

L. M. DeVantier · G. De'ath · E. Turak  
T. J. Done · K. E. Fabricius

## Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef

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**Abstract** Species richness, cover and community structure of reef-building corals were assessed at 599 sites on 135 reefs along the Great Barrier Reef (GBR) between 1994 and 2001, with focus on the nearshore area. Communities were described hierarchically, with smaller regional communities forming part of higher level communities at increasing spatial scales. Site richness increased from the coast to the mid-continental shelf, declining on the outer shelf. Richness also increased with depth to 5 m, stabilizing thereafter. An anomaly was present in a 400 km section adjacent to the northern, 'wet tropics' coast, where site richness was 67 and 41% lower than the adjacent far northern and central GBR, respectively; this was probably due to the disturbance regime, with an apparent anthropogenic component. Site richness also declined in the Southern GBR, probably due to naturally marginal conditions. All indicator species had highest values in five small Far Northern and Central GBR communities. In the eight depauperate communities no indicator species had high values, indicating that these communities represent degraded, yet potentially transitional forms of the more diverse communities of the Far Northern and Central GBR. The study shows that on the GBR, disturbance results in the local removal of corals rather than a shift to suites of other coral species.

**Keywords** Species richness · Community structure · Biogeography · Disturbance · Multivariate regression trees · Indicator

### Introduction

Australia's Great Barrier Reef (GBR) comprises more than 3,000 reefs distributed over > 1,800 km and covers 350,000 km<sup>2</sup>, including adjoining inter-reefal areas. Most reefs (~2,400) are platform reefs developed well offshore from the mainland coast on the mid- and outer-continental shelf. There are also many (~600) that are located nearshore, either as fringing reefs around continental islands and along the mainland coast or as small, detached patch or platform reefs (Hopley et al. 1989). The biological structure and ecological status of many nearshore reefs remain relatively poorly understood, with previous coral community studies on the GBR (Done 1982; van Woesik and Done 1997; DeVantier et al. 1998) having restricted geographical ranges: their applicability to the broader GBR ecosystem is uncertain. We addressed this gap in knowledge by undertaking the first broad-scale assessment of nearshore reefs along > 75% of the length of the GBR, from 14°S to 23°S, focusing on patterns in the species composition, richness and community structure of reef-building corals.

Other studies have demonstrated broad-scale latitudinal and cross-shelf variability in coral community structure. Latitudinally, there is a net decline in species richness from north to south, with some species replacement in southern areas (Veron 1986, 2000) consistent with global patterns (Willig et al. 2003; Mora and Robertson 2005). Veron (1995, 2000) reported 77 genera and 396 species of reef-building corals on the GBR, 324 species in the north, 343 species in the central GBR and 244 species in the south. Many coral species exist all the way across the continental shelf, but there are major differences in richness and relative abundance of species across the shelf (Done 1982). These differences were

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L. M. DeVantier · G. De'ath · T. J. Done · K. E. Fabricius (✉)  
Australian Institute of Marine Science, and Cooperative Research  
Centre for the Great Barrier Reef World Heritage Area,  
PMB 3, Townsville MC, QLD 4810, Australia  
E-mail: k.fabricius@aims.gov.au  
Tel.: +61-7-47534444  
Fax: +61-7-47725852

E. Turak  
1 Rue François Villon, 95000 Cergy, Paris, France

attributed to contrasting habitat diversity, disturbance histories, gradients in wave energy and water clarity, depth and terrestrial influences.

The surveys reported here were undertaken during a period of time (1994–2001) when the state of the GBR coral communities was still considered by many to be largely unaffected by human activity due to its size, remoteness and low population density. However, assertions are being increasingly voiced that the GBR is being influenced by human impacts (e.g. Pandolfi et al. 2003): there are reports that some reefs are either degraded or under serious threat from a cumulative array of impacts (Bell and Elmetri 1995; Seymour and Bradbury 1999). Within the last 10 years, evidence has increased that terrestrial run-off of fertilizers and silt from rivers onto the shallow and wide continental shelf is a significant problem for some of the nearshore reefs (van Woesik et al. 1999; Brodie 2002; Furnas 2003; Fabricius and De'ath 2004; Fabricius et al. 2005), but again, these studies had restricted spatial ranges. The findings of our broad-scale assessment of nearshore reefs, describing regional differences in species richness and community structures, therefore have to be interpreted in the context of both natural gradients and natural and potentially anthropogenic disturbance histories.

## Materials and methods

### Field surveys

A total of 599 sites on 135 reefs were surveyed between 1994 and 2001 (Fig. 1) using a standard method of Rapid Ecological Assessment (DeVantier et al. 1998). During this period, different areas of the GBR were subjected to disturbances of varying spatial scale and intensity, including cyclones, flooding, bleaching, particularly in 1998, and continuing predation by crown-of-thorns seastars. The surveys provided a broad spread, both latitudinal and with distance from the mainland. There were 109 reefs surveyed in the nearshore (inner- or inner mid-continental shelf,  $\leq 35\%$  relative distance across the shelf) and 26 reefs on the mid- or outer shelf ( $> 35\%$  across the shelf). Sampling intensity was not consistent along or across the GBR, primarily because of logistic constraints. This was not a 'regional' study per se, rather gradients, discontinuities and changes in the nearshore coral communities were investigated along the GBR, albeit in an uneven manner, opportunistically over a 7 year period.

All data were recorded by observers experienced in the field identification of reef-building corals using SCUBA and snorkel from haphazardly chosen starting positions that were recorded with a portable Global Positioning System. On each reef, 1–31 habitats were surveyed in up to three depth zones (sites), comprising (a) the shallow reef flat and crest; (b) the shallow reef slope (between 3 and 7 m depth); and (c) the deeper reef slope (maximum depth of 16 m), respectively. Only

habitats considered suitable for development of coral-dominated communities were chosen, and hence flats of nearshore reefs, which often support abundant macroalgae and/or seagrasses and very sparse coral cover, were not surveyed. Similarly, headlands without reef development were avoided.

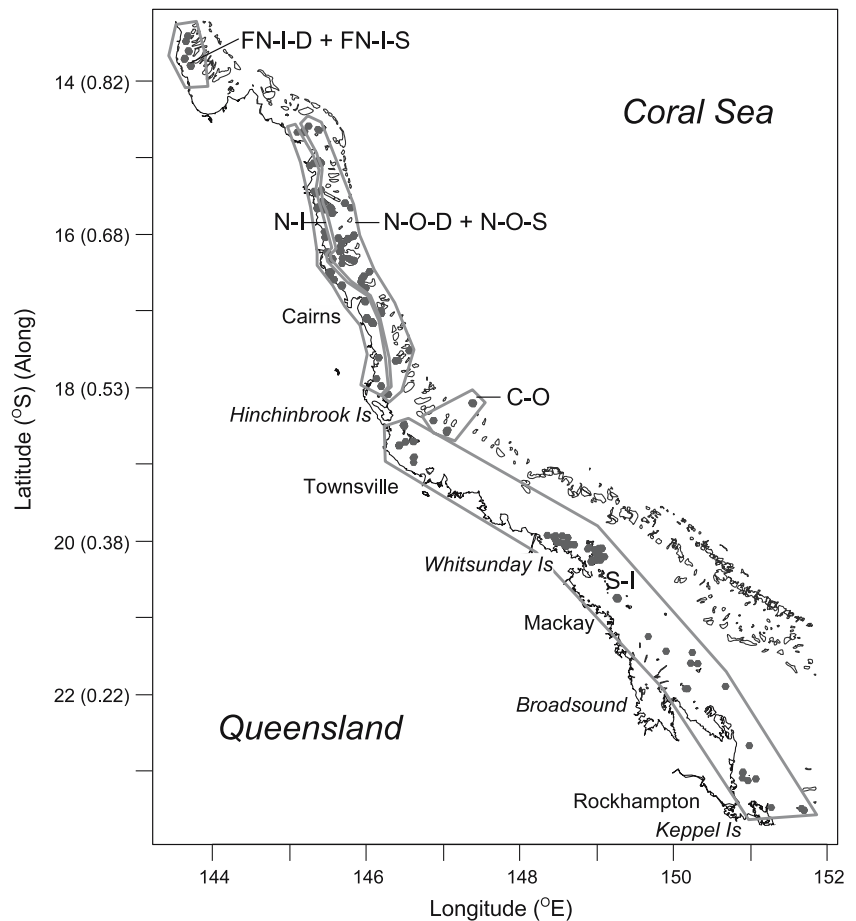
At each site, an inventory of reef-building corals was compiled (Class Anthozoa, Order Scleractinia). The swims took an average of 45 min and covered varying distances along the slope; generally areas were surveyed until no new taxa had been encountered for some time. Prior analysis of relations between species richness and duration of survey demonstrated a very weak relationship (DeVantier et al. 1998). Corals were identified to species level wherever possible (taxonomic references reviewed in Veron 1986, 2000), otherwise to genus and growth form (e.g. massive *Porites*). At the end of each site survey, the abundance of each taxon was recorded in six broad abundance categories—absent, rare, uncommon, common, abundant or dominant—analogueous to those used in vegetation analysis (Jongman et al. 1995). A visual estimate of average cover of live hard coral was also made, recorded in six categories: 0 = 0%, 1 = 1–10%, 2 = 11–30%, 3 = 31–50%, 4 = 51–75%, 5 = 76–100% (Miller and Muller 1999).

### Data analysis

Data were analysed at the level of individual sites. The positions of the sites were defined by mean depth and relative distance across and along the GBR (Fabricius and De'ath 2001; distance across takes the value 0 on the coast and 1 on the outermost edge of the continental shelf, and distance along takes the value 0 on the southern edge of the GBR World Heritage Area and 1 on the northern edge). The species richness of hard corals was calculated for each site (henceforth termed 'site richness'). Site richness and hard coral cover (0–5 rating scale) were estimated by assessing their dependency on location (relative distances across and along the GBR) and depth using linear models. Smooth terms in the three explanatory variables were included and the degree of smoothness was determined by cross-validation (Wood 2000). Interactions between the explanatory variables were included in initial models. Reefs were included as random effects, and the significance of effects was assessed by likelihood ratio tests.

Coral community composition was assessed using two methods. First the joint abundance ratings (untransformed) of the observed species were analysed using multivariate regression trees (MRT; De'ath 2002). MRT used sums of squares (Euclidean distance) for splitting and the explanatory variables were relative distances across and along the GBR and depth. The best-sized tree was selected by cross-validation and the 1 – SE rule (De'ath and Fabricius 2000) based on reefs to account for inter-site correlation within reefs. The tree

**Fig. 1** Map of the Great Barrier Reef (GBR) showing locations of 599 survey sites on 135 reefs. Broad geographic regions containing seven coral community groups (two of the regions contain deep and shallow groups) are also shown; the community groups are Far North Inner Deep and Shallow (FN-I-D and FN-I-S), North Inner (N-I), North Outer Deep and Shallow (N-O-D and N-O-S), Central Outer (C-O) and South Inner (S-I). The vertical scale bar also indicates the relative distance along the GBR, ranging from 0 at the southern to 1 at the northern edge of the GBR World Heritage area



defines a hierarchy of species communities and their spatial values that locate them on the GBR. This hierarchical approach can be used with any clustering method (constrained as is the case here with MRT or unconstrained). It also identifies groups of species that co-occur at varying spatial scales to form communities. This contrasts with non-hierarchical methods which derive mutually exclusive clusters at a single spatial scale, thereby lacking high-level (broad spatial scale) structure and ignoring information from highly prevalent species. The homogeneity of the clusters formed by MRT (from one through to seven nodes) was compared with similar numbers of unconstrained cluster groups, using *K*-means clustering and Euclidean distance.

Indicator values (DLI; Dufréne and Legendre 1997) were calculated for each species for each node of the tree. For a given species and a given group of sites, the DLI is defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups (a type of specificity), times the proportion of sites within the group where the species occurs (fidelity), multiplied by 100. DLI takes a maximum value of 100 if the species occurs at all sites in the group and nowhere else. Each species was associated with the tree node (community)

where its maximum DLI value occurred, and the numbers of indicator species and their values were used to characterize each node of the tree. Species with high DLIs were used as characteristic members of each community, and the spatial extent of the group indicated the region where the species was predominantly found.

A principal components analysis of abundance rating data (untransformed) was used to further illustrate the community structure within and between the groups formed by the multivariate tree analysis.

All analyses used the R statistical package (R Development Core Team 2005) including packages mvpart, vegan and mgcv.

## Results

### Patterns in species richness and cover

In total, 362 coral species from 75 genera in 15 scleractinian families were recorded in the 599 sites. Of these 359 species in 74 genera were hermatypes, excluding the dendrophylliid *Tubastrea*. Site richness averaged 39.5 over all sites (range 0–128; Table 1). Rank-ordered species richness was sigmoidal (Fig. 2a): 1.1% of sites had high species richness (> 100 species per site), ~30%

**Table 1** Means, standard deviations and ranges of site richness and cover (in ratings) of the coral communities of the whole GBR and the seven terminal community groups

Group	N	Richness			HC cover (ratings)		
		Mean	SD	Range	Mean	SD	Range
GBR	599	39.5	21.8	0–128	2.18	1.12	0–5
FN-I-S	13	85.3	19.4	52–128	3.85	0.99	2–5
FN-I-D	12	90.8	15.9	63–118	2.83	0.83	2–4
N-I	159	28.8	15.7	0–83	2.11	1.23	0–5
N-O-S	133	42.7	16.6	1–96	2.09	0.94	1–5
N-O-D	122	25.9	10.7	6–66	1.91	0.79	1–4
C-O	15	61.9	18.0	39–93	3.00	0.82	2–4
S-I	144	48.9	20.8	4–111	2.31	1.24	1–5

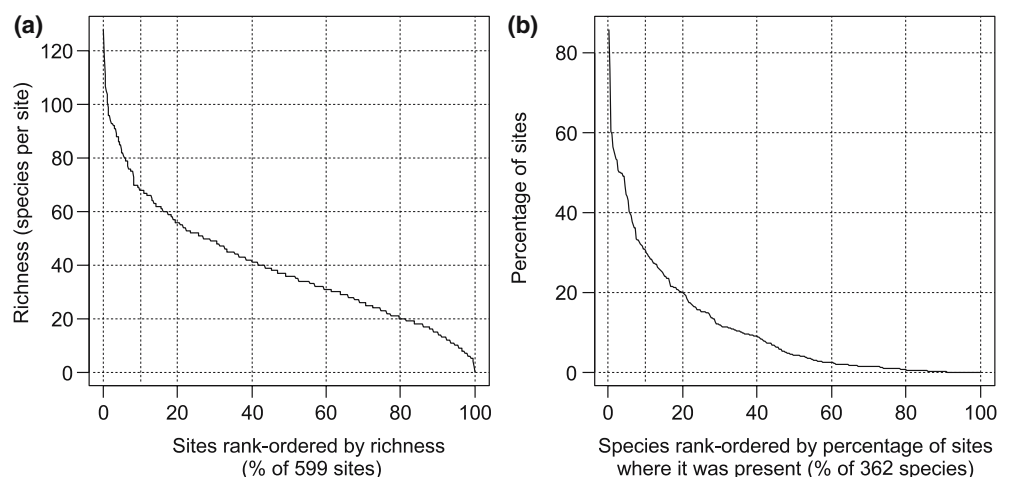
For abbreviations of the group names see Fig. 1  
 N number of sites per group

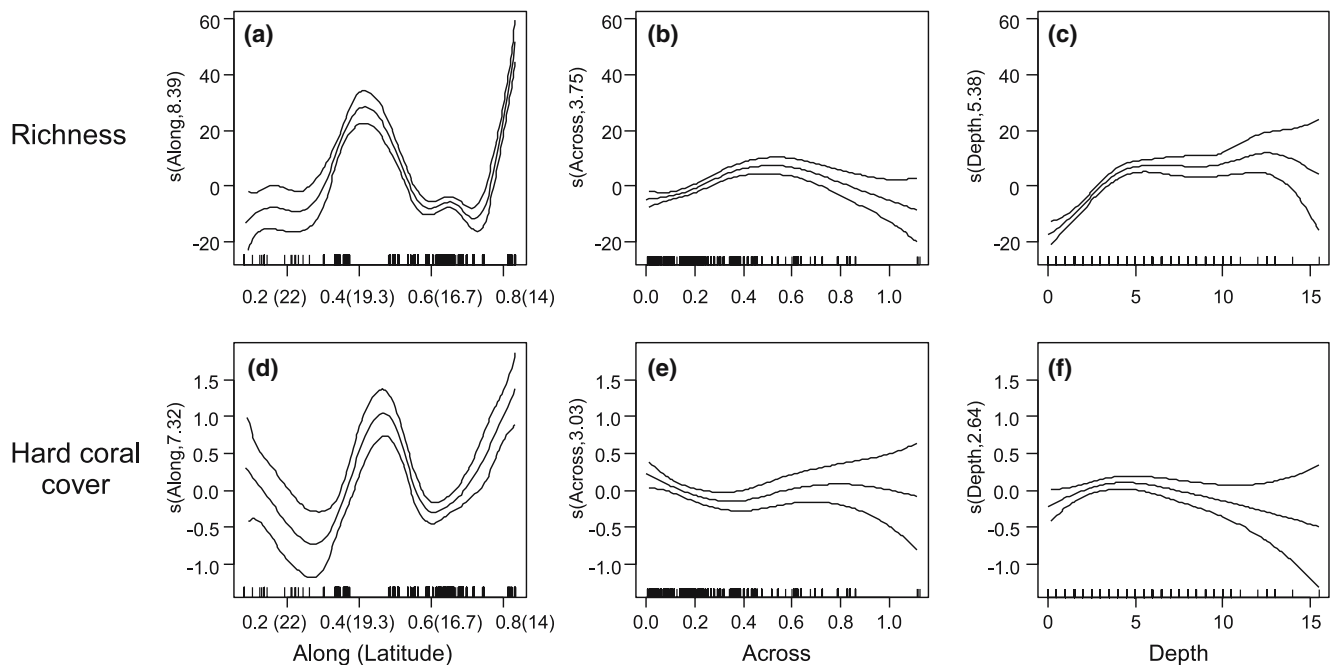
of sites had moderate richness (> 50 species), while ~ 20% of sites had low richness (< 20 species). Most of the 362 recorded species were rare or uncommon, occurring in only a small percentage of the sites surveyed (Fig. 2b). Eighty percent of the species were recorded in less than 20% of the sites and 18% were recorded only 1–3 times, with 32 species recorded only once. Only 10% of the species were moderately abundant, occurring in ≥30% of the sites, and of these, only 2 taxa (*Pocillopora damicornis* and massive *Porites* spp.) were recorded in > 80% of the sites.

Only four species were found exclusively on mid- and outer-shelf reefs (*Acropora multiacuta*, *Acropora polystoma*, *Pocillopora woodjonesi* and *Porites myrmidonensis*). Nine species were recorded only in the tropical waters of the far northern and northern reefs, all being new distribution records for the GBR (based on the distribution maps of Veron 2000): *Astreopora randalli*, *Pectinia maxima*, *Mycedium robokaki*, *Echinomorpha nishihirai*, *Oxypora crassispinosa*, *Turbinaria irregularis*, *Cantharellus jebbi*, *Lobophyllia dentatus* and *Oulophyllia levis*. Conversely, a small suite of ~10 characteristic ‘sub-tropical’ GBR taxa occurred predominantly in the southern GBR: *Acropora solitaryensis*, *Acropora glauca*,

*Acropora lovelli*, *Acropora chesterfieldensis*, *Acropora spicifera*, *Acanthastrea lordhowensis*, *Acanthastrea hillae*, *Scolymia australis*, *Turbinaria radicalis* and *Turbinaria heronensis*.

There was greater variation in site richness along the GBR than across the shelf or with depth (Fig. 3a–c). Controlling for distance across and depth effects, estimated richness was highest along the GBR in the Far North (~14°S) and in the Townsville (Palm Islands)–Whitsunday Islands region (~20°S), with 45 and 30 species per site above the mean value, respectively. Between these regions—in the Northern region (~15°S–18°S)—there was a sharp decline in richness. This ~400 km long stretch had 35–50 fewer species per site compared to the adjacent Far Northern and Townsville–Whitsunday Islands regions (~67 and 41% reductions, respectively; Fig. 3a). A second major decline in estimated site richness occurred south of 21°S (Northumberland Islands to Broad Sound), similar in magnitude to the Northern trough. Across the continental shelf, estimated site richness was ~10 species greater in mid-shelf sites than in either nearshore or outer-shelf sites (Fig. 3b). Richness was lower on the innermost mainland fringing reefs and the outer-shelf platform and

**Fig. 2** Distribution plots of rank-ordered **a** site richness (mean = 39.5, range 0–128) and **b** species abundances (the percentage of sites where each species was encountered)



**Fig. 3** Dependency of site species richness and hard coral cover (ratings) on relative distance along (a, d) and across (b, e) the reef and depth (c, f). The plots show partial effects of smooth trends based on linear regression models. Distance along the reef ranges from 0 at the southern end of the GBR to 1 at the far northern end (corresponding degrees in latitude are given in brackets). Distance across takes the value 0 on the coast and 1 on the 80 m contour of

the outer shelf. Hard coral cover was estimated as ratings as follows: 0 = 0%, 1 = 1–10%, 2 = 11–30%, 3 = 31–50%, 4 = 51–75%, 5 = 76–100%. For site richness ( $R^2 = 0.54$ ) all effects were significant ( $P < 0.01$ ), whereas for hard coral cover ( $R^2 = 0.18$ ) only the change with relative distance along the reef was significant ( $P < 0.05$ ). The short dashed lines (rugs) along the x-axis indicate the location of the survey sites

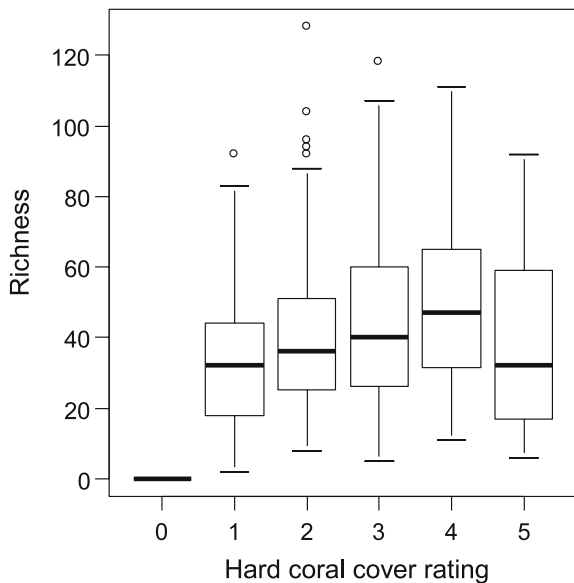
ribbon reefs and peaked in the middle section (~30–60% across the GBR, including the island fringing reefs of the inner mid-continental shelf and the mid-shelf platform reefs). Along the depth gradient, site richness was highest in >5 m depth, remained near-constant to the deepest depths surveyed (~15 m) and declined linearly at shallower depths (<5 m), losing ~5 species  $m^{-1}$  (Fig. 3c).

Hard coral cover varied with distance along the GBR, but was unrelated to relative distance across the GBR or depth (Fig. 3d–f). Along the GBR, the systematic variation was similar to that of richness, but changes were relatively smaller. Estimated cover was low in the Northern region (~15°S–18°S) and in Broad Sound (~21°S–23°S) and highest in the Far North and the Whitsunday Islands. Unlike richness, estimated cover increased weakly from Broad Sound towards the southern-most region of the GBR. There was a weak positive relationship between richness and hard coral cover ( $R^2 = 0.06$ ,  $P < 0.01$ ; Fig. 4). Such a weak relationship is not unexpected, given that on nearshore reefs, whole sites can be occupied by extensive beds of just a few species of genera such as *Goniopora*, *Porites*, *Alveopora*, *Echinopora* or *Leptoseris*. Conversely, other sites that were recovering from a past disturbance may be species rich, even at low levels of hard coral cover.

### Patterns in coral communities

Hierarchical coral communities were defined by MRT based on explanatory variables of relative distance along and across the GBR and mean depth of the sites. A tree with seven terminal nodes was selected with splits based on the three explanatory variables (Figs. 1, 5). Trees of size 7–22 predicted within 1 – SE of the best predictor and could be considered as representing a reliable community structure, with 7 being the most parsimonious structure. The seven groups of sites represent spatially contiguous clusters of similar species composition. Comparison of the homogeneity of clustering from 1 to 22 nodes with similar numbers of unconstrained cluster groups (using K-means clustering and Euclidean distance) showed that the constrained and unconstrained groupings were similarly homogeneous. This suggests that the species clusters are spatially contiguous and that the three spatial variables explain the groupings adequately. The 7-group tree explained only 13.3% of the variation in the species data, not unusual with large numbers of species of low abundance (G. De'ath, personal observation). The distribution plots of species abundances at each of the terminal nodes show that most species had consistently higher abundances in the three groups FN-I-D, FN-I-S and C-O compared to the four remaining groups.





**Fig. 4** Box and whisker plots showing the relationship between site species richness and hard coral cover (ratings: 0 = 0%, 1 = 1–10%, 2 = 11–30%, 3 = 31–50%, 4 = 51–75%, 5 = 76–100%). The horizontal bars indicate median values, boxes envelope the inner quartiles (middle half) of the data, whiskers mark 1.5 times the ranges of these inner quartiles (or the maximum data values, whichever is smaller) and circles denote extreme values

The analysis of indicator values was conducted for all 13 nodes of the regression tree, from the root node (representing the entire GBR) to the 7 terminal nodes. Of the 362 species, 188 had DLI values  $\geq 20$ , and 69 had DLI values  $\geq 50$ . All but four of these 188 high-DLI species occurred in five dominant community nodes, namely the two higher level communities of the whole GBR and FN-I and the three rich terminal groups FN-I-D, FN-I-S and C-O (Fig. 5, Table 2). The number of high-DLI indicator species (DLI values  $\geq 20$ ) found in the rich communities were, in order of decreasing spatial scale: the whole GBR = 32 spp., FN-I = 104 spp., FN-I-D = 75 spp., FN-I-S = 30 spp. and C-O = 51 spp. (Fig. 5). Importantly, none of the remaining eight northern (N) and southern (S) community nodes contained any indicator species with moderate to high values: the highest DLI within these groups was 12. These communities are hence dominated by the five rich hierarchical communities with many species indicators, in the sense that all species they contain also occur in higher numbers elsewhere.

The 32 indicator species with DLI maxima at the root node ('whole GBR') occur across most sites, whereas species of highest indicator values further down the tree are located in FN-I-D, FN-I-S and C-O. The eurytopic 'whole GBR' indicator species are generally ubiquitous and widely distributed beyond the GBR, and include species such as *P. damicornis*, *Stylophora pistillata*, *Galaxea fascicularis* and *Acropora hyacinthus* (Table 2).

The Far Northern community nodes (FN-I, FN-I-D and FN-I-S) contained 37 of the 69 species with DLI

values  $\geq 50$  and in total  $> 65\%$  of the species with high DLI values ( $\geq 20$ ), although they comprised only 25 of the 599 sites. The offshore group C-O, containing only 16 sites, also hosted a high number of indicator species with high DLI values, such as *Favia stelligera*, *Acropora humilis* and *Acropora secale*, *Pocillopora verrucosa* and *Pocillopora eydouxi* and *Porites lichen*. Therefore, most strikingly, the two regions FN-I and C-O, comprising  $< 7\%$  of all sites, contained community groups that included over 85% of all species and were associated with indicators for over 260 of the 362 observed species. An important point here is that these communities may be more widely distributed than the data suggest, since the number of reefs sampled was limited in the far northern and central offshore parts of the GBR (Fig. 1); while such limited sampling prevented reliable estimates of the regional species pool, it does not influence the estimates of richness at site level as shown in this analysis.

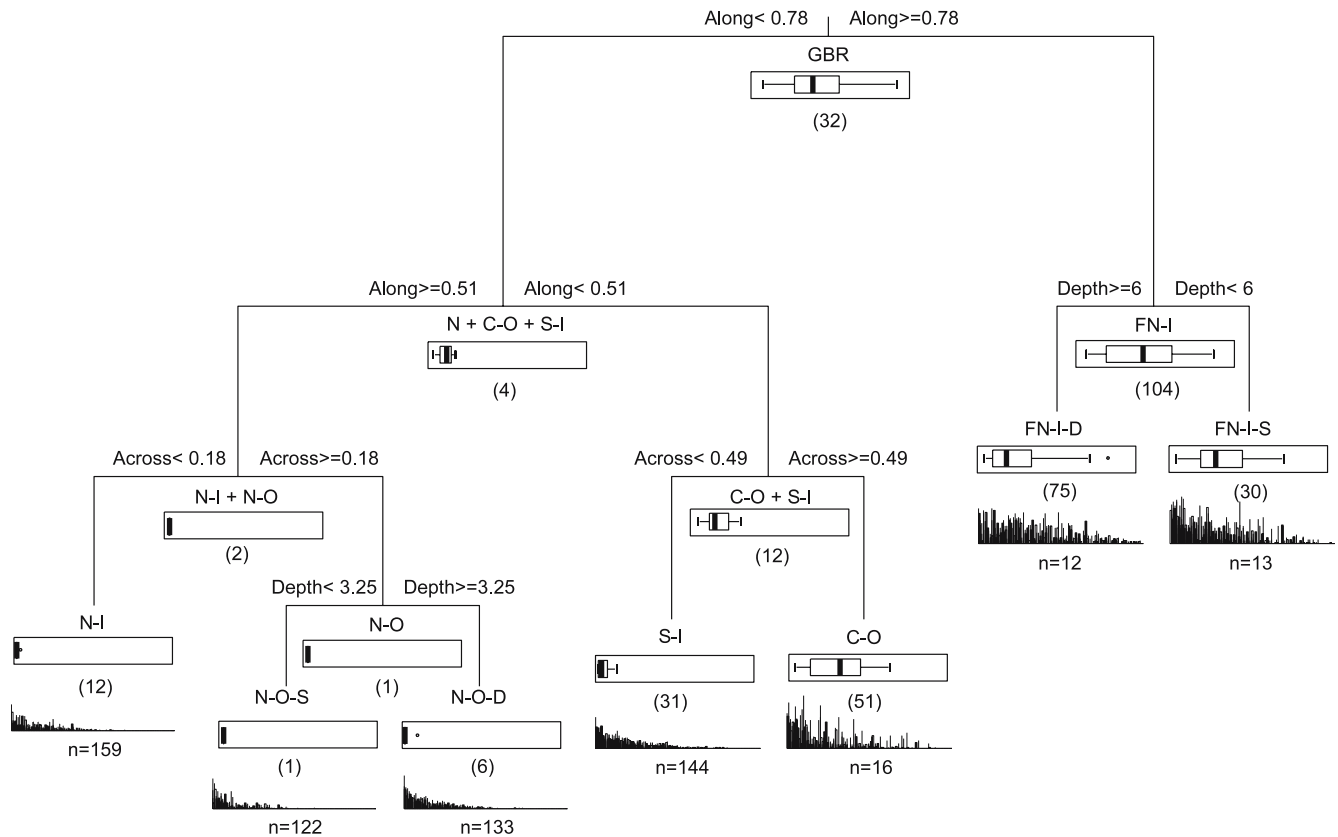
The principal components analysis also shows the dominance of species in the three communities FN-I-D, FN-I-S and C-O over the other terminal four groups (Fig. 6). The consistent direction of the species vectors towards the sites of these three groups shows that none of the 362 species were strongly affiliated with the remaining four terminal groups. The species associated with the Far Northern sites belonged to a wide range of genera and families, whereas most of the species associated with the offshore group C-O belonged to the genus *Acropora* (Table 2).

Cumulative species richness in FN-I-D, FN-I-S and CO had not approached an asymptote (Fig. 7). The two Far Northern communities had the fastest rates of species' accumulation, and these communities are substantially richer than described here. In three of the other four communities, cumulative richness was of the order of ca. 250 spp., with lower richness (ca. 175 spp.) in N-O-S (Fig. 7). This showed that the low mean site richness of the regions N-I, NO-D and S-I was due to a low representation of taxa at individual sites, rather than due to small regional species pools.

## Discussion

### The Great Barrier Reef fauna

A total of 362 species in 75 genera of reef-building corals were recorded in the surveys, representing  $\sim 91\%$  of species and 97% of genera known from the GBR (Veron 2000). The present study supports previous estimates of GBR richness and yielded new distribution records for nine species and one genus, the monotypic pectiniid *Echinomorpha* (*Echinomorpha nishiharai*). This raises the total species and generic richness of the GBR to  $\sim 405$  species in 78 genera. The species tally was lower than Veron (2000) partly because most of the species of massive *Porites* and some of the encrusting *Montipora* were not distinguished to species level in the field. The three previously recorded genera we did not encounter



**Fig. 5** Multivariate regression tree analysis defining coral communities (362 species) in terms of relative distance along and across the GBR and depth (599 sites). The terminal nodes represent seven communities (FN-I-D and FN-I-S, N-I, N-O-D and N-O-S, C-O and S-I; see Fig. 1 for abbreviations and locations) corresponding with different regions of the GBR, and the higher level nodes represent the six higher level communities. The bar plots show the distribution of species abundances at each of the terminal nodes, with each vertical bar representing the mean abundance of a species at that group. The numbers under the bar plots indicate the number ( $n$ ) of sites within each group. Each species is associated with the region where its Dufréne–Legendre indicator value (DLI, see

Materials and methods) is maximized. Box and whisker plots show the median and distribution of the DLI values at each node, and the number in round brackets below it is the total number of indicator species whose DLI was maximum at that node. The species with DLI maxima at the root node (all data) occur across most sites, whereas species with DLI maxima at the terminal nodes are predominantly located in restricted regions. Three of the seven terminal groups (FN-I-D, FN-I-S and C-O) and two higher level regions (GBR and FN-I) contain all species with high indicator values ( $DLI \geq 0.2$ ), whereas the other groups have only few indicators with very low indicator values ( $DLI < 0.2$ )

were the monotypic *Stylaraea* (Poritidae, *Stylaraea punctata*) and *Heterocyathus* (Caryophylliidae, *Heterocyathus aequicostatus*), which are found typically free-living in shallow and deep sandy areas, respectively, and the colonial mussid *Micromussa* (*Micromussa amakusensis*).

Most species present in the GBR were widely distributed across regions, but sparse in abundance across sites. Eighty percent of the species were recorded in less than 20% of the sites and 18% were recorded only 1–3 times. Just 4 of these 362 species were recorded only on mid- or outer-shelf reefs, confirming that a large majority of taxa can live (albeit some in low numbers) on nearshore reefs where water may be turbid from terrestrial influences and sediment resuspension. Nine species were recorded only in the tropical far northern and northern waters (all being new records for the GBR); for these species the northern GBR appears to represent the margin of their distri-

bution ranges (Veron 2000). In contrast, most of the 10 ‘sub-tropical’ GBR species found exclusively, in this study at least, in the southern and central GBR, but not in the north, also occur in sub-tropical or tropical regions elsewhere in the Indo-Pacific (Wallace 1999; Veron 2000), and the reasons for such apparently disjunct distribution and absence from the intensely surveyed more northern inshore areas of the GBR are unclear.

The taxonomic inventory in this study for the remote Far Northern communities is clearly an underestimate of the total regional richness, as the species-abundance curves were not yet saturated (Fig. 7). Mean site richness in the Far Northern GBR (Fig. 3) was as high as that recorded at the Indonesian Sangihe-Talaud and Banda Islands, which are located within the Indonesia–Philippines–New Guinea centre of diversity (Turak, unpublished site richness data). However, mean site richness in the Far Northern GBR was lower than that within the

**Table 2** Coral indicator species for the community groups identified at several hierarchical scales (see Fig. 5)

Community group	Species	DLI	Community group	Species	DLI
Whole GBR	<i>Porites massive</i>	86	FN-I	<i>Porites annae</i>	57
Whole GBR	<i>Pocillopora damicornis</i>	76	FN-I	<i>Seriatopora hystrix</i>	56
Whole GBR	<i>Stylophora pistillata</i>	60	FN-I	<i>Heliofungia actiniformis</i>	56
Whole GBR	<i>Galaxea fascicularis</i>	60	FN-I	<i>Fungia horrida</i>	55
Whole GBR	<i>Acropora hyacinthus</i>	56	FN-I	<i>Sandalolitha robusta</i>	54
Whole GBR	<i>Platygyra daedalea</i>	55	FN-I	<i>Astreopora myriophthalma</i>	54
Whole GBR	<i>Acropora millepora</i>	54	FN-I	<i>Goniopora minor</i>	53
Whole GBR	<i>Favites abdita</i>	53	FN-I	<i>Ctenactis echinata</i>	53
Whole GBR	<i>Acropora tenuis</i>	51	FN-I	<i>Favia pallida</i>	53
FN-I	<i>Fungia paumotensis</i>	83	FN-I	<i>Favites russelli</i>	51
FN-I	<i>Echinopora horrida</i>	73	FN-I	<i>Polyphyllia talpina</i>	50
FN-I	<i>Hydnophora rigida</i>	72	FN-I-D	<i>Mycedium mancaoi</i>	78
FN-I	<i>Merulina scabricula</i>	70	FN-I-D	<i>Herpolitha weberi</i>	67
FN-I	<i>Echinopora lamellosa</i>	69	FN-I-D	<i>Montipora turgescens</i>	61
FN-I	<i>Echinopora pacificus</i>	68	FN-I-D	<i>Oulophyllia bennettiae</i>	59
FN-I	<i>Goniopora columna</i>	67	FN-I-D	<i>Pectinia alvicornis</i>	57
FN-I	<i>Fungia concinna</i>	67	FN-I-S	<i>Platygyra ryukyuensis</i>	69
FN-I	<i>Herpolitha limax</i>	66	FN-I-S	<i>Acropora spathulata</i>	60
FN-I	<i>Ctenactis crassa</i>	66	FN-I-S	<i>Montipora spumosa</i>	54
FN-I	<i>Lobophyllia hemprichii</i>	65	FN-I-S	<i>Platygyra verweyi</i>	52
FN-I	<i>Leptastrea purpurea</i>	62	FN-I-S	<i>Pavona venosa</i>	51
FN-I	<i>Pachyseris speciosa</i>	62	FN-I-S	<i>Fungia repanda</i>	51
FN-I	<i>Podabacia crustacea</i>	61	C-O	<i>Favia stelligera</i>	61
FN-I	<i>Favia fava</i>	61	C-O	<i>Acropora humilis</i>	60
FN-I	<i>Pavona decussata</i>	61	C-O	<i>Pocillopora verrucosa</i>	59
FN-I	<i>Montipora hoffmeisteri</i>	61	C-O	<i>Porites lichen</i>	59
FN-I	<i>Pectinia lactuca</i>	61	C-O	<i>Acropora secale</i>	58
FN-I	<i>Psammocora digitata</i>	61	C-O	<i>Pocillopora eydouxi</i>	58
FN-I	<i>Merulina ampliata</i>	61	C-O	<i>Montastrea curta</i>	57
FN-I	<i>Fungia danai</i>	59	C-O	<i>Acropora abrotanoides</i>	57
FN-I	<i>Goniastrea pectinata</i>	59	C-O	<i>Acropora clathrata</i>	54
FN-I	<i>Favites halicora</i>	59	C-O	<i>Acropora gemmifera</i>	53
FN-I	<i>Montipora danae</i>	59	C-O	<i>Acropora robusta</i>	53
FN-I	<i>Psammocora contigua</i>	58	C-O	<i>Montipora foveolata</i>	51
FN-I	<i>Oulophyllia crispa</i>	57			

Only species with DLI  $\geq 50$  are listed

core of the Indo-west Pacific centre of diversity (Veron 1995; Briggs 1999; Allen 2000), including site richness recorded at Rajah Ampat, Wakatobi, Derawan and Bunaken Islands in Indonesia and Milne Bay in Papua New Guinea (Devantier et al. 2006; Turak and Devantier, unpublished site richness data).

### Coral community hierarchies

Patterns and processes governing species richness and community structure are complex and scale-dependent (Murdoch and Aronson 1999; Pandolfi 2002; Willig et al. 2003; Ricklefs 2004; Rahbek 2005). The hierarchical community structure based on MRT shows communities at varying spatial scales, with the seven GBR communities (terminal nodes of the tree) forming part of larger communities that in turn are part of the whole GBR community and larger communities of the Coral Sea Basin. Finer-scale structure of coral communities described in more geographically restricted analyses (Done 1982; van Woesik and Done 1997; Devantier et al. 1998) was not revealed in the 7-node tree selected here; however, larger trees with up to 22 nodes were all

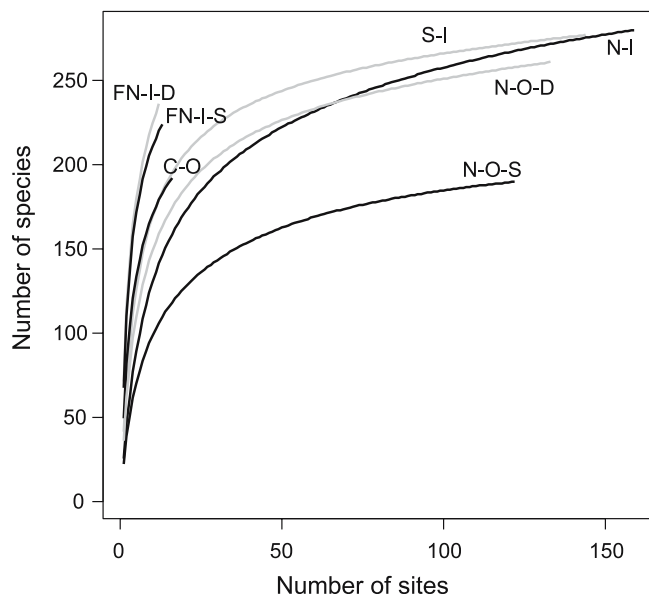
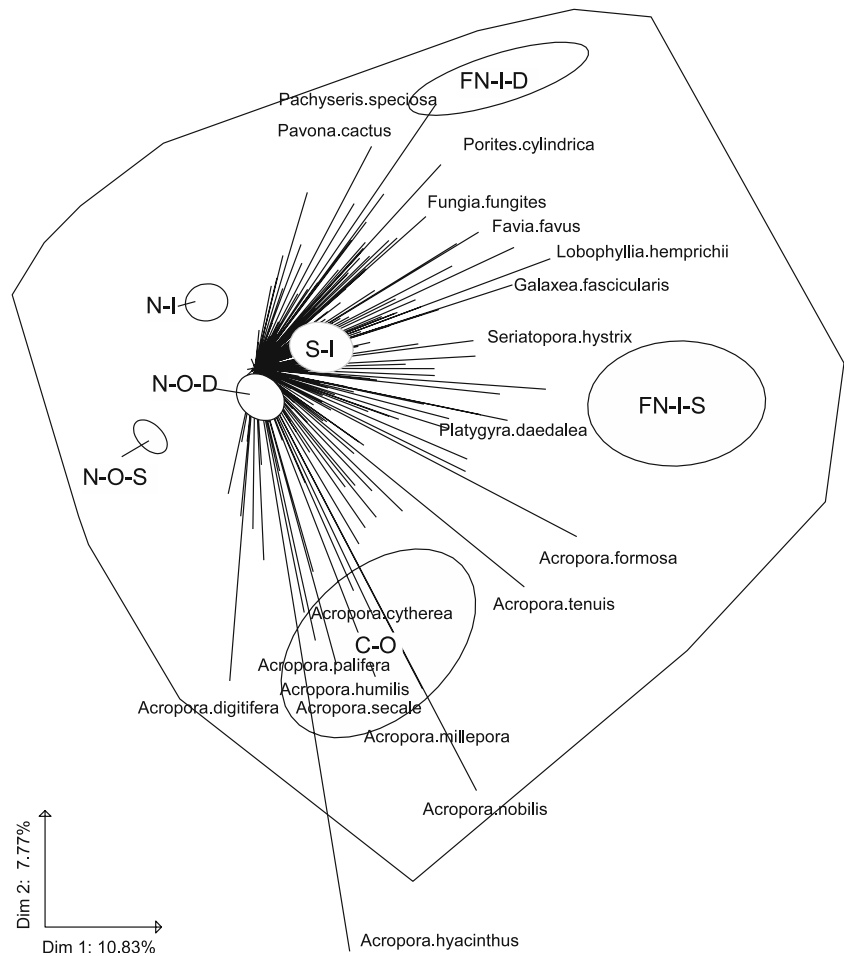
within 1 – SE of the best model, thus suggesting additional community types at finer spatial scales.

The indicator species show some species are predominantly associated with single communities and spatial regions and depths, but many communities also share a substantial proportion of their coral species complement, a phenomenon also reported elsewhere (e.g. Red Sea; Sheppard and Sheppard 1991; Devantier et al. 2000). Thus a continuum of community structure exists over space and depth, as shown here using regression tree analyses. This continuum is consistent with Ricklefs (2004) who argued that local and regional mechanisms influence species richness and interact on a continuum of time and space, with regional species pools shaped by the history of colonization and species' evolution and local richness shaped by local environmental determinants and regional species' interactions.

The two best differentiated communities were those of the Far North (FN-I), characterized by a species pool rare or absent from more southerly reefs, and the Central Offshore community (C-O) of mostly stout branching and massive corals (Fig. 5, Table 2). These included *Acropora palmerae*, *Acropora abrotanoides*, *A. polystoma*, *A. multiacuta*, *Acropora monticulosa*,



**Fig. 6** Principal component analysis biplot of the 362 hard coral species occurring in the 599 survey sites. The centroids of the seven community groups (FN-I-D and FN-I-S, N-I, N-O-D and N-O-S, C-O and S-I; see Fig. 1 for abbreviations) are marked by 95% confidence intervals (ellipses), while the total spread of the 599 sites is contained in the *convex hull*. The species' labels identify the 5% of species with greatest variation in the first two dimensions of the PCA; all other species names were removed for clarity. The species vectors point with a few minor exceptions towards three of the seven community groups (FN-I-D, FN-I-S and C-O), consistent with the fact that no species occurs at high levels in the four remaining groups that does not occur at high levels in the three dominant groups



**Fig. 7** Species-accumulation curves for the seven regional communities. For abbreviations of the region names see Fig. 1

*Acropora lutkeni*, *F. stelligera*, *P. verrucosa*, *P. eydouxi* and *P. woodjonesi*. On the GBR, these species occur mostly on offshore reefs, with relatively clear waters,

suggesting that their local populations are strongly phototrophic.

The varying degrees of differentiation in structure among the community groups (Figs. 5, 6) are partially explained by the differences in species' trophic modes and levels of trophic plasticity. The inshore communities (FN-I-D, FN-I-S, N-I, S-I) were typically characterized by euphylliids (*Euphyllia divisa*, *Euphyllia glabrescens*), pectiniids (*Mycodinium*, *Pectinia* spp.), faviids (notably *Echinopora* spp.), dendrophylliids (e.g. *Turbinaria*, *Duncanopsammia* spp.), poritids (e.g. *Goniopora*, *Alveopora* spp.) and fungiids. Although only a few species have been studied to date, at least some of these taxa are strong particulate feeders well suited to turbid habitats where relatively high concentrations of fine suspended sediments and particulate matter not only provide a food source (Anthony 1999), but also affect illumination and potentially smother corals (Stafford-Smith and Ormond 1992). Other, more widespread species have the capacity for trophic plasticity and local acclimation (e.g. the near-ubiquitous *Goniastrea retiformis*), maintaining a positive energy balance across a broad range of environmental conditions (Anthony and Fabricius 2000). Such capacity for plasticity is likely to contribute to a broad niche and a low indicator value for any one of the communities (low community fidelity). Of the few

species studied to date, *Montipora digitata*, *Acropora millepora* and *P. damicornis* display particle ingestion rates that increase linearly across a wide range of particle concentrations (Anthony 1999, 2000); all these species are widespread and common (Fig. 5). In contrast, *Porites cylindrica* apparently lacks trophic plasticity (Anthony and Fabricius 2000), possibly explaining its absence from our sites in the Broad Sound area with its very high turbidity (Kleypas 1996).

#### Regional trends in ecological status

The GBR coral communities have developed during the mid to late Holocene in a disturbance regime dominated by tropical storms and river floods. These regimes vary among our seven regions. Massel and Done (1993) suggest there is a peak in coral dislodging forces generated by cyclone waves near where our C-O and S-I communities adjoin, and King et al. (2001) show much shorter return periods between low salinity events in the depauperate wet tropics region than along other sectors of the inshore GBR. The recurrence intervals between such extreme events may be important drivers of richness and cover at site scale. These natural disturbance regimes have been augmented in recent times by human changes to the river systems, increasing fishing pressure, major population outbreaks of crown-of-thorns seastars *Acanthaster planci* and mass coral bleaching, among other impacts. Most of the present study was undertaken prior to the 1998 mass bleaching episode, hence the apparent poor condition of the Northern communities, both inshore and offshore, must be attributed to other causes. Importantly, the regional species pool of the Northern community was still quite rich, with >280 species recorded in total, and thus low site richness scores in the Northern community do not simply reflect a depauperate regional pool.

The Northern Inshore community closest to the 'Wet Tropics' rivers (community N-I) was highly depauperate at site level and comprised of mostly widespread species in low abundance (low indicator scores, Fig. 5). This is consistent with the increasing evidence that reefs lying in direct influence of these heavily modified rivers, with their major inputs in fine sediments, nutrients and pesticides and several outbreaks of crown-of-thorns starfish, are adversely impacted (Sweatman et al. 1998; Haynes et al. 2000; Wolanski 2001; Furnas 2003; Fabricius and De'ath 2004; Fabricius et al. 2005). Taxa with low trophic plasticity will be at significant risk if their habitat conditions change, likely exemplified by sites in the Northern inshore community N-I, with major reductions or absences of characteristic taxa and generally low abundances of even the ubiquitous species.

The Northern Offshore communities (N-O-S and N-O-D) also had low site richness, low coral cover and also lacked strong indicator species at time of survey in 1995–1997. This was more than a decade after the previous

highly destructive seastar outbreak series there, and coincidentally just prior to the next outbreak wave (Sweatman et al. 1998). It is possible that there had been insufficient time for establishment of the full potential richness and abundance at these sites. In contrast, the C-O had high richness at the time of survey, despite similar recovery time from the 1980s seastar outbreaks. At C-O, recovery was well underway (however, most of these and the Northern reefs have subsequently been impacted again by the seastars).

The poorer communities, and especially the Northern Inshore and Offshore communities did not contain any strong indicator species. This suggests that there has been little to no species replacement or shifts in community composition from one species suite to another following disturbance. Rather, there was a generally low representation of a wide range of species. The sites likely represent degraded, yet potentially transitional, forms of the more diverse communities to their north and south (Figs. 1, 6; see also DeVantier et al. 1998). In these respects, current ecological status, as exemplified here by site richness and cover, related as it is to disturbance regime and resilience, is superimposed on the intrinsic latitudinal, cross-shelf and depth effects on community structure.

In the central and southern GBR, the Palm Islands and Whitsunday Islands had generally higher site richness and cover than adjacent inshore areas to their north (Wet Tropics, in N-I) and south (Broad Sound–Keppel Islands; Figs. 1, 2, 3). The shallow, turbid and macrotidal Broad Sound region is known to be naturally marginal for coral growth and reef development (Kleypas 1996). Coral richness and cover in the late 1980s tended to increase with increasing distance offshore from Broad Sound and northwards to the Northumberland Group (van Woesik and Done 1997). Further to the south away from Broad Sound, low cover and richness at many of our sites at the Northumberland and Keppel Islands, at the time of survey in 1997, were legacies from the major coral mortality caused by a low salinity plume from the flooding Fitzroy River in 1990 (van Woesik et al. 1995) and a limited time for recovery. The lack of strong indicator species in the central and southern inshore communities was attributed to two factors. First, the sub-tropical coral species described above were uncommon and sparsely distributed, and thus did not score highly on the DLI. Second, the disturbance and geographic effects described above were manifested as a lack of species, rather than replacement by another suite of species between disturbances.

#### Resilience in a changing disturbance regime

Since the undertaking of most of this study, many GBR reefs have been affected by mass bleaching events in 1998 and 2002 (Hoegh-Guldberg 1999; Lough 2001; Berkelmans et al. 2004), and many have been subjected to the third destructive outbreak of *A. planci* since the

1960s. With likely synergistic effects of future mass bleaching episodes, *A. planci* outbreaks and river runoff, the capacity for recovery of the inshore reefs may be severely put to test. It is conceivable the depauperate characteristics of the communities N-I, N-O-S and N-O-D will become more widespread, through a region-wide depletion and loss of less tolerant, more specialized taxa and loss of their reproductive outputs. Such changes would represent a severe reduction in ecological complexity and diversity. It would likely cascade from reef to reef, through a weakening supply of larvae of many species of reef-inhabiting organisms, and from corals to other faunistic groups (Jones et al. 2004). The best presently available strategy to counter such possibility would appear to be a patchwork of strategically placed no-take zones across the length and breadth of the Great Barrier Reef. Such a patchwork now exists (currently covering 33% of the GBR's total area); however, it remains to be seen whether and for how long such networks will counteract predicted increases in the frequency of major disturbances.

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