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Species Richness and Community Structure on a High Latitude Reef: Implications for Conservation and Management

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Abstract: In spite of the wealth of research on the Great Barrier Reef, few detailed biodiversity assessments of its inshore coral communities have been conducted. Effective conservation and management of marine ecosystems begins with fine-scale biophysical assessments focused on diversity and the architectural species that build the structural framework of the reef. In this study, we investigate key coral diversity and environmental attributes of an inshore reef system surrounding the Keppel Bay Islands near Rockhampton in Central Queensland, Australia, and assess their implications for conservation and management. The Keppels has much higher coral diversity than previously found. The average species richness for the 19 study sites was ~40 with representatives from 68% of the ~244 species previously described for the southern Great Barrier Reef. Using scleractinian coral species richness, taxonomic distinctiveness and coral cover as the main criteria, we found that five out of 19 sites had particularly high conservation value. A further site was also considered to be of relatively high value. Corals at this site were taxonomically distinct from the others (representatives of two families were found here but not at other sites) and a wide range of functionally diverse taxa were present. This site was associated with more stressful conditions such as high temperatures and turbidity. Highly diverse coral communities or biodiversity 'hotspots' and taxonomically distinct reefs may act as insurance policies for climatic disturbance, much like Noah's Arks for reefs. While improving water quality and limiting anthropogenic impacts are clearly important

management initiatives to improve the long-term outlook for inshore reefs, identifying, mapping and protecting these coastal 'refugia' may be the key for ensuring their regeneration against catastrophic climatic disturbance in the meantime.

Keywords: coral; diversity; biodiversity; inshore reef

1. Introduction

In spite of their preeminence as one of the most biologically diverse ecosystems on earth, coral reefs have declined in biodiversity, habitat quality and area over the past two to three decades. A prime example of this is the Indo-Pacific region, which encompasses 75% of the world's tropical reefs, and has experienced an estimated decline of ~1–2% per year in coral cover over the past few decades [1-3]. Many coral species are now listed as "critically endangered" (6 spp.), or "endangered" (23 spp.) or "vulnerable" (199 spp.) by the International Union for Conservation of Nature [4,5]. A recent study of massive *Porites* colonies on the Great Barrier Reef has also revealed an alarming 21% decline in calcification rates since 1994 suggesting that not only are reefs losing species and habitat but that massive corals are struggling to maintain their pre-1994 accretion rates [6,7]. Although some reefs have demonstrated strong regeneration following disturbance [8], reefs can only recover if they have a good supply of larvae and the conditions are conducive to settlement and growth. The influence of land runoff on water quality [9] means that many reefs are no longer able to recover and many have already undergone phase shifts [10]. Remote and isolated reefs are also starved of larval supply and shorter return times between disturbances puts more and more reefs at risk of undergoing phase shifts [11]. Complex recovery trajectories also mean that recovering reefs do not necessarily return to their original species composition [12,13].

The causes of coral reef degradation vary both locally and regionally but the trends of declining species diversity, coral cover and calcium carbonate accretion are expected to continue given that global sea temperatures and $p\mathrm{CO_2}$ are expected to increase by 2050 [14]. While current global management models are focused on implementing marine reserves and are showing promise for the protection of fish stocks [15], insuring against predator outbreaks [16] and promoting coral cover following disturbance [17]; the loss of species diversity that can accompany such disturbance and recovery may mean that recovered reefs are less functionally diverse. The alarming trends of declining species diversity, loss of reef habitat and accretion rates call for an urgent re-assessment of current management models and practices and an improved understanding of the key factors that contribute to regional scale variations in reef resilience.

The biological diversity of the corals found on reefs is inextricably linked to ecosystem function and their capacity to return to former states following disturbance [18]. Even pristine reefs can rapidly undergo phase shifts [19] to macro-algal dominated states that may take decades to return to coral dominance [20]. High species diversity contributes greater potential variation in the reef's response to disturbance whilst still remaining in a coral-dominated state [21] because a variety of species provides enhanced functional complementarity [22]. The addition or removal of one or a few species has the potential to have profound impacts on the dynamics and persistence of other marine fauna in the

system [23,24]. Coral biodiversity is influenced in part by competition between species and by the availability of a variety of habitat types suitable for growth [25]. Maintenance of coral biodiversity is therefore contingent on protection from processes that reduce this competition as interruptions to species competition can shift the whole system to a stable but functionally less diverse state [26] with ultimate consequences for other marine organisms [27].

Regional-scale coral cover and biodiversity patterns vary according to the availability and area of suitable habitat that suit particular functional groups [28] as well as the reefs history and response to disturbance [29]. In particular, near-shore reefs are most at risk of coral losses because they typically experience more frequent and severe temperature stress [30,31], have higher sedimentation and dissolved inorganic nutrient levels [9] and lower coral biodiversity [32]. The lower baseline diversity on inshore reefs may make them more vulnerable because important family or functional groups that are capable of responding to environmental variability may already be missing or present in low abundance. Causal factors such as post-European deterioration in water quality associated with increased sediment [9,33] and nutrients from coastal catchments [34,35] are all argued to be contributing to habitat declines in near-shore reefs. Because of their vulnerability and their importance to coastal towns, natural resource managers often must rapidly assess and interpret localized changes in coral reef communities following disturbance in order to make decisions about the most appropriate measures to ensure their protection and continued survival.

In spite of the wealth of research on the Great Barrier Reef, to date, few detailed biodiversity assessments of its inshore coral communities have been conducted. Logistical constraints, lack of adequate expertise in identifying corals to a high enough taxonomic resolution and the vast scale of many reef areas all contribute to this inadequacy. On a broad scale, the cover and diversity of coral species on the Great Barrier Reef varies with both latitude and distance from the coastline along it's >1800 km length. In general, northern and central, outer-shelf reefs have been described as having the highest diversity while southern, inner-shelf fringing reefs have been described as having the lowest species diversity [32,36-38]. North-south variation is overshadowed by cross-shelf species variation which increases with distance from the sediment and silt-affected mainland coastline. In the Southern Great Barrier Reef, decline in species richness is also due to naturally marginal environmental conditions [39], isolation [40] and high disturbance regimes [11]. While broad-scale assessments can be useful in comparing regional reef areas in terms of species diversity and coral cover, without finer scale assessments of inshore reefs it may be impossible to tease out future anthropogenic effects from natural historical trends [41]. This may be particularly true for isolated coastal reef systems because of their lack of connectivity and their reliance on self-recruitment. Effective conservation and management of a marine ecosystem must therefore necessarily begin with fine-scale biophysical assessments focused on the diversity of the architectural species that build the structural framework of the reef [13,42].

The aim of this study was to conduct a detailed assessment of coral biodiversity and abundance as well as a number of key physical parameters (temperature, light, habitat profile, reef rugosity and current strength) on an inshore reef system to elucidate patterns, linkages and implications for conservation. The Keppel Islands region in the southern Great Barrier Reef was chosen for the study because it is a relatively small and isolated inshore fringing reef system that has a history of frequent disturbance and strong regeneration between events.

2. Experimental Section

The Keppel Island group (Keppels) is a group of 15 continental islands situated along the inner shelf of the Great Barrier Reef near Rockhampton (23.1 °S, 150.9 °E, Figure 1). The islands are surrounded by a patchwork of fringing reefs with relatively high coral cover (~67%) compared to the rest of the Great Barrier Reef [3]. Radio carbon dating of similar reefs ~100 km to the north (Percy Islands) suggests that reefs in the Keppel group are relatively young, having developed only ~1500 years ago in the late Holocene following landward migration of the terrigenous sediment wedge and sea level fall [43,44]. Keppel Bay is essentially an ancient flood plain, in-filled with accumulated coastal sediment from the Fitzroy River following sea level rise in the early Holocene (~9000 years ago). Sediment continues to accumulate in the river mouth and inner Keppel bay north spreading along the coast during short duration episodic high discharge fluvial events [45,46]. However, there is relatively low sediment accumulation around the islands in the outer part of the bay. In general, leeward bays are dominated by shallow reef flats (where the geomorphology allows adequate flushing of fluvial and accumulated sediments) while eastern shores and rocky headlands comprise deeper reef slopes.

Figure 1. Map of the study sites in the Keppels.

A number of disturbances have impacted on the Keppel reef communities in the last few decades causing concerns about loss of reef quality [30,47-50] and severe bleaching in 2006 [51,52]. A flood in 1991 caused mortality of almost 85% to corals to a depth of ~1.3m below datum on leeward island reefs. Assessments of reef impact were conducted by van Woesik [47] and Byron and O'Neill [53]. A bleaching event in 2006 resulted in a 40% loss of corals (unpublished data). Two earlier bleaching events in 1998 and 2002 also caused significant coral mortality [30]. In spite of these disturbances, the high coral growth rate observed in the Keppels has allowed significant recovery [54].

2.1. Field Surveys

A total of 19 sites were surveyed between March 2008 and April 2009 (Table 1). A combination of high resolution aerial photographs and local knowledge was used to ensure that all significant reef systems in the central Keppel Island group were represented. Aerial photos were geo-rectified in Google Earth ™ and reef area estimated by tracing the outline of the reef which was clearly visible in the photos. Coral species and their abundance (ranked % abundance) were assessed during a random swim over ~60 minutes at each of the 19 sites. Species lists were limited to scleractinian corals. Most coral species could be adequately identified in the field with the exception of those in the Poritidae (massive growth form) and Fungiidae genera which were counted as one species if these were present. Digital still photographs of the features of each species were taken to verify identity. Each species was ranked in terms of abundance and compared to the total live hard coral cover using a scale of 0–5 (0 = none present; 1 = 1–10%; 2 = 11–30%; 3 = 31–50%; 4 = 51–75%) as per de Vantier *et al.* [38].

Table 1. The study sites in the Keppels and their abbreviations.

Location	Abbreviation	Latitude south (decimal degrees)	Longitude east (decimal degrees)	Reef area (Ha)
Bald Rocks	Bald	23.17108	150.9938	10.0
Barren Island	Barren	23.15674	151.0253	31.0
Clam Bay	Clam	23.187	150.9782	45.0
Egg Rock	Egg	23.20004	151.0993	4.5
Halftide Rocks	Halftide	23.15352	150.9385	8.0
Halfway Island	Halfway	23.2011	150.9729	45.0
Humpy Island	Humpy	23.21639	150.9744	68.0
Leekes Creek	Leekes	23.16712	150.9519	0.5
Man and Wife Rocks	Man and Wife	23.11836	150.9916	4.0
Miall Island	Miall	23.1539	150.9038	27.0
Middle Island	Middle	23.16235	150.9205	28.0
Monkey and Shelving Points	Monkey	23.19491	150.9362	10.5
North Keppel Island	Nth Keppel	23.08477	150.8987	44.0
Outer Rocks	Outer	23.06545	150.9521	10.0
Parkers Bommie	Parkers	23.15407	150.9768	8.0
Passage Rocks	Passage	23.16865	150.9287	4.5
Pelican Island	Pelican	23.24123	150.8769	41.0
Pumpkin Island	Pumpkin	23.09211	150.9028	11.0
Wreck Bay	Wreck	23.1601	150.9768	4.5

2.2. Benthic Cover

The cover of benthic communities was assessed for 17 of the 19 sites (benthic cover was not measured for Leeke's Creek and Clam Bay) along two haphazard 50 m transects on the reef flat (0–2.0 m at chart datum, 2.4–4.8 m at mean sea level) and reef slope (6.0–12.0 m at chart datum, 8.4–14.4 m at mean sea level). Transects were photographed every 2 m at a height of 1 m above the substratum using a digital still camera (4 Mp) fitted with a 16 mm wide angle lens. To enable calculation of the average gradient between the reef flats and slopes, geo-referenced images were obtained for each transect using a towed GPS set to record a track at 5 second intervals which was later matched to the images using the software RoboGeo[TM] according to the methods of Roelfsema and Phinn [55]. Digital still images were analysed using 20 random points per image with the program CPCe[TM] v3.1 [56]. Cover was assessed as the percentage of the total biotic and abiotic benthos averaged across the replicate transects on reef flats and slopes. Benthic cover was classified into the proportion of macro-algae, abiotic, coralline algae, turf algae, hard live coral and soft coral.

2.3. Environmental Variables

To assess their influence on the coral species assemblage, three key environmental variables, light, temperature and habitat profile were directly measured at 18 of the 19 study sites (light and temperature loggers were not deployed at Leeke's Creek). In addition, current strength and reef rugosity (3-D habitat complexity) were subjectively categorized for each site based on observations as potential influences on diversity.

2.3.1. Light Attenuation Coefficient—K_d

To assess the variation in light levels across sites, predominantly due to variation in turbidity, the light attenuation coefficient (K_d) was derived from photosynthetically active radiation (PAR) loggers (Odyssey, Dataflow Systems, NZ) at each site deployed at a depth of 5–7 m. The PAR loggers were fitted with custom-built wipers to prevent fouling of the sensor by sediment and algal growth. These wipers brushed the PAR sensor three times in quick succession every two hours. Light was recorded every 10 minutes for periods of 1–12 weeks.

Average daily cumulative PAR light between 10 am and 3 pm was determined for each site using only data from cloud-free days. Cloud-free days were easily identified in the dataset by their smooth diurnal light curves. K_d, was calculated from the average cumulative underwater irradiance (I) at depth (z) and the theoretical cloud-free irradiance at the surface ($I_{surface}$), derived using the software PARCAL (AIMS, version 01.03.08), using the equation:

$$[d_{site} = Ln\,[(I/I_{surface})]/z \tag{1}$$

All K_d values were standardized to values at Miall Island, our reference site, to account for non-synchronous deployments of light loggers at some sites. Odyssey PAR loggers were calibrated in air using theoretical clear-sky midday irradiances derived from by PARCAL. Theoretical midday irradiances were checked against a calibrated LI-COR[®] sensor and the maximum error was found to be <3%.

2.3.2. Temperature

Sea temperatures (SST) were recorded at half-hourly intervals using Odyssey temperature loggers (Dataflow Systems Pty Ltd, NZ) deployed on the reef slope (5–7 m at LAT). Loggers were calibrated against a NATA certified Hart 1522 reference thermometer (Hart Scientific, UT, USA) in a water bath to a final accuracy of <0.1 °C. The total number of days where the maximum daily temperature exceeded 28 °C (days >28 °C) was calculated for each site.

2.3.3. Habitat Profiles

Habitat profiles were estimated by measuring the gradient (slope) between the start of reef flat and slope transects for each site from the geo-rectified images using Google Earth[TM]. The depth at the reef flat was subtracted from the depth at the reef slope and then divided by the distance between the points.

2.3.4. Current

To assess the influence of current flow on the species assemblage at each site, current strengths were catagorized based on local knowledge as: 1 = strong tidal combined with longshore currents; 2 = medium current (mainly tidal) but some longshore current influence; 3 = mostly diurnal tidal currents which are protected from strong longshore currents and ocean swell.

2.3.5. Habitat Rugosity

To assess the influence of 3-D habitat complexity (rugosity) on the coral species assemblages at the 19 sites, each site was subjectively categorized as: 1 = high rugosity as a result of bommies and rocks creating high 3-D habitat structure and a range of habitat types; 2 = average rugosity with reef flats and slopes exhibiting range of coral growth morphologies and scattered bommies; and 3 = low rugosity (reef flats and slopes with extensive mono-specific stands dominated mainly by *Acropora* spp.) [57].

2.4. Statistical Analyses

Data for species abundance, benthic cover, and environmental variables were analyzed using the statistical software Primer v6 [58-60] and SPSS v17 (SPSS Inc.). Missing values for benthic cover variables were replaced using the expectation maximum likelihood algorithm which assumes a multi-normal distribution model for the data. A range of coral community-based statistical methods, as described in the following sections, were used to explore the sites according to their species assemblage and environmental variables. Multivariate analysis of variance was used to investigate the significance of differences in the benthic variables among site groups. The model residuals were examined to verify the validity of the assumption of normality and Levene's test was used to verify the homogeneity of variances. Simple pair-wise comparisons were performed to further investigate significant differences between groups of sites.

2.4.1. Multivariate Analyses of Species Assemblage

A resemblance matrix based on Bray Curtis similarities was constructed from the species presence/absence data for the 19 sites. Agglomerative CLUSTER analysis was used to group the sites according to the presence or absence of coral species using group average linkage distances. Objective grouping of clusters was based on the SIMPROF routine [61]. The validity of the site groupings derived from CLUSTER analysis were further explored using non-metric multidimensional scaling analysis (MDS) following the recommendations of Legendre and Legendre [62].

2.4.2. Univariate Measures of Community Structure: Species Richness S and Average Taxonomic Distinctness (Δ+)

Species richness S and average taxonomic distinctness Δ+ were determined for each site [63,64]. Following Somerfield *et al.* [65] the branch lengths between taxonomic levels (ω) were weighted using the species richness information gained from the full species inventory. Higher branch lengths were assigned to consecutive taxonomic levels according to differences in species richness whereby taxonomic groups with the same species richness were assigned branch lengths of zero. The species list from each site was compared with the full species inventory for the study and the resulting values of Δ+ were displayed using a funnel plot under the null hypothesis that the assemblages are a random selection from the regional species pool but adjusts probabilities to account for commonness/rarity [63,66,67].

2.4.3. Environmental Variables Contributing to Coral Community Structure

To examine the structuring forces behind the species assemblage, the 7 environmental variables (light extinction coefficient index, average and maximum daily temperatures, number of days >28 °C, habitat profile, current and rugosity) and 6 benthic variables (% coral, macro-algae, turf algae, coralline algae and soft coral cover) were explored using BEST [60] using Spearman's rank correlations (ρ) as a measure of resemblance. The environmental data were then compared with the benthic cover and species assemblage data in the same way.

2.4.4. Coral Genera Contributing to Community Structure

The coral taxa contributing to the multivariate species community structure were investigated using the SIMPER procedure run on data aggregated to genus level [60]. Coral genera contributions were visualised by superimposing bubble plots across the species assemblage 2-D MDS plot.

3. Results

3.1. Species Lists

In total, 167 species from 48 genera in 13 scleractinian families were recorded at the 19 sites. Average species richness among sites was 39.5, the same as the mean species richness found for the Great Barrier Reef between Townsville and Rockhampton by de Vantier (39.5) [39]. Humpy had much

greater species richness than any other site (70 species compared to the next highest, 53, at Passage), and the lowest species richness was found at Egg (24 species).

3.2. Benthic Cover

Coral cover varied from 29% to 94% with an overall average of 52% ± 19% (Figure 2). Reef flats had only slightly lower coral cover than reef slopes (48 ± 21% cf 53 ± 20%). The highest mean coral cover was found on the south eastern side of Humpy Island (88 ± 10%) and the lowest cover was found around Egg Rock (33 ± 16%). Soft corals comprised only 6 ± 1% of the benthic cover. Macro algal cover comprised 8 ± 1% of the benthic cover and was dominated by a single species, *Lobophora variegata*.

Figure 2. Percentage benthic cover (percentage of total benthic cover) on reef flats (F) and slopes (S) in the Keppels.
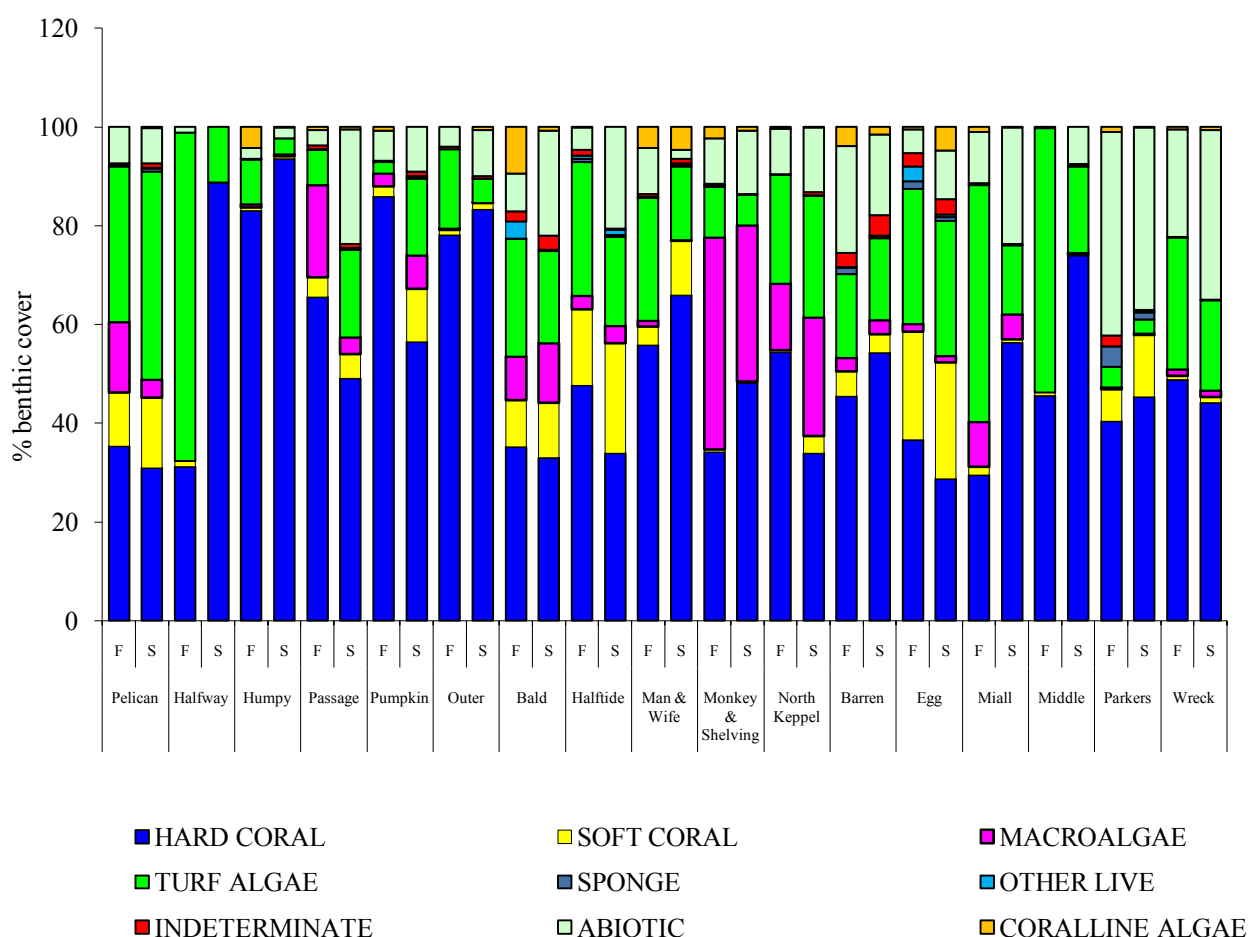
Species from the Families Acroporidae and Faviidae were the best represented with 61 and 57 species, respectively (Table 2). Species from the branching genus *Acropora* dominated the species assemblage in the Keppels in both species richness (43 out of a total of 167 species) and contribution to hard coral cover (80%). The remaining 20% non-acroporid coral community had a mean site abundance of <10% (mostly non-branching species except for pocilloporids).

Table 2. The 13 Scleractinian coral families comprising 167 species in 48 genera identified in the Keppels.

Family	# Species per family	Genus	# Species per genus
Acroporidae	61	*Acropora*	43
		Montipora	14
		Astreopora	4
Agariciidae	1	*Coelosceris*	1
Astrocoeniidae	1	*Palauastrea*	1
Dendrophylliidae	8	*Turbinaria*	8
Faviidae	57	*Barabattoia*	1
		Cyphastrea	5
		Diploastrea	1
		Favia	15
		Favites	8
		Goniastrea	8
		Leptastrea	4
		Leptoria	1
		Montastrea	5
		Moseyela	1
		Oulophyllia	1
		Platygyra	6
		Plesiastrea	1
Fungiidae	1	*Fungia*	1
Merulinidae	3	*Hydnopora*	3
Mussidae	12	*Acanthastrea*	5
		Blastomussa	1
		Lobophyllia	4
		Scolymia	1
		Symphillia	1
Pectiniidae	4	*Echinophyllia*	2
		Mycedium	1
		Oxypora	1
Pocilloporidae	3	*Pocillopora*	2
		Stylophora	1
Poritidae	10	*Goniopora*	5
		Porites	5
Sidastreiidae	5	*Coscinaraea*	2
		Psammocora	2
		Pseudosiderastrea	1

3.3. Multivariate Analyses of Species Assemblage

CLUSTER analysis separated the sites into four groups (A–D, Figure 3). 2-D plots of the MDS axis were overlaid with the groups derived using the SIMPROF routine. Group A comprised a single site, Pelican with 28 species. Group B included Humpy, Outer, Passage and Pumpkin with 52 ± 13 species.

Group C included Barren, Egg, Miall, Man and Wife, Parkers and Wreck with 31 ± 6 species. Group D included Bald, Clam, Halftide, Leekes, Halfway, Middle, Monkey and North Keppel with 41 ± 7 species.

Percentage coral cover and turf algal cover varied between the sites groups (Figure 4A–B). Group B sites had the highest coral cover, more than double that of Pelican and 1.5 times that of the other two groups. Turf algal cover showed the reverse pattern.

Figure 3. 2-D Multidimensional scaling analysis (MDS) plot based on Bray Curtis similarities between coral species assemblages at 19 sites in the Keppels depicting three groups based on 28% similarity (circles) and four groups distinguished by CLUSTER analysis (symbols). Aqua symbols represent sites in group A, red symbols represent sites in group B, blue symbols represent sites in group C and green symbols represent sites in group D.
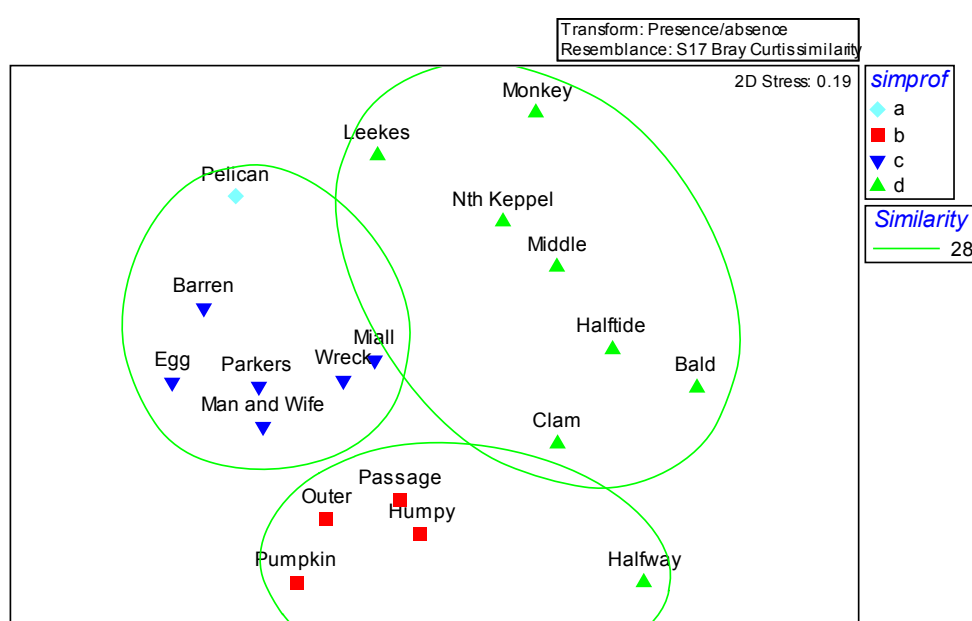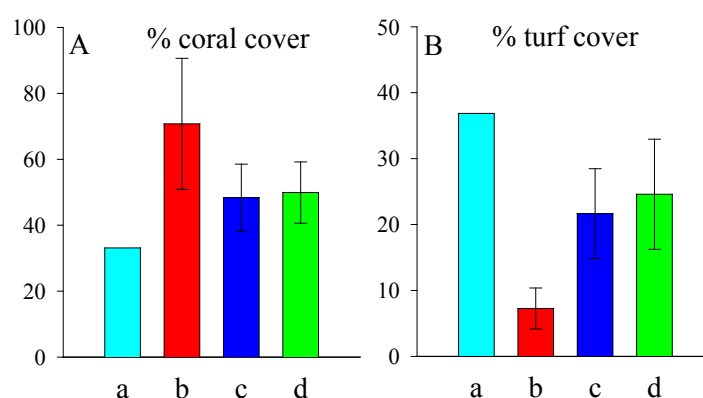

Figure 4. Bar graphs showing the mean percentage of (**A**) coral and (**B**) turf cover across the 4 site groups chosen using CLUSTER analysis. Aqua bars represent sites in group A, red bars represent sites in group B, blue bars represent sites in group C and green bars represent sites in group D.

3.4. Species Richness S and Average Taxonomic Distinctness AvTD (Δ+)

There was a gradient of species richness and taxonomic distinctness across the four groups of sites (Figures 5 and 6). Pelican (Group A) had the highest taxonomic distinctness but low species numbers. The frequency-based mean taxonomic distinctness for the full species list was ~86. Seven sites had frequency-based values of Δ+ above the mean including Pelican which had the highest taxonomic distinctness followed by Halfway, Leekes, Humpy Pumpkin, Clam and Passage. Five sites (Egg, Barren, Miall, Halftide and Wreck) had taxonomic distinctness values below the 95% probability limit.

Figure 5. Species numbers for the 19 sites in the Keppels. Thin dotted line represents the mean species number (39 species) for the 19 sites and bars represent the actual species number for individual sites. Aqua bars represent sites in group A, red bars represent sites in group B, blue bars represent sites in group C and green bars represent sites in group D.
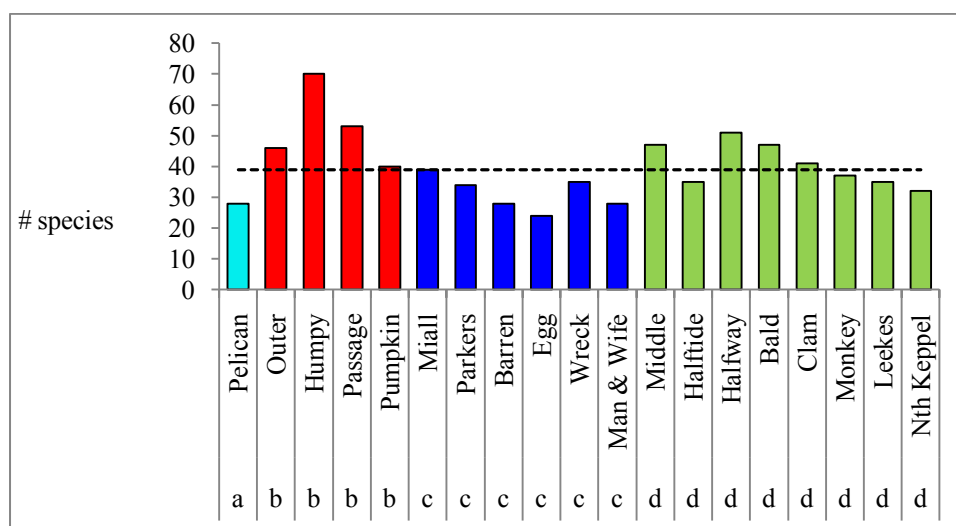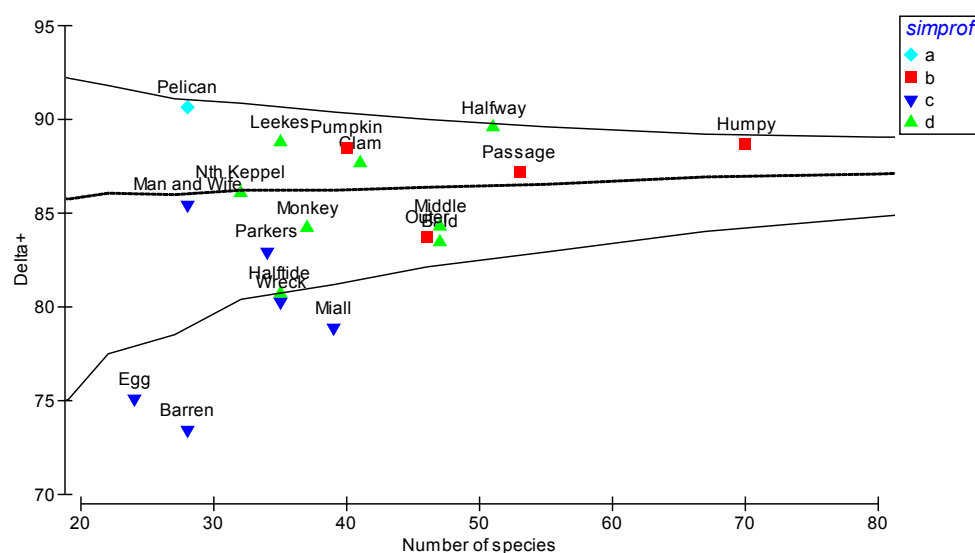

Figure 6. Funnel plots for simulated Δ+ *versus* species numbers. The broken line indicates the mean Δ+ for the full species inventory and thin lines represent the 95% probability limits. Aqua symbols = group A sites, Red = group B sites, Blue = group C sites and Green = group D sites.

Overall, there is a suite of sites that have relatively higher values for species richness, taxonomic distinctiveness and coral cover: the four sites in Group B, Humpy, Passage, Pumpkin and Outer plus two more sites in Group D, Halfway and Middle (Figure 7). A further site was added to this group, Pelican, on the basis of its taxonomic distinctiveness and provision of habitat for stress tolerant corals not found at the other 18 sites.

Figure 7. 3-D plot of species richness, taxonomic distinctiveness and coral cover for the 19 sites.
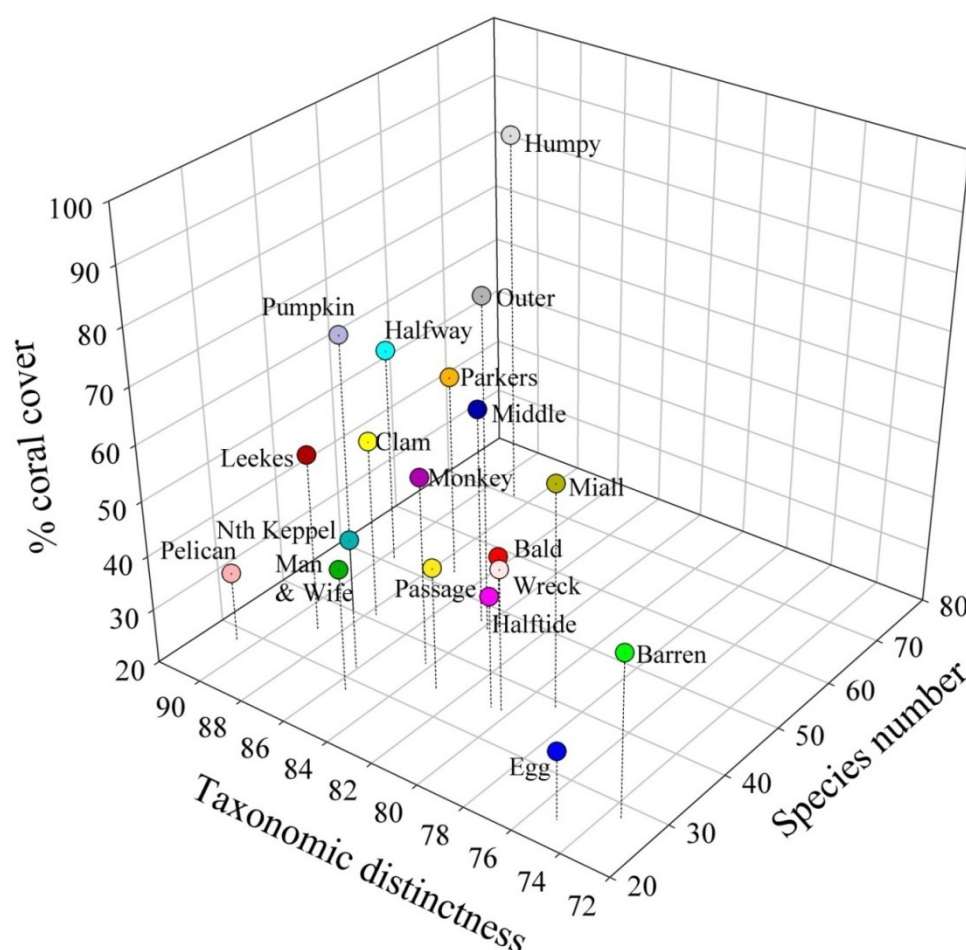
3.5. Environmental Variables Contributing to Coral Community Structure

None of the environmental variables significantly explained the species assemblage (Figure 8). There was also no statistically significant relationship between the resemblances based on the coral community structure and that of the full suite of environmental variables. It is likely that there is insufficient replication of suites of particular abiotic variability to obtain a statistically robust analysis [68] or that the community structure does not respond to the chosen variables, at least not over the scales at which they were measured.

Figure 8. Bubble plots of the five environmental variables. **(A)** light extinction coefficient (K_d = 0–1); **(B)** temperature (days >28 °C); **(C)** current (1 = strong; 2 = medium; 3 = weak); **(D)** rugosity (1 = high rugosity; 2 = average rugosity; and 3 = low); and **(E)** reef profile (0–0.5) superimposed on the 2-D MDS plot of sites of the Bray Curtis similarities based on the presence/absence of 167 scleractinian coral species at 19 sites in the Keppels. Bubble scales for each variable are shown to the right of the plots.
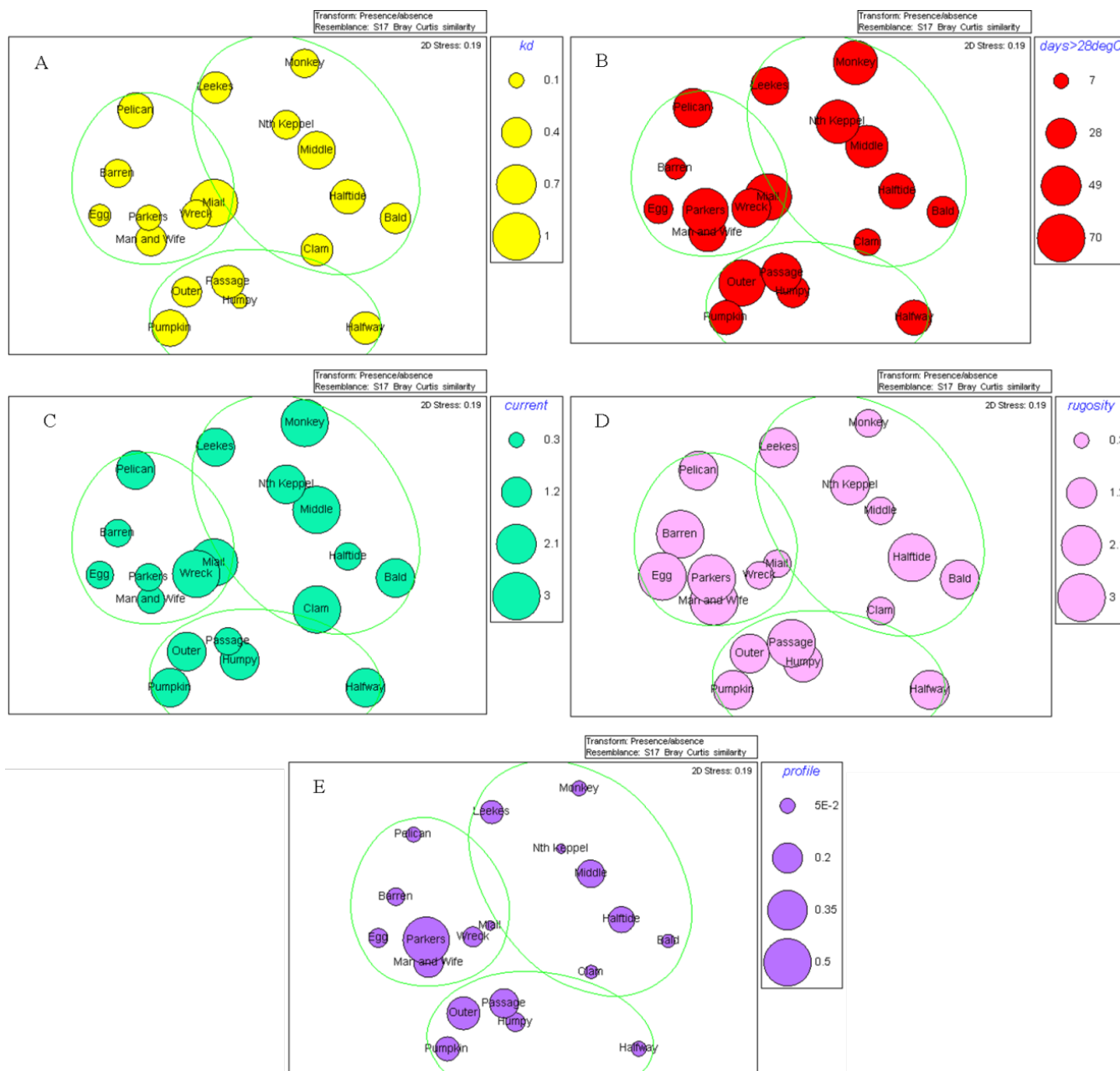
3.6. Coral Genera Contributing to Community Structure

There was little structure to the species comparisons among the sites which was dominated by *Acropora* (30–60% contribution). More detailed comparisons were conducted following removal of *Acropora* from the dataset. SIMPER analysis showed that the average similarity amongst the four sites in Group B (Humpy, Outer, Passage and Pumpkin) was 64%. Five genera comprising

Turbinaria (15%), *Goniastrea* (13%), *Acanthastraea* (12%), *Favia* (12%) and *Montipora* (11%) contributed most to the group similarities.

The average similarity between the sites in group C (Barren, Egg, Miall, Man and Wife, Parkers, Wreck) was 52%. Eight non-*Acropora* genera comprising *Platygyra* (13%), *Acanthastrea* (13%), *Pocillopora* (12%) and *Turbinaria* (10%) contributed to the similarities between site groups.

The average similarity between the sites in group D (Bald, Clam, Halftide, Leekes, Middle, Monkey, North Keppel) was 58%. *Favia* species contributed 19% to the similarity. Three other taxa comprising *Montipora* (13%) *Platygyra* and *Favites* (9%) contributed to the similarities between groups.

The relationship between the site groups and the cumulative ranked abundance of corals in each genus was apparent from the bubble plots superimposed on the MDS of species assemblage. For instance, species from the genera *Acanthastrea* were more abundant in Group B sites (Figure 9).

Figure 9. Bubble plot of the abundance of coral species from the genus *Acanthastrea* superimposed on the 2-D MDS plot of sites of the Bray Curtis similarities based on the presence/absence of 167 scleractinian coral species at 19 sites in the Keppels. Bubble key shows the ranked % abundance whereby each species was ranked in terms of abundance and compared to the total live hard coral cover using a scale of 0–5 (0 = none present; 1 = 1–10%; 2 = 11–30%; 3 = 31–50%; 4 = 51–75%).
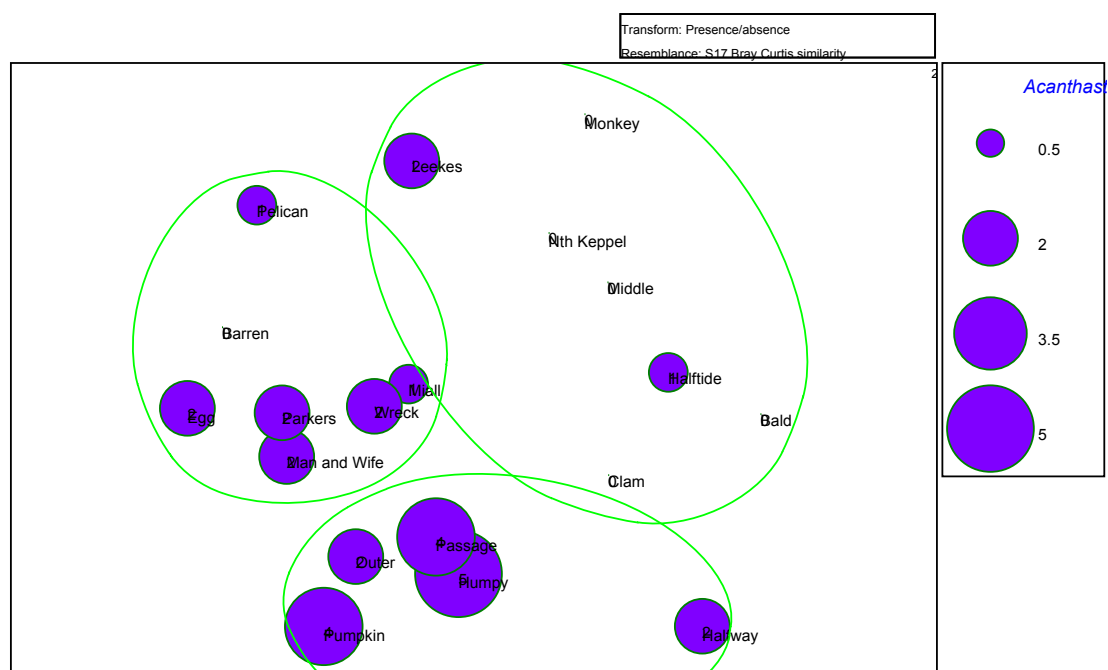
Coral species from the family Poritidae, specifically in the genus *Goniopora* were strongly represented at sites in group C which had 1–4 species at 6 sites whereas only one site in each of group B (two species at one site) and C (one species at one site) had species from this genus. Sites in groups B and C had a greater abundance of coral species from the family Merulinidae specifically the genus *Hydnophora* (1–2 spp) compared to only 1 species at two sites in group D (bubble plots not shown).

4. Discussion

Six of the 19 reefs were identified as coral biodiversity hotspots within the Keppel Island group (Keppels). The survey sites in the southern bays at Humpy, Middle and Halfway Islands, reef surrounding Passage Rocks, Outer Rocks and Pumpkin Island were typified by relatively high species richness, taxonomic distinctiveness and coral cover, and low turf-algal cover compared to other sites. These six sites are likely to be more resilient to disturbance than the other sites in the study because high taxonomic diversity is implicated in ecosystem stability [69]. For much of the year prevailing southeast trade winds drive surface currents northwest, connecting four of the sites, Humpy, Passage, Halfway and Pumpkin oceanographically to sites such as Clam Bay, Haftide Rocks, and North Keppel Island [70]. These sites therefore represent potential 'refugia' (source reefs) in the Keppels, from which propagules from a wide range of coral species can spread to surrounding sites of lower diversity (sink reefs) following the annual mass coral spawning. Knowing what taxa exist on which reefs that are connected to each other oceanographically can provide information about sites that are of high conservation value and therefore are a priority for enhanced management efforts if regeneration of surrounding sites becomes important. On the GBR, de Vantier [39] conducted broadscale assessments of >75% of the nearshore reef-building coral communities between 14 °S and 23 °S. These assessments supplemented previous work by Veron [37,71,72] and contributed to an improved understanding of both the natural and anthropogenic influences structuring inshore GBR coral communities. Whilst coral species community assessments must be interpreted with care in the context of differential coastal geomorphology, habitat diversity, disturbance history, connectivity and terrestrial influences, they contribute to a more robust contextual framework against which researchers and reef managers can predict and model changes. Care must be taken when making qualitative comparisons between coral communities because many of the sediment-tolerant taxa are particularly sparse and restricted to small reef areas [73]. As such, fine-scale mapping can contribute to more robust study design by elucidating smaller, low-diversity sites which have an abundance of stress-tolerant taxa but would otherwise have been considered of 'low' conservation value. In addition, fine-scale mapping can be used as a baseline to investigate the impacts of anthropogenic disturbance, such as dredging, on coral communities [74-76]. A note of caution must also accompany any discussion of augmented management intervention in order to enhance overall reef resilience. It remains to be seen whether past intervention (the implementation of no-take zones) has been effective in protecting coral biodiversity due to the potentially over-riding influences of other major structuring forces like terrestrial runoff, thermal stress and cyclones [11,77,78].

The concept of marine 'refugia' is not new. No-take areas focused on the preservation of the commercially harvested marine species have historically been used as a key management tool to enhance the resilience of reefs [79]. However, recent evidence strongly suggests that although no-take areas enhance the capacity of corals to recover following disturbance [17] and protect fish stocks [15,79], as a management tool they may not necessarily protect coral biodiversity [1,80,81]. An example of this can be found in the Red Sea [82] whereby the species diversity on a protected reef failed to recover to pre-disturbance diversity after catastrophic exposure because of chronic pollution. A second example can be found on Kenyan reefs following the 1998 bleaching [83] whereby the colony sizes of some coral species were affected regardless of reef protection status. Natural influences

also structured the complement of species that re-colonized both polluted and unpolluted reefs in the Gulf of Eilat where fast-growing and competitively superior branching *Acropora* species monopolized recovered reef flats [82]. There are multiple other examples of reefs that have undergone coral community composition changes following disturbance. Among these are those that have been influenced by bleaching [20,42,84,85], herbivore reductions [86-88], coral carnivore (*Acanthaster planci*) invasions [89-91], siltation [74-76,92] and commercial collection [93,94]. In some cases, combinations of multiple influences have driven longer-term changes in coral community composition [11,86]. Choice of marine protected areas must therefore not only take into account coral biodiversity but must also consider the key natural and anthropogenic structuring influences such as space limitation, temperature, water quality and fishing pressure which can all ultimately exert influence on coral communities [91].

Loss of the biodiversity of the structurally important coral species that underwrite ecosystem stability could have devastating long-term consequences on reefs [13,24,95-97]. Most coral taxa are functionally distinct and therefore respond in varying ways to specific environmental conditions. The higher the number of species such variability is averaged across, the less variable is the total system [98]. Pelican (Group A) had a more random assemblage of coral species but low species number compared to all other sites in the Keppels because the coral communities surrounding Pelican have probably already responded to past disturbance by shifting to stress tolerant species. On sites with high coral diversity or taxonomic distinctness, equilibrium may have been reached whereby competitive interactions between species prevent stronger species from overcoming weaker ones, thereby averting the assemblages from becoming mono-specific. Whilst the fast-growing *Acropora* species are clearly the most dominant feature on most reefs in the Keppels, they are also vulnerable to temperature and low salinity. The low *Acropora* abundance surrounding Pelican Island confirms that these species are not able to withstand chronic disturbances such as bleaching and flood impacts in much the same way that mono-specific plant communities are vulnerable to disease and predation [99]. And yet, the persistence of a wide diversity of less abundant but stress-resilient species has helped to sustain Pelican reefs under a frequent disturbance regime. It is unclear whether these species are 'reef-builders' capable of building the substrate for future reefs [100]. Until their contribution has been determined, and considering that they probably contribute to functional diversification, it is imperative that future management efforts are directed towards maintaining and protecting existing levels of coral biodiversity in order to augment the resilience of the system as a whole. The threats posed by increased temperature, ocean acidification, rising sea level, land runoff, changing hydrodynamics and increasing severity of storms and floods are predicted to escalate. There is also a strong likelihood of a corresponding decline in the resources available to management initiatives to protect coral reefs. It may also be necessary to prioritize the protection of sites based on their potential to provide the seed stock for regeneration on surrounding reefs when and if the threats abate: Noah's arks for reefs.

The main characteristics responsible for distinguishing sites in the Keppel Islands were the richness (number) and taxonomic distinctness of coral taxa. These sites were also characterized by high coral cover combined with a low percentage of turf-algal cover but there was no evidence that these were structuring factors. The lack of correlation between the species assemblage and environmental variables may be a result of a lack of replication of sites with similar biotic and abiotic characteristics. Study sites were chosen based on their likelihood of supporting high coral species diversity without

regard for replicating environmental characteristics. The design of future studies should comprise control sites and widely spaced replicates within each sites with appropriate randomization in sampling. The availability of a variety of habitat types and strong tidal flushing are also expected to support species biodiversity however we found no evidence for these factors structuring the species assemblages among the sites chosen for the study. Restricted habitat rugosity has previously been identified as a potential factor in limiting the diversity of species assemblages because of the importance of a range of suitable habitat types for settlement and survival of functionally diverse coral taxa [101]. Clearly, in the Keppels factors other than high habitat rugosity are at play in determining biodiversity but there is evidence of this factor limiting species diversity. For instance, shallow reef flats such as Monkey that lie in sheltered bays and are prone to temperature extremes are likely to have a more restricted range of species than sites such as Passage Rocks which have high rugosity. In contrast, Egg Rock is clearly an important fish habitat because of its geographic isolation and strong ocean currents but these factors and the lack of a variety of substrates at depths suitable for coral growth may limit biodiversity. Neither Egg Rock nor Monkey Point reefs represent significant coral biodiversity hotspots. Shallow reef flats such as those at those at Middle, Halfway, Monkey and Clam are also prone to high temperatures and flood impacts. Frequent disturbance with limited time for recovery is clearly a factor in structuring their species assemblages which are dominated by fast growing branching and corymbose *Acropora* species. Space limitation on the reef flats is another factor that limits diversity. Where space is limited and conditions like temperature and light are stochastic, single functional opportunists e.g., *Acropora* species, tend to monopolize the resources available [82,91]. In contrast, sites such as Humpy, Passage and Pumpkin with adequate tidal flushing, which prevents water temperatures and turbidity from frequently reaching stressful levels and encourages the exchange of coral propagules with surrounding sites, have much higher coral cover and species diversity. It is possible that many of the study reefs are not yet in a state of equilibrium, *i.e.*, that disturbance is so frequent that the coral communities have not yet reached the point at which they are structured by environmental factors such as temperature, light and rugosity, but rather that they are in a state of recovery from past disturbance [82].

Oceanographic connectivity is central to the concept of coral 'refugia'. Tidal and oceanic currents provide a means by which coral propagules can potentially be transported between sites during the annual spring coral spawning. For instance, Passage Rocks was found to have surprisingly high species-richness despite its relatively small size and high turbidity. Situated between Middle Island and Great Keppel Island, it is prone to strong tidal- and wind-driven currents. These currents connect Passage to other sites, making it a potential source of coral propagules during the annual mass spawning and thus an important site for management [25,102]. Studies of the genetic flow between such sites combined with detailed hydrodynamic modeling are urgently needed in order to understand the importance of these small, deepwater refuges of coral biodiversity in this region. Without such information, reef managers may struggle to prevent further fragmentation and loss of coral biodiversity [102].

Two sites stood out as having strongly contrasting species attributes in the Keppels. Pelican had the lowest species number but a highly distinctive species assemblage whereas Humpy had many more species than the other 18 study sites (70 compared with a range of 24 to 53). Humpy and Pelican have distinctively different disturbance histories. The survey site at Pelican is on the northern side of the

island which is away from the mouth of the Fitzroy River and, although protected from the prevailing south easterly winds, it is prone to frequent freshwater influx, sediment accumulation and warmer than average temperatures. These factors may have encouraged the proliferation of stress tolerant species at Pelican, which resulted in a distinctive but restricted species complement compared with other, less stressful sites. Sediment-tolerant species from the family Pectinidae and the genus *Echinophyllia* (specifically *E. aspera* and *E. orpheensis*) were identified at Pelican but were not found on any other reefs in the study. However, the low abundance of *Acropora* species is the most distinctive feature of the coral species assemblage at Pelican. Only 10 out of 43 coral species from the family Acroporidae were present (comprising 23% of the total species found in the Keppels) whereas all other sites had between 30% and 55% of the *Acropora* species. The synergistic effects of temperature, turbidity and sediment at Pelican probably deter the proliferation of anything but the most stress-tolerant species.

This study has shown that the Keppels has more than double the coral species richness than previously described by van Woesik [103]. We identified a total of 167 species in the Keppels compared to 70 species described by van Woesik [103]. Mean species richness was ~40, which is almost the same as the mean of ~39.5 reported by de Vantier [39] for the Great Barrier between Townsville and Rockhampton. Sixty eight percent of the 244 species reported by Veron [104] for the southern Great Barrier Reef were found in the Keppel group. The apparent anomalies between species diversity in the present study and that found previously is probably a result of the much higher number of sites surveyed (19 sites compared to 8 sites in van Woesik's study), the use of random swims compared to the 1989 study which used set 200 m^2 transects. . The finding of higher species diversity in this study compared to the 1989 and 1997 studies could also lie in the time elapsed since major disturbance. De Vantier *et al.* [39] conducted their surveys in 1997, approximately 6 years after the 1991 flood [105] whereas the reefs had had a further 11 years to recover for the current study. De Vantier compared the relatively lower species diversity in the Keppels to the northern Great Barrier Reef and attributed it to the higher disturbance history in the Keppels and the fact that although many of the sub-tropical indicator species were present they were sparsely distributed. Species may have been present but may not have had time to proliferate between disturbance events [11]. More species may be present in the Keppels than have been described in these latest surveys but they may exist in numbers so low and in areas so small that they are seldom found. The classification of Keppel reef biodiversity as 'low' may therefore be inaccurate in light of the species richness found in this study [106]. The Keppels may instead be considered truly biologically distinct because of its unique geographic location and relative abundance of stress tolerant species such as those from the Mussidae, Faviidae, Dendrophylliidae, Merulinidae, Poritidae and Sidastreiidae families [78].

While coastal geomorphology, oceanographic connectivity, and the geological history of reefs in the Keppels are probably structuring coral assemblages in the longer term, more localized short term changes are within anthropogenic control. Maintaining water quality, reducing anchor damage and preventing the loss of the less abundant but stress-tolerant species through commercial coral collection will go a long way towards maintaining reef resilience in the shorter (10 year) timeframe. Due to the global market demand for small and vibrantly colored corals for use in domestic aquaria, the commercial marine coral fishery in Queensland has recently begun targeting species from the coral taxa Faviidae, Euphyllidae and Mussidae (specifically species from the genera *Acanthastrea, Scolymia,* and *Blastomussa*) in the Keppels [107]. Over 12,000 specimens from the Mussidae family

were collected in the year between 2008 and 2009 from the Keppels compared to only ~4000 from the larger collection area on reefs off Cairns in the northern Great Barrier Reef and compared to <6000 specimens from the Keppels in the year between 2007 and 2008. Little is currently know of the functional role and regeneration capacity of these rare taxa. Undermining functional diversity by removing less abundant coras which are vulnerable to localized depletions due to their limited distributional range could hasten the compositional change of species-assemblages [108,109]. Altered community structure can rapidly disrupt ecosystem function [110,111]. Another important influence is that of water quality on marine coastal coral biodiversity. Over geologic time, runoff from land can be a stronger factor in shaping coral community structure than even temperature variability [112]. Runoff not only damages corals, it also diminishes substrate quality for larval settlement and can lead to algal proliferation, which is a key factor for declining recruitment success [113]. Worm *et al*. [109] have established a link between marine biodiversity and coastal water quality. Wooldridge [31] estimates that improved local management has a potential benefit equivalent to 2.0–2.5 °C improvement in temperature tolerance to inshore reefs that run the highest risk of damage from dissolved inorganic nitrogen. Similarly, Negri *et al*. [114] have suggested that reducing herbicides by 1.2 mg L^{-1} was equivalent to reducing thermal stress on *Acropora* corals by 1.0–1.8 °C. Therefore, improved water quality in reef lagoons is one of the key protective measures to augment the capacity of reefs to survive climate change.

5. Conclusions

The way that we manage our reefs now is critical to Australia's future economic and maritime security as they protect our vulnerable coastlines and provide food, employment and recreation. This study presents a detailed assessment of the coral species assemblage of a small and geographically isolated system of fringing reefs in the Keppel Islands region that assist in protecting the coast and islands in the southern region of the Great Barrier Reef. Six coral biodiversity hotspots were identified based on the richness and distinctness of the coral taxa present. These sites are considered coral 'refuges' based on their high species numbers and connectivity to sites with lower species numbers and coral cover. Further molecular studies of the main structural species and the hydrodynamics between sites are required to investigate the connectivity between these biodiversity hotspots and other sites in the Keppels. Reefs with high coral diversity and those at the extreme environmental tolerance range for coral survival may need to be earmarked by marine and natural resource managers for increased protection from anthropogenic influence. Assessments of the species assemblages of the structurally important reef corals on inshore reefs provide a clear and practical model to identify reefs that has important implications for economically and ecologically effective marine management intervention.

Acknowledgements

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