespread and prevalent BRH was canopy algae, occurring in all regions surveyed (Figure 4a). Sites in the barren BRH were highly concentrated on the New South Wales coast, together with a few sites on the Victorian and eastern Tasmanian coasts (Figure 4b). Epiphytic algae–understorey BRH occurred in a patchy range of locations in southern Australia and Tasmania (Figure 4c), whereas the turf BRH occurred at six distinct locations on the Australian coast (Figure 4d).

Tropical BRHs showed a greater mosaic in geographical distribution compared with the temperate BRHs (Figure 4e–i). In addition, the tropical BRHs were less clearly defined by particular substratum groups, with all BRHs except the foliose algae BRH containing a mix of coral categories (Table 1).

The 'coral' BRH occurred in nearly all regions around tropical Australia, although it was concentrated on the inshore Queensland coast, inside the Great Barrier Reef. The 'turf–coral' BRH occurred at most survey locations. 'Coral–bacterial mat' occurred in patchy distribution across the tropical realm. The 'calcified algae–coral' BRH occurred at the most sites and dominated the offshore locations (the Coral Sea and the North West Shelf). 'Foliose algae' was confined to the southern part of the tropical region in North East Australia, whereas on the west coast this habitat was evident as far north as the Kimberleys. The turf BRH did not occur at sites surveyed around most of northern Australia and the Great Barrier Reef.

3.2 | Environmental and anthropogenic correlates

DISTLM marginal tests for the temperate sites identified all covariates to have a significant 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%, $p < .001$), whereas the human population index explained 6.1% of variation ($p < .001$). The best model for the temperate realm included all variables and explained 23.5% of total variation. However, sequential tests showed mean SST, mean nitrate, estuarine index and SST standard deviation (henceforth SST *SD*) cumulatively to explain a major proportion, 19.1%, of total variation.

The DISTLM marginal tests for the tropical sites showed that SST *SD* explained 7.3% ($p < .001$) of the variation in the data cloud. Distance to coast and mean SST explained similar proportions: 7.2 ($p < .001$) and 5.9% ($p < .001$), 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 (Supporting Information Appendix S7).

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 (Figure 5a). Comparison of the dbRDA ordination to the corresponding PCO based on temperate data (Figure 3a) indicated that 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–understorey 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.

The first two axes of the tropical dbRDA ordination explained 78.0 and 18.3% of the fitted and total variation, respectively (Figure 5b). As for the temperate case, comparison of the dbRDA plot with the corresponding PCO plot (Figure 3b) showed distortion between the model representation and the true ordination. The calcified algae–coral BRH sites were densely clustered and loosely aligned with increasing distance from the coast, decreasing human population index and increasing mean SST and site depth. Both the turf–coral and the foliose algae groups appeared to align with increased SST *SD* and decreasing mean SST. Coral–bacterial mat aligned loosely with increasing human population indices. The coral BRH was comparably scattered and with no obvious alignment with variables in the dbRDA model.

3.3 | Environmental and anthropogenic variables as predictors for habitat

Tropical and temperate RF models built from the environmental and anthropogenic variables 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 (percentage of sites classified incorrectly). The RF variable importance plots (Figure 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.

Depending on the BRH, different variables were more important for prediction and therefore more highly correlated with a particular BRH (Figure 7). Partial dependence plots (Supporting Information 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 (Figure 7).

Nitrate was the most important predictor variable for the canopy algae BRH, although 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 (Figure 7a; Supporting Information Appendix S8). The barren BRH was best predicted by mean SST, with partial dependence plots indicating that this habitat was more likely with greater mean SSTs as well as increases in human population index and mean nitrate (Figure 7b). RF models found that epiphytic algae–understorey BRH was

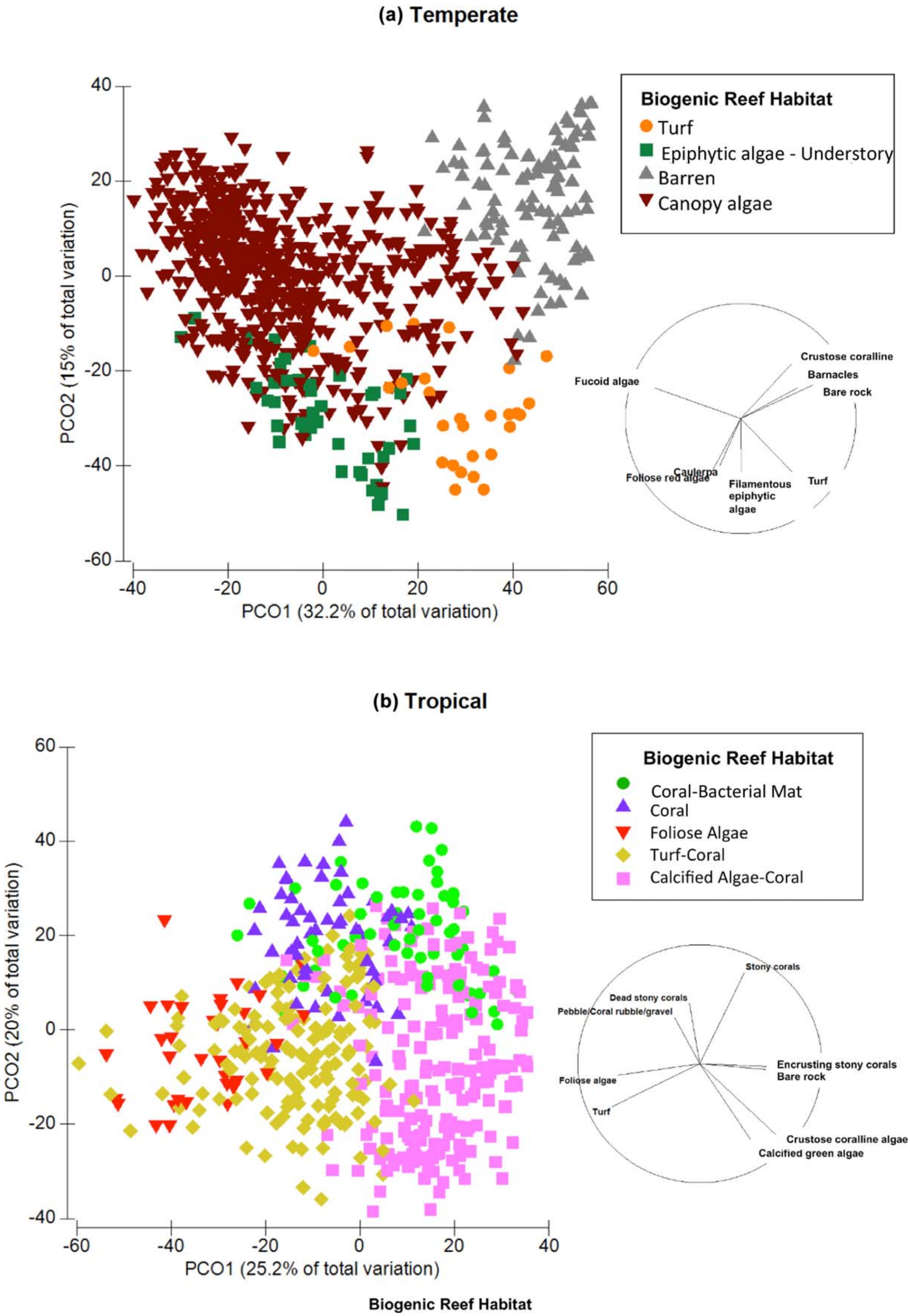

FIGURE 3 Principal coordinates ordination (PCaO) plot of (a) temperate sites and (b) tropical sites based on the estimated cover of substratum biota. The colours/shapes show, in (a) the four and in (b) the five biogenic reef habitats (BRHs) formed from hierarchical cluster analysis. Vector overlays show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

TABLE 1 Nine clusters classified from analyses of sites in the tropical and temperate realms with the mean percentage cover of each of the Reef Life Survey substratum biota categories

Biogenic reef habitat	Temperate				Tropical				
	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**

Note. Percentage cover has been rounded to zero decimal places. Reef Life Survey substratum biota categories with $<$ 5% cover in any biogenic reef habitat (BRH) are not shown here. The full table is available for reference in Appendix S6 in Supporting Information. Bold and italics numbers are those with $>$ 5% cover.

best predicted by exposure, with mean SST and human population also highly ranked. Partial plots did not show a clear relationship for exposure; this BRH was encountered at sites with both low and high exposure values, with lower frequency between. Exposure and SST mean and *SD* were the most important predictors for the turf BRH. As both exposure and SST *SD* increased, the probability of turf decreased, whereas a clear relationship with mean SST was not evident.

The tropical BRHs also showed variability in the most highly ranked predictor variables (Figure7e–i). Coral–bacterial mat BRH was most closely associated with the variables *SD* and mean SST, with partial dependence plots showing that this habitat was unlikely at SST *SD* $<$ 1.5 °C, and likelihood increased at high *SD* values. As mean SST increased from 22 to 24 °C the likelihood of this habitat increased, but at higher temperatures the relationship became variable and noisy (Supporting Information Appendix S8). The coral BRH was most closely associated with distance to coast and SST *SD*; however, the relationship with distance to coast varied in a complex manner. Coral BRH was more likely at mean SST $>$ 27 °C and at low *SD*s.

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 SST and increasing distance to coast. Calcified algae–coral was best predicted by distance to coast, being most probable farther from shore, at low SST *SD* and high mean SST. The foliose algae BRH was most closely associated with human population, distance to coast and mean SST. The relationship with distance to coast was not obvious, but partial dependence plots showed higher likelihood at high human population indices and as mean SST decreased.

4 | DISCUSSION

4.1 | Biogenic reef habitats

On the basis of quantitative analyses, the present study identified nine distinct broad-scale 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

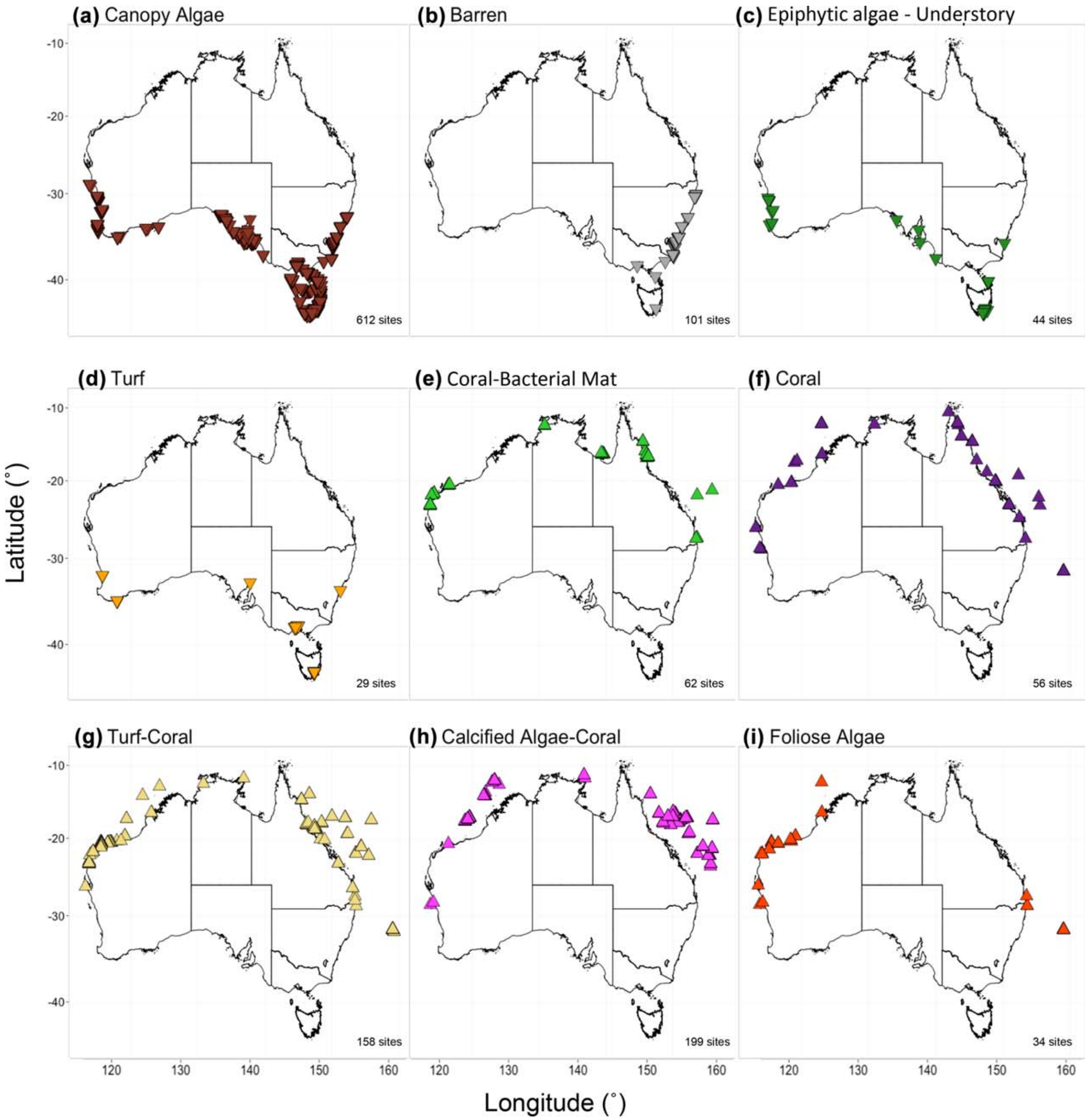

FIGURE 4 Geographical distribution of the nine biogenic reef habitats (BRHs), defined through hierarchical cluster analyses. Panels (a–d) show Australia with south-facing triangles indicating the distribution of the four temperate BRHs: (a) canopy algae, (b) barren, (c) epiphytic algae–understorey and (d) turf. (e–f) 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, respectively

'biological facies' or 'map-able units characterized by groups of particular species of coral, sponges, algae and other macrobiotic groups'). Last et al. (2010) considered that, although species are the fundamental units of biodiversity, biological facies comprise the smallest practical unit for conservation management at regional scales.

The major demarcation between tropical and temperate realms, when assessed at the coarse spatial resolution of 1° × 1° latitude–longitude grid cells, was expected given the known differences in species distributions in tropical versus temperate Australia, and matched the bioregional realms previously defined by Spalding et al. (2007): the Central Indo-Pacific and the Temperate Australasian.

Four BRHs were defined in the temperate realm and five in the tropical realm, each distinguished by a particular make-up of substratum biota. However, distinctions were subtler than expected, particularly in the tropical realm. Most BRHs contained a mixture of substratum functional groups that co-occurred in different proportions, rather than pure stands of a particular functional group (e.g., corals were conspicuous elements of four of the five tropical BRHs). Inshore reef habitats appear to be considerably more complex than generally recognized in subjective habitat classifications where dominant functional groups are recognized (e.g., kelp, turf). Thus, at the 50–200 m span of sites examined, functional groups such as branching coral did

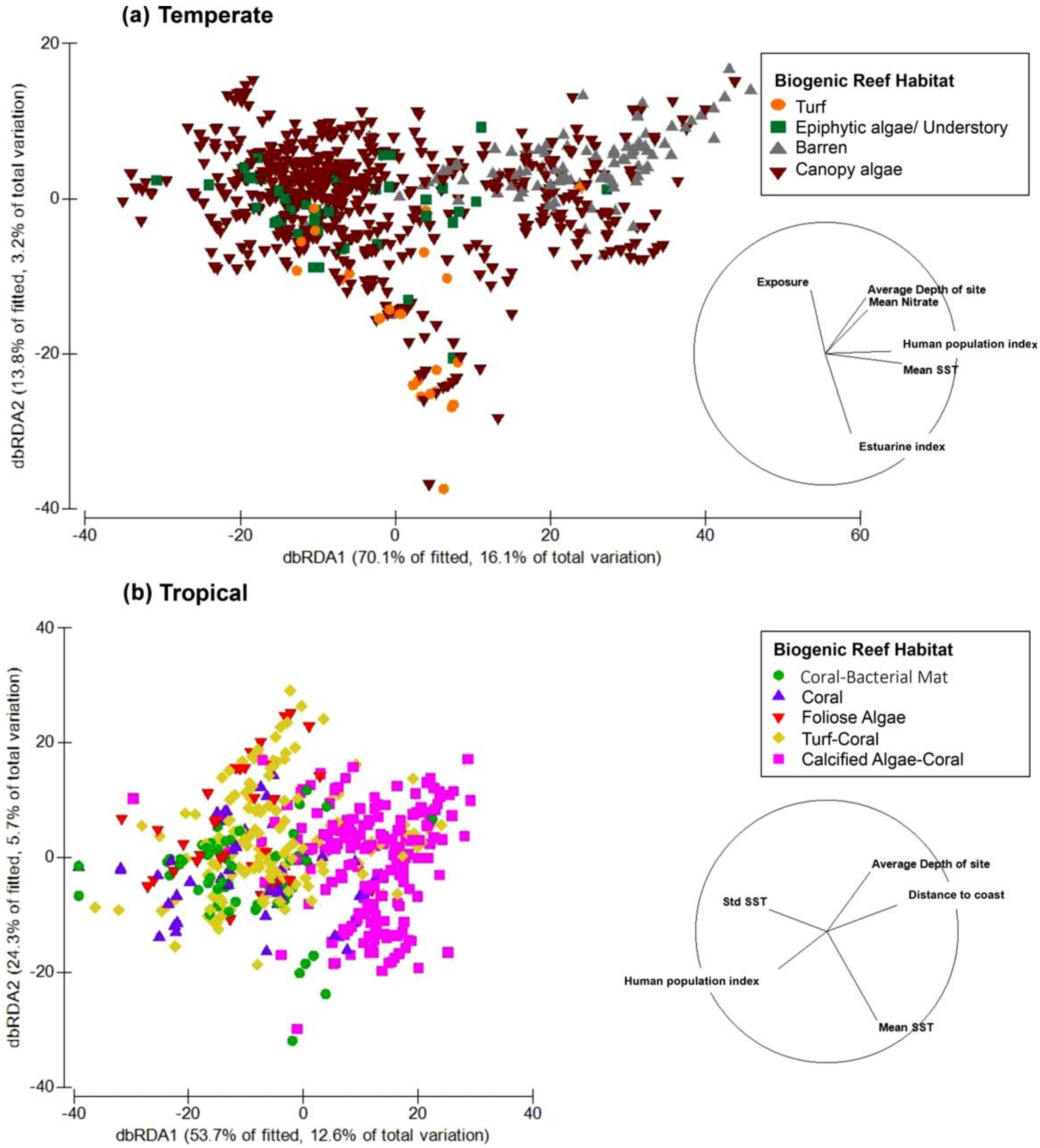

FIGURE 5 Distance-based redundancy analysis (dbRDA) ordinations of (a) temperate sites and (b) tropical sites identifying the greatest variation between sites based on the cover of substratum functional groups. The vector overlay shows the most strongly correlated environmental variables calculated from the multiple partial correlations ($r > .4$)

not consistently occur as monotypic entities, but were interspersed with soft corals, dead coral, turf and a variety of other coral forms (including massive and encrusting corals).

4.2 | Temperate habitats

The dominant habitat identified in temperate Australia is characterized by large brown canopy-forming macroalgae (Fucales and Laminariales). A similar habitat is present in most of the world's temperate oceans (Bolton, 2010; Steneck et al., 2002). Globally, altered environmental regimes, some the direct result of anthropogenic stressors, such as pollution, and others more indirect, arising from flow-on effects of fishing and climate change, are leading to widespread loss of structurally complex habitats that support diverse communities (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Connell et al., 2008; Johnson et al., 2011). Airoldi, Balata, and Beck (2008) describe this change as a 'flattening' of the marine environment, with replacement of structurally complex habitats by more two-dimensional counterparts. Canopy algae and epiphytic algae–understorey BRHs in the present study represent architecturally complex habitats that are juxtaposed with the barren BRH, characterized by bare rock and crustose coralline algae, and turf BRH, characterized by low-lying mats of turfing algae.

Mean SST was found to be the most important correlate of tropical and temperate BRHs. Increased SST was positively correlated with

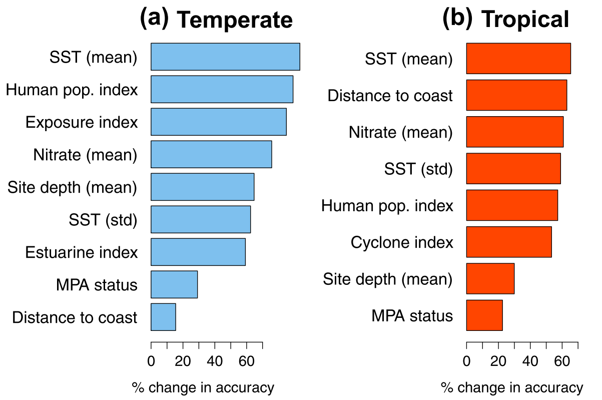

FIGURE 6 Random forest variable importance plots for (a) the temperate model and (b) the tropical model. Classification errors associated with temperate and tropical models were 15.3 and 24.6%, respectively. Plots show the relative importance of the (a) nine and (b) eight covariates in correctly predicting the habitat at a given site. The percentage change in accuracy for a given predictor variable is measured by the change in error rate between models that include or do not include that predictor variable (i.e., a larger value means that variable was more influential in correctly predicting habitat type). Model output is based on 2,500 trees

the 'flat' habitats (the barren and the turf BRH) and negatively correlated with the structurally complex canopy algae and epiphytic algae–understorey BRHs. This is a concern given increasing ocean temperatures observed and predicted, suggesting that long-term warming could contribute to the 'flattening' of marine habitats. Furthermore, human population was the second most important predictor variable for the temperate RF model and was positively correlated with barren BRH and negatively correlated with canopy algae and epiphytic algae–understorey. Thus, our results consistently suggest that increasing sea temperature and human population growth both represent key threats to reef habitats and biodiversity via impacts to structurally complex habitats that support diverse reef-associated communities. For future studies, examining structural complexity more quantitatively at the site level would be beneficial; however, this metric was not available for all sites in the present study (Alexander, Barrett, Haddon, & Edgar, 2009).

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

High human population indices were also associated with the barren BRH, perhaps a consequence of fishing pressure for the key predators of the urchins responsible for creating this BRH, such as the southern rock lobster (*Jasus edwardsii*), blue groper (*Achoerodus viridis*) and pink snapper (*Pagras auratus*) (Ling, Johnson, Frusher, & Ridgway, 2009; Pederson & Johnson, 2006). 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).

4.3 | Tropical habitats

Tropical coral reefs support some of the most diverse marine ecosystems on earth (Green, Bellwood, & Choat, 2009; Sala & Knowlton, 2006), but vary substantially both in the amount of live coral cover and their structural complexity. Five distinctive tropical BRHs were identified here, namely coral, coral–bacterial mat, calcified algae–coral, turf–coral and foliose algae. These were arranged in a complex manner, both in composition and in spatial distribution.

As for the temperate realm, the major correlate of BRHs in the tropical realm was mean SST according to both DISTLM and RF results. Variation in SST was a stronger correlate in the tropical realm than the temperate, perhaps reflecting low tolerance of corals and other tropical sessile biotic groups to variation in temperature anomalies. The coral BRH was characterized by a diverse array of different coral elements (the genera *Pocillopora* and *Acropora*, bleached and dead coral, branching, massive, encrusting and soft corals) and possessed a strong negative relationship with SST variability. This, in combination with the coral BRH occurring frequently at some of the warmest Australian locations ($>$ 27 °C mean SST), indicates vulnerability to bleaching if the frequency of warm-water events continues to increase.

Turfing algae is a common feature on most coral reefs. This habitat supports a diverse array of herbivores (Green et al., 2009), which use production generated by fast growth and high turnover regardless of low standing biomass. The turf–coral BRH had *c*. 40% mean cover of turfing algae and was associated with high mean SST and large distances offshore. It was present at 158 of 509 tropical survey sites in almost all surveyed regions. Although 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.

A turfing algae-dominated state has been proposed to occur as an alternative stable state to coral in tropical ecosystems (Green et al., 2009; Norström, Nyström, Lokrantz, & Folke, 2009). In addition to herbivorous fishes, nutrient and light levels are considered important variables in transitions, with high nutrients and low light levels providing turfing algae with a competitive advantage over corals, particularly after disturbances such as cyclones (Hughes et al., 2007). In the present study, the turf–coral BRH was positively associated with mean nitrate

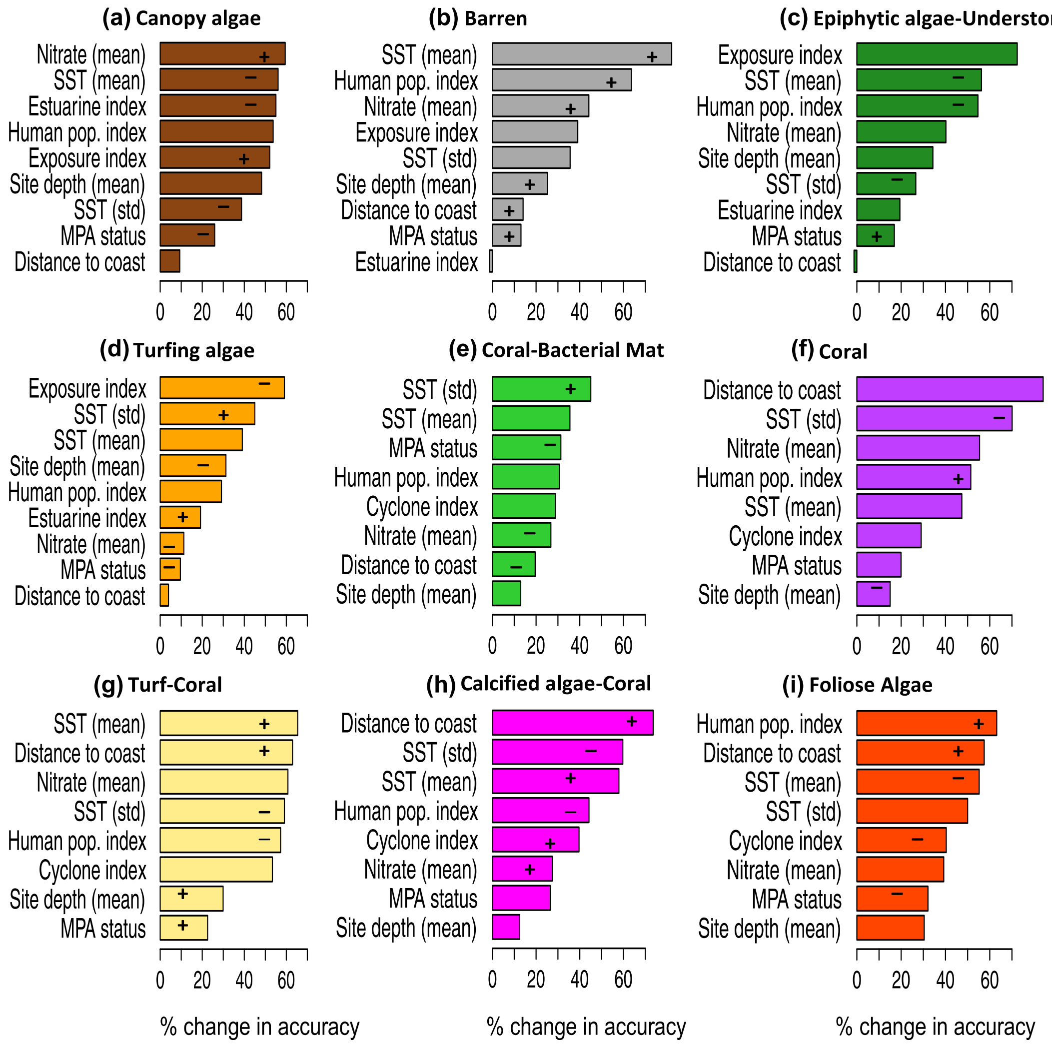

FIGURE 7 Results of random forest analyses showing the relative importance of the (a–d) nine and (e–i) eight covariates used to predict the habitats at a given site. (a–d) The relative importance of the predictors for each temperate biogenic reef habitat (BRH) and (e–i) the relative importance of the predictor variables for each of the tropical BRHs. The percentage change in accuracy for a given predictor variable is measured by the change in error rate between models that include or do not include that predictor variable (e.g., if mean nitrate is excluded from the model, what does that mean for the prediction accuracy for each habitat?). 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

concentrations, whereas the coral BRH was negatively associated with nitrate concentrations, supporting the hypothesis that elevated nutrients provide a potential competitive advantage for turfs.

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 was most prevalent in areas of high variation in SST. The geographical distribution of the coral–bacterial mat BRH did not give a clear indication of oceanic conditions associated with this habitat. Turbidity might 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, but was not considered in the present study (Fabricius, De'ath, McCook, Turak, & Williams, 2005). Coral–bacterial mat occurred in locations with high amounts of suspended sediment in the water column attributable to large tidal movement in northwestern Australia and in the Gulf of Carpentaria (Burford, Alongi, McKinnon, & Trott, 2008; Somers & Long, 1994).

Foliose algae, with a distribution on the east coast localized near the Queensland–New South Wales 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 might signify that more frequent anthropogenic disturbance is decreasing coral resilience and allowing macroalgae to expand, although given this habitat occurred most frequently in the temperate–tropical realm transition, competition between tropical and temperate species is perhaps a more likely driver.

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

The DISTLM models captured only a small proportion of total variation in the tropical models, suggesting that 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 present study but will 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 because of the coarse grain of available covariate data (typically *c.* 5 km; Supporting Information Appendix S5).

4.4 | Conclusions

This study examined patterns associated with reef habitat types over a continental scale using field survey data and includes important inference about process at the habitat level. Nine BRHs were delineated, four in the temperate realm and five in the tropical realm, all characterized by unique functional sets of algae, sessile invertebrates and corals. Relationships identified between the objectively defined BRHs and environmental variables allowed formulation of conceptual models associated with potential threats to coastal systems (such as increasing mean SST will lead to decline in the canopy algae and increase in the barren BRHs). Further research might allow these relationships to be extended to predict the likelihood of a BRH persisting through time in any given location, ultimately allowing environmental covariates to be used as surrogates for cost-effective monitoring. Such an approach should nevertheless be regarded as an addition rather than alternative to ongoing benthic monitoring, given that important covariates were probably overlooked in our study, and unrecognized ecological interactions were probably also present. Improved ecological monitoring can be achieved through extended application of citizen science, such as through the Reef Life Survey programme. Further monitoring will allow conceptual models to be tested and refined, using the current distribution of habitats as a baseline for assessing future change. Models outlined indicate likely influences of local as well as global stressors, providing guidance to management efforts.

In particular, the association of many BRHs with temperature, human population and proximity to major cities provides a clear warning in the context of changing climate and increasing anthropogenic stress to global marine systems. Particular habitats, including some previously considered common, such as canopy-forming algae and coral communities, are threatened.

DATA ACCESSIBILITY

See Supporting Information for more detailed information on analyses, and for the geographical locations of sites within each habitat type see Appendix S9.

ACKNOWLEDGMENTS

We would like to thank all contributors to the Reef Life Survey and Temperate Australian Marine Protected Areas monitoring programmes with special thanks to all persons involved in the analysis of photoquadrats. Analyses were facilitated by the Australian Research Council and the Marine Biodiversity Hub, a collaborative partnership supported through the Australian Government's National Environmental Science Programme. We acknowledge the CSIRO Marine Laboratories as the source of the CARS2009 environmental data. We gratefully acknowledge Toni Cooper and Just Berkhout for assistance with the RLS dataset. Thanks also to Simon Wotherspoon, Nicole Hill, Martin Marzloff, Nick Perkins, Amelia Fowles and Luis Antipa for their interest and advice regarding the research; to Stuart Kininmonth for contributing the human population index; to Geoff Hosack for matching the cyclone data to the study sites; and to George Cresswell and Susan Blackburn for effective and valuable editing and comments on drafts.

ORCID

Anna K. Cresswell http://orcid.org/0000-0001-6740-9052
Graham J. Edgar http://orcid.org/0000-0003-0833-9001
Rick D. Stuart-Smith http://orcid.org/0000-0002-8874-0083

REFERENCES

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., . . . Colquhoun, J. (2015). A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: the CATAMI classification scheme. *PLoS One*, *10*, e0141039.

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 3019–3025.

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. Plymouth, U.K.: PRIMER-E.

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.

Bolton, J. J. (2010). The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgoland Marine Research*, *64*, 263.

Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., & Smith, M. D. (2014). Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution*, *5*, 65–73.

Burford, M. A., Alongi, D. M., McKinnon, A. D., & Trott, L. A. (2008). Primary production and nutrients in a tropical macrotidal estuary, Darwin Harbour, Australia. *Estuarine, Coastal and Shelf Science*, *79*, 440–448.

CIESIN. (2014). *Gridded population of the world, version 4 (GPWv4) 2010*. Columbia University, NY: Center for International Earth Science Information Network.

Clarke, K. R., & Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth, pp. 192.

Connell, S. D., & Irving, A. D. (2008). Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *Journal of Biogeography*, *35*, 1608–1621.

Connell, S., Russell, B., Turner, D., Shepherd, A., Kildea, T., Miller, D., . . . Cheshire, A. (2008). Recovering a lost baseline: missing kelp forests from a metropolitan coast. *Marine Ecology Progress Series*, *360*, 63–72.

Costello, M. J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., & Miloslavich, P. (2010). A census of marine biodiversity knowledge, resources, and future challenges. *PLoS One*, *5*, e12110.

Cracknell, A. P. (1999). Remote sensing techniques in estuaries and coastal zones an update. *International Journal of Remote Sensing*, *20*, 485–496.

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, *88*, 2783–2792.

Daniel, W. W. (1990). *Applied nonparametric statistics* (2nd ed.). Boston, MA: Houghton Mifflin.

Diaz, R. J., Solan, M., & Valente, R. M. (2004). A review of approaches for classifying benthic habitats and evaluating habitat quality. *Journal of Environmental Management*, *73*, 165–181.

Douvere, F. (2008). The importance of marine spatial planning in advancing ecosystem-based sea use management. *Marine Policy*, *32*, 762–771.

Drew, E. (1983). Halimeda biomass, growth rates and sediment generation on reefs in the central great barrier reef province. *Coral Reefs*, *2*, 101–110.

Edgar, G. J., & Stuart-Smith, R. D. (2009). Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Marine Ecology Progress Series*, *388*, 51–62.

Edgar, G. J., & Stuart-Smith, R. D. (2014). Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data*, *1*, 140007.

Fabricius, K., De'ath, G., McCook, L., Turak, E., & Williams, D. M. (2005). Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin*, *51*, 384–398.

Gorgula, S., & Connell, S. (2004). Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology*, *145*, 613–619.

Green, A. L., Bellwood, D. R., & Choat, H. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience. A practical guide for coral reef managers in the Asia Pacific Region*. Gland, Switzerland: IUCN. Retrieved from http://cmsdata.iucn.org/downloads/resilience_herbivorous_monitoring.pdf

Halpern, B. S., McLeod, K. L., Rosenberg, A. A., & Crowder, L. B. (2008). Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean and Coastal Management*, *51*, 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 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*. Canberra, ACT, Australia: Geoscience Australia. csiro: EP104155.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., . . . Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, *17*, 360–365.

Irving, A. D., Connell, S. D., & Gillanders, B. M. (2004). Local complexity in patterns of canopy–benthos associations produces regional patterns across temperate Australasia. *Marine Biology*, *144*, 361–368.

Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J. . . . 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.

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.

Liaw, A., & Wiener, M. (2002). Classification and regression by random forest. *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 USA*, *106*, 22341–22345.

Marzinelli, E. M., Williams, S. B., Babcock, R. C., Barrett, N. S., Johnson, C. R., Jordan, A., . . . Steinberg, P. D. (2015). Large-scale geographic variation in distribution and abundance of Australian deep-water kelp forests. *PLoS One*, *10*, e0118390.

McArthur, M. A., Brooke, B. P., Przeslawski, R., Ryan, D. A., Lucieer, V. L., Nichol, S., . . . 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., . . . Williams, A. (2011). Effectiveness of biological surrogates for predicting patterns of marine biodiversity. *PLoS One*, *6*, e20141.

Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S., & Crowston, K. (2012). The future of citizen science: Emerging technologies and shifting paradigms. *Frontiers in Ecology and the Environment*, *10*, 298–304.

Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: Beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series*, *376*, 295–306.

O'Hara, T. D., & Poore, G. C. B. (2000). Patterns of distribution for southern Australian marine echinoderms and decapods. *Journal of Biogeography*, *27*, 1321–1335.

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.

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ridgway, K. R., Dunn, J. R., & Wilkin, J. L. (2002). Ocean interpolation by four-dimensional least squares_application to the waters around Australia. *Journal of Atmospheric and Oceanic Technology*, *19*, 1357.

Roff, J. C., & Evans, S. M. J. (2002). Frameworks for marine conservation — Non-hierarchical approaches and distinctive habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *12*, 635–648.

Sala, E., & Knowlton, N. (2006). Global marine biodiversity trends. *Annual Review of Environment and Resources*, *31*, 93–122.

Seddon, S., Connolly, R. M., & Edyvane, K. S. (2000). Large-scale seagrass dieback in northern Spencer Gulf, South Australia. *Aquatic Botany*, *66*, 297–310.

Somers, I., & Long, B. (1994). Note on the sediments and hydrology of the Gulf of Carpentaria, Australia. *Marine and Freshwater Research*, *45*, 283–291.

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., ... Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience*, *57*, 573–583.

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, *29*, 436–459.

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., ... Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, *501*, 539–542.

Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Bates, A. E., Baker, S. C., Bax, N. J., ... Brock, D. J. (2017). Assessing national biodiversity trends for rocky and coral reefs through the integration of citizen science and scientific monitoring programs. *BioScience*, *67*, 134–146.

Tilman, D., & Lehman, C. (2001). Human-caused environmental change: Impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences USA*, *98*, 5433–5440.

Underwood, A. J., Chapman, M. G., & Connell, S. D. (2000). Observations in ecology: You can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*, *250*, 97–115.

WAMDI Group. (1988). The WAM model—A third generation ocean wave prediction model. *Journal of Physical Oceanography*, *18*, 1775–1810.

Wernberg, T., Thomsen, M. S., Connell, S. D., Russell, B. D., Waters, J. M., Zuccarello, G. C., ... Gurgel, C. F. (2013). The footprint of continental-scale ocean currents on the biogeography of seaweeds. *PLoS One*, *8*, e80168.

Williams, A., Bax, N. J., Kloser, R. J., Althaus, F., Barker, B., & Keith, G. (2009). Australia's deep-water reserve network: Implications of false homogeneity for classifying abiotic surrogates of biodiversity. *ICES Journal of Marine Science*, *66*, 214–224.

Wondolleck, J. M., & Yaffee, S. L. (2017). *Marine ecosystem-based management in practice: Different pathways, common lessons*. Island Press, Washington, pp. 271.

BIOSKETCH

The authors' research focuses on better understanding of broad-scale trends in rocky and coral reef biodiversity related to pressures such as fishing, ocean warming, invasive species and pollution. Analysis of data collected using standardized methods from the Reef Life Survey programme allows the tackling of uniquely broad questions, which encompass not only coral reefs but also rocky reefs from the Antarctic to the Arctic. The research group's ultimate goal is to improve monitoring, reporting, management and protection of marine biodiversity.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Cresswell AK, Edgar GJ, Stuart-Smith RD, Thomson RJ, Barrett NS, Johnson CR. Translating local benthic community structure to national biogenic reef habitat types. *Global Ecol Biogeogr*. 2017;00:1–14. https://doi.org/10.1111/geb.12620