Report

Assembly Rules of Reef Corals Are Flexible along a Steep Climatic Gradient

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Summary

Coral reefs, one of the world's most complex and vulnerable ecosystems, face an uncertain future in coming decades as they continue to respond to anthropogenic climate change, overfishing, pollution, and other human impacts [1, 2]. Traditionally, marine macroecology is based on presence/absence data from taxonomic checklists or geographic ranges, providing a qualitative overview of spatial shifts in species richness that treats rare and common species equally [3, 4]. As a consequence, regional and long-term shifts in relative abundances of individual taxa are poorly understood. Here we apply a more rigorous quantitative approach to examine large-scale spatial variation in the species composition and abundance of corals on midshelf reefs along the length of Australia's Great Barrier Reef, a biogeographic region where species richness is high and relatively homogeneous [5]. We demonstrate that important functional components of coral assemblages "sample" space differently at 132 sites separated by up to 1740 km, leading to complex latitudinal shifts in patterns of absolute and relative abundance. The flexibility in community composition that we document along latitudinal environmental gradients indicates that climate change is likely to result in a reassortment of coral reef taxa rather than wholesale loss of entire reef ecosystems.

Results and Discussion

The accelerating impact of climate change on coral reefs is of major concern worldwide [2, 6–8]. Contemporary research on how climate change affects coral reefs has matured beyond the simplistic "canary in the coal mine" concept to a more nuanced recognition that climate-related pressures such as bleaching (due to the loss of symbiotic zooxanthellae) and ocean acidification do not affect all species equally (e.g., [2, 6, 7, 9–11]). In this context, a critical issue for the future status of reefs will be their ability to maintain functional capacity in the face of the changes in species composition

that are already underway due to multiple anthropogenic impacts [1, 6, 12, 13]. To date, all regional-scale assessments of coral reef condition have been based on the relatively crude metric of total coral cover, masking the extent of changes in relative abundances [1]. Here we explicitly examine regional-scale patterns in the composition of coral reef assemblages along the full length of the Great Barrier Reef, which spans a latitudinal environmental gradient from 10°S to 23°S (Figure 1). Average summer sea surface temperatures (SSTs) in the northern Great Barrier Reef exceed southern winter temperatures by at least 8°C–9°C [14], and even larger deviations occur in shallow reef habitats or during warm or cold spells. Our multiscale sampling and analyses are uniquely designed to compare local and regional variation in coral assemblages and to test the extent to which individual taxa change in abundance at multiple scales. Our results provide the first quantitative evidence of spatial shifts in the assemblage structure of contemporary corals (as distinct from counts of species) at a hierarchy of scales, placing local variation in assemblage structure among sites, reefs, and habitats in a broader biogeographical perspective.

The structure of coral assemblages changes substantially at regional scales along the Great Barrier Reef, with important functional components exhibiting large shifts in relative and absolute abundance (Figure 2; Table 1). Coral assemblages in two key habitats (reef crests at 1–2 m depth and reef slopes at 6–7 m) also have highly distinctive faunas, which differ from each other as much as the Great Barrier Reef regions separated by up to 1740 km (Figure 2). Our data show that crest and slope assemblages along the Great Barrier Reef do not exhibit a monotonic trend with latitude or latitude-related temperature gradients, because some taxa increase in abundance as others decrease or remain relatively constant among regions (Figures 2 and 3). On reef crests, 9 of the 12 major taxa that comprise these assemblages varied significantly among regions. Similarly, on slopes, seven taxa showed significant regional-scale variation in abundance (Figure 3). Only *Montipora* spp. were uniformly abundant along the Great Barrier Reef on both the crests and slopes. The other 11 taxa exhibited significant regional-scale variation on the reef crests and/or slopes, regardless of their susceptibility or resistance to thermal stress and bleaching (Table 1). For 7 of the 12 taxa, 20%–44% of the overall variation in their abundance in at least one habitat occurred at this largest, regional scale. These findings indicate that assembly rules at a regional scale are surprisingly flexible and do not show a consistent latitudinal response to climatic drivers (Figure 2).

In comparison to regional differences in species abundances, variation among adjacent reefs was generally small, whereas variation among sites on individual reefs was often comparable to or greater than among regions (Figure 3). Only two taxa (Poritidae and *Montipora*, both on crests), showed reef-scale differences that accounted for >12% of the total variation. In contrast, on both crests and slopes, all taxa showed significant differences in abundance among sites that typically account for 15%–30% of the overall variation in abundances (Figure 3).
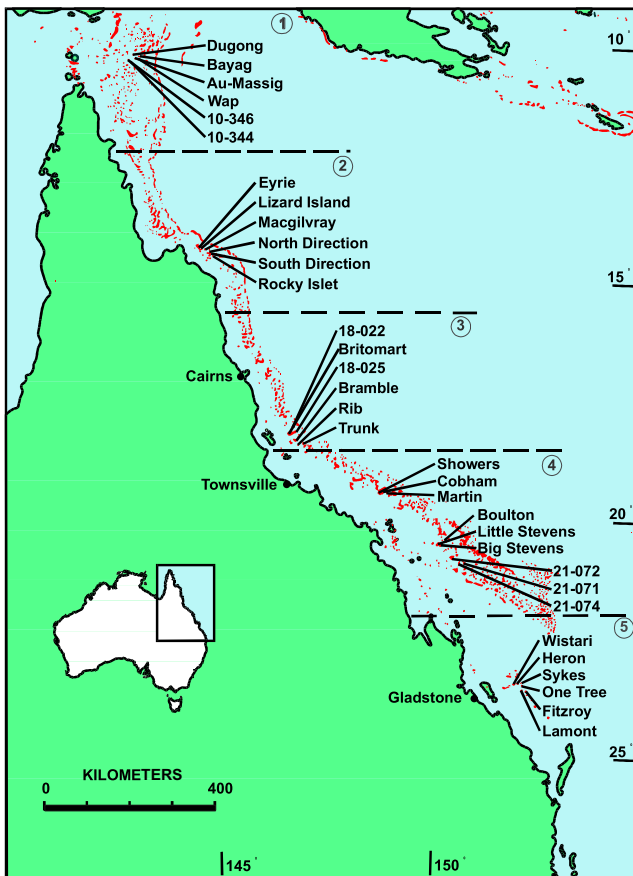
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Figure 1. Map of the Great Barrier Reef Showing the Locations of Five Regions and Thirty-Three Reefs Where Abundances of Corals Were Measured on the Reef Crest and Slope
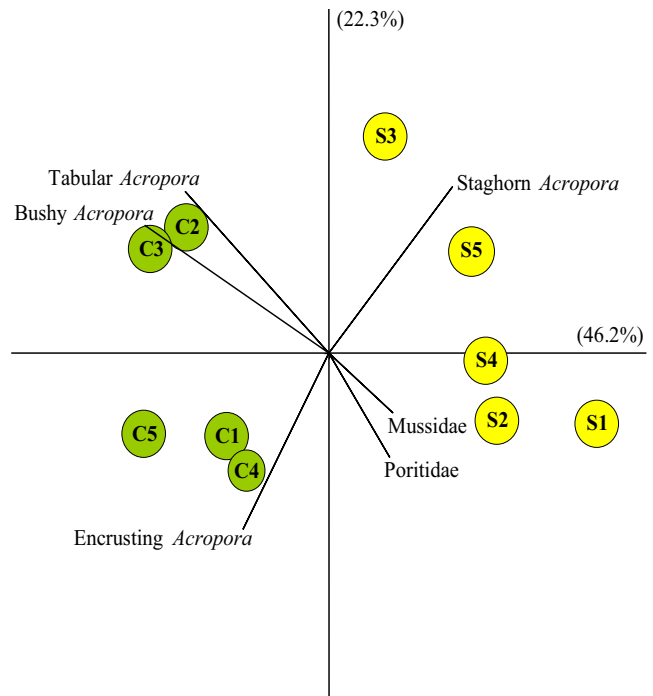
Figure 2. Spatial Variation in Community Structure of Coral Assemblages Revealed by Canonical Discriminant Analysis, Based on Percent Cover of Twelve Taxonomic Categories Measured on 1,320 Ten-Meter Transects

The ten circles depict assemblage structure in two habitats (C, crest; S, slope) in each of five regions, numbered 1–5 from north to south along the Great Barrier Reef (see Figure 1). The diameter of the circles indicates that reef-scale variation in assemblage structure is uniformly small in comparison to differences among regions or habitats. The vectors (for clarity, only 6 of 12 are shown) indicate which taxa are primarily responsible for discriminating among habitats and regions.

Shallow-water reef crests are readily distinguished from deeper slopes (multivariate analysis of variance $F_{region*habitat}$ = 24.55, df = 48, 5,156, p < 0.001; Figure 2). Intuitively, crests have higher abundances of wave-tolerant taxa (encrusting, bushy, and/or tabular species of *Acropora*), whereas many slopes are dominated by more delicate staghorn *Acropora* that are virtually absent from crests (Figure 2). The crest assemblages in some regions overlap slightly (regions 2 and 3 and regions 1 and 4; see Figure 1 for locations), whereas the slope assemblages in different regions are all distinctive (Figure 2). On crests, the total abundance of corals (all taxa combined) was remarkably uniform among regions and among adjacent reefs but differed substantially at smaller scales (see the right-hand hatched bars in Figure 3). On slopes, total abundances varied significantly among regions and to a lesser extent among reefs. However, like the crests, much greater differences in total coral cover (>65% of the overall variation) occurred locally among and within sites.

These multiscale patterns in assemblage structure align with the spatial scales of variation in demographic processes (recruitment, growth, and mortality) that affect the abundance of different coral taxa. Recruitment by brooding and spawning corals on the Great Barrier Reef also varies latitudinally among regions, among depths, and among local sites but is relatively uniform among adjacent reefs [22, 23]. Similarly, growth of corals varies among habitats with changes in depth and exposure [24] and regionally in response to latitudinal gradients in light, water flow, and temperature [25, 26]. However, colony growth is unlikely to vary significantly among neighboring reefs that share similar physical conditions, a pattern that is consistent with our finding that species abundances vary least at this intermediate scale. Persistent, larger-scale differences in some sources of mortality may also contribute to patterns of abundance among regions. For example, outbreaks of crown-of-thorns starfish, *Acanthaster planci*, are less prevalent at either end of the northern Great Barrier Reef, and cyclones are 4–5 times more frequent in the central Great Barrier Reef compared to northern or southern regions [14].

An unknown amount of the multiscale spatial variation we describe could be due to recent disturbance events such as cyclones, crown-of-thorn starfish predation, episodes of bleaching, or to pulses of recruitment. Major, regional-scale bleaching due to thermal stress has affected the Great Barrier Reef twice since scientific observations began more than 60 years ago, in 1998 and in 2002 [27]. Adjacent reefs tended to bleach (or not) in clusters at scales of tens of kilometers, with strong bleaching recorded in each of the events on 18% of reefs scattered throughout most of the length of the Great Barrier Reef [27]. In the most extreme case, the spatial variation among regions, reefs, and sites that we have documented could simply represent otherwise identical assemblages that are transiting through a successional trajectory that converges in theory to the same climax community at all spatial scales,
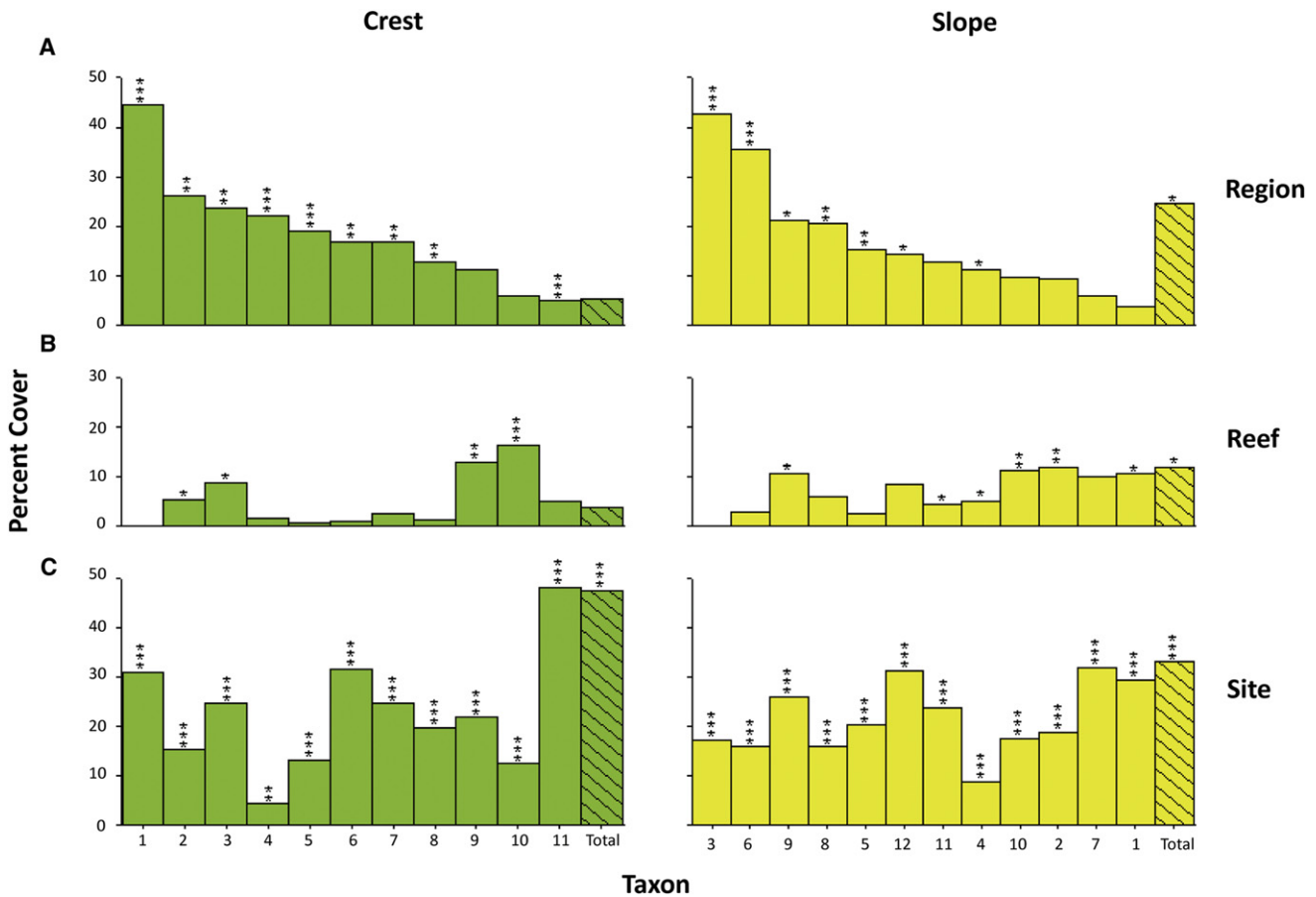
Figure 3. Components of Variation in Percent Cover of Corals at Three Spatial Scales, Region, Reef, and Site, on Reef Crests and Slopes

Crests are colored green; slopes are yellow. Individual species are grouped here into 12 taxa according to their taxonomic, morphological, and ecological traits (Table 1). The order of taxa is arranged from high to low amounts of regional-scale variation in either habitat. The taxonomic groups are: 1, encrusting *Acropora*; 2, Faviidae; 3, tabular *Acropora*; 4, Mussidae; 5, Pocilloporidae; 6, bushy *Acropora*; 7, soft corals; 8, other sessile animals; 9, Poritidae; 10, *Montipora*; 11, other scleractinians; 12, staghorn *Acropora* (slopes only). The hatched bars show variation in total cover of all taxa combined. Asterisks indicate significant differences in abundance among regions (A), reefs (B), or sites (C): *p < 0.05; **p < 0.01; ***p < 0.001.

as cover increases. However, we find no evidence of such convergence. At the regional and reef scale, we see no logical ordering of crest or slope assemblages (e.g., from low cover by newly recruited corals to high cover by competitive dominants) that is consistent with an ecological succession (Figure 2; Table 1). Among habitats, the divergence between crests and slopes is clearly not a temporary phenomenon and is consistent with many studies that have documented coral reef zonation along environmental gradients [28–32]. At longer evolutionary time frames, the relative abundances of abundant species in time-averaged fossil coral assemblages in the Caribbean varied most at regional and local scales, but only a little at an intermediate scale among adjacent reefs [33], the same pattern we have found here for extant assemblages in the Pacific (Figure 3). We conclude that a relatively small amount of the spatial patterns that we recorded among habitats and regions of the Great Barrier Reef (Figure 2) is likely to be attributable to temporal variation. Longer-term influences such as physiological tolerances of individual taxa and spatial patterns of mortality, growth, and larval recruitment appear to be the major drivers of multiscale spatial variation in these coral assemblages among habitats and along the length of the Great Barrier Reef.

Implications for the Future of Coral Reefs

Our results have profound implications for the future expectations of regional-scale impacts of climate change on coral reefs. Importantly, the susceptibility of corals to thermal stress and bleaching, reduced alkalinity, and other climate-related phenomena all vary substantially within and between taxa (e.g., [2, 6, 7, 10, 15, 30, 34]). For example, some coral genera and species, such as slow-growing, massive *Porites* and *Leptastrea*, bleach far less readily than faster-growing branching and tabular *Acropora* (e.g., [6, 10, 16]; Table 1). Similarly, in short-term experiments, some corals retain their calcifying abilities over a realistic range of aragonite concentrations, whereas others are much more sensitive [2, 9, 35]. Furthermore, recolonization and recovery after disturbances such as cyclones or bleaching events varies greatly among species (e.g., [22, 36, 37]). Species such as *Acropora* and *Pocillopora* that are susceptible to bleaching and other mortality agents can also be good colonizers (Table 1), complicating our capacity to predict future assemblage structures on tropical reefs.

Our results show that the diverse pool of species that we sampled along a latitudinal gradient can assemble in markedly different configurations (Figures 2 and 3) across a wide range

Table 1. Twelve Taxonomic Groups, and Their Ecological Characteristics, Used to Quantify Changes in Composition of Reefs along the Length of the Great Barrier Reef

Taxon	Growth Form	Susceptibility to Bleaching [7, 10, 15–17]	Life History Traits [18–21]
1. Encrusting *Acropora*	encrusting mounds	high	moderate growth rate, often long-lived, resistant to cyclones, brooders
2. Faviidae	massive, encrusting, less commonly plate-like	low to medium	slow-growing, long-lived, resistant to cyclones, broadcast spawners
3. Tabular *Acropora*	tabular, foliaceous	high	fast-growing, competitive dominants, highly susceptible to cyclones, spawners
4. Mussidae	massive, encrusting	low	slow-growing, long-lived, resistant to cyclones, aggressive competitors, broadcast spawners
5. Pocilloporidae	small bushes	medium to high	moderate growth rate, short-lived, usually brooders
6. Bushy *Acropora*	small to medium bushes	high	moderate growth rate, short-lived, broadcast spawners
7. Soft corals	encrusting, tree-like	high	often highly clonal and persistent
8. Other sessile animals	mixed	usually low	often cryptic and ephemeral
9. Poritidae	massive, finger-like	low	slow-growing, long-lived, resistant to cyclones, mixed spawners and brooders
10. *Montipora*	sheet-like, foliaceous, submassive	medium to high	variable growth rates, often long-lived, resistant to cyclones, spawners
11. Other scleractinians	mixed	low to medium	tend to be rarer species, with mixed life histories
12. Staghorn *Acropora*	tall, loosely branching	high	fast-growing, highly clonal, highly susceptible to cyclones, spawners

of contemporary environments [14, 38]. These findings, combined with the emerging literature on widespread shifts in species composition of coral reefs in recent decades (e.g., [1, 39]) and on range expansions by coral reef species [40, 41], support the hypothesis that coral reef assemblages will change substantially but could continue to function as highly altered systems in the future if emissions of CO_2 and other greenhouse gasses are reduced sufficiently to avoid a complete collapse of reefs. Furthermore, the geographic ranges of 93% of the 416 coral species found on the Great Barrier Reef extend northwards toward the equator (e.g., to Papua New Guinea, the Solomon Islands, and/or the Indonesian archipelago), and 46% are also found in colder conditions further to the south [5]. Average SSTs on the Great Barrier Reef in the past 30 years (1976–2005) have risen by 0.25°C in the north and 0.4°C in the south compared to the earliest instrumental records from 1871 to 1900, and they are projected to rise by 1°C–3°C by 2100 under "business as usual" carbon emission scenarios [14]. Consequently, average thermal conditions in the southern Great Barrier Reef are unlikely to exceed those now being experienced by these same species in the more equatorial regions of their current geographic ranges.

Compared to temperature, spatial and temporal patterns of pH and aragonite saturation state on coral reefs are poorly understood, because global and regional patterns are well described only for the open ocean. Furthermore, separating the extent to which aragonite concentrations and temperatures control reef growth or physiology at relevant scales is difficult because both are strongly correlated with each other and with latitude [2]. Tropical oceans will remain saturated with aragonite unless extreme levels of atmospheric CO_2 occur (approximately 1700 ppm, or six times preindustrial levels) [35]. Globally, ocean surface pH has decreased by 0.1 unit since 1750 due to the uptake of atmospheric CO_2, with a smaller 0.06 decline recorded for the tropics [35]. In comparison, contemporary variation in pH among reef habitats on the Great Barrier Reef and among short-term replicate measurements spans a range of 0.39 units, from 8.37 to 7.98 [42]. This short-term and habitat-scale variability swamps latitudinal trends, which were undetectable on reef habitats along

510 km stretching from the northern to central Great Barrier Reef [42]. Some individual *Porites* colonies on the Great Barrier Reef exhibit a small reduction in growth rate in recent years due to unknown causes, as reveled by skeletal growth bands [43]. However, other colonies show no decline. A similar study along the length of the western coast of Australia found no change in calcification rates in the 20th century, whereas growth of high-latitude corals is increasing in response to rising temperatures [26].

Using natural gradients in pH close to volcanic carbon dioxide seeps, Fabricius et al. [11] compared coral cover and assemblage structure under a range of conditions that mimic future climate change scenarios. Coral cover did not change between "low pCO₂ sites" (pH range 7.97–8.14) and "high pCO₂ sites" (pH range 7.73–8.00). Cover of massive *Porites* was double under the less alkaline conditions, whereas branching and other three-dimensional corals were less abundant [11]. These studies and our large-scale analysis of coral assemblages all point to a surprisingly resilient response by some elements of coral assemblages to spatial and temporal shifts in climatic conditions. Nonetheless, the impacts of climate change on more vulnerable taxa are already substantial [7, 44–46]. Key areas for future research include the capacity of coral reef organisms to acclimate and adapt to rapidly changing conditions, the abilities of warm-adapted genotypes to disperse, and the dynamics and resilience of altered and depleted assemblages [2, 6].

In conclusion, our multiscale spatial analyses demonstrate that assembly rules of coral assemblages are flexible, as indicated by the individualistic variation in abundance of each taxon (Figure 3). In the past three decades, corals have shown a wide range of susceptibilities to episodic bleaching events (and to other climate-related phenomena such as cyclones and emergent diseases), depending on their physiology, life history, morphology, and spatial distribution ([10, 15, 16, 30]; Table 1). Different reef taxa will continue to react to environmental change at a variety of scales, both in time (e.g., behavioral, physiological, and evolutionary responses) and in space (e.g., changes in growth form, local abundance, and geographic ranges). At any one location, some coral reef taxa

that are currently dominant are likely to decline or disappear while others may simultaneously increase or expand their geographic range from elsewhere, producing highly altered assemblages analogous to the evolution of novel terrestrial plant assemblages that occurred in response to Quaternary climate change [47]. However, in the case of corals and other reef organisms, these alterations are likely to be much more rapid and unpredictable because of the rapid pace of anthropogenic climate change and the greater potential for dispersal of marine larvae compared to most terrestrial plants [48]. As with Pleistocene marine and terrestrial assemblages [41, 47], many of these novel coral reef communities are likely to lack contemporary analogs, with unknown but potentially far-reaching consequences for the ecology and evolution of reef organisms.

Experimental Procedures

Multiscale Sampling Design
We used a hierarchical, nested sampling design to quantify scale-dependent patterns of coral abundances. Five regions of the Great Barrier Reef were sampled from north to south, each 250–500 km apart. Within each region, we sampled three to six midshelf reefs, separated by approximately 10–15 km. A total of 33 reefs were sampled over a 12-month period. On each reef, four sites were located 0.5–3 km apart. Coral composition and abundances (number of colonies and percent cover) were measured at each of the 132 sites using ten replicate 10-meter-long line intercept transects placed a few meters apart following the depth contour. Thus, our sampling protocol is based on 1,320 standardized sampling units (each transect) that were spaced apart at different scales from meters to hundreds of kilometers. Using this multiscale sampling design, abundances were measured in each of two habitats: the reef crest (1 m below datum) and the reef slope (6 m below datum).

We identified and measured a total of 35,428 coral colonies on 33 reefs. We categorized each colony that we encountered (including the majority of species that are too rare to analyze individually) into ecologically relevant groups depending on their physiology, morphology, and life history (see Table 1) and then quantified multiscale variation in abundance of each those groups. The most common species and genera (in parentheses) in each of the 12 taxonomic groups were: 1, encrusting and submassive *Acropora* (*A. palifera*, *A. cuneata*); 2, Favidae (*Cyphastrea*, *Echinopora*, *Favia*, *Favites*, *Goniastrea*, *Leptastrea*, *Montastrea*, *Platygyra*); 3, tabular *Acropora* (*A. cytherea*, *A. hyacinthus*, *A. paniculata*); 4, Mussidae (*Acanthastrea*, *Lobophyllia*, *Symphyllia*); 5, Pocilloporidae (*Pocillopora*, *Stylophora*, *Seriatopora*); 6, bushy *Acropora* (*A. gemmifera*, *A. humilis*, *A. loripes*, *A. nasuta*, *A. secale*, *A. tenuis*, *A. valida*); 7, soft corals (alcyonaceans, zooanthids); 8, other sessile animals (sponges, tunicates, mollusks); 9, Poritidae (*P. annae*, *P. cylindrica*, *P. lobata*); 10, encrusting and submassive *Montipora* (*M. foliosa*, *M. grisea*, *M. hispida*, *M. montasteriata*, *M. tuberculosa*); 11, other scleractinians; 12, staghorn *Acropora* (*A. danai*, *A. florida*, *A. formosa*, *A. intermedia*, *A. microphthalma*, *A. robusta*). The amount of variation at the regional scale exhibited by each of the 12 taxonomic groups was independent of their species richness ($r^2 = 0.27$ and 0.04 on crests and slopes, respectively), indicating that the large-scale predictability of these functional components (Table 1) is insensitive to the classification we used.

Statistical Analyses
The sampling was designed for a three-factor nested analysis of variance where regions, reefs, and sites were random factors, with the residual within-site variation among replicate transects represented by the error term. Heterogeneity of variances was removed using log (x+1) transformations. Analyses based on cover and on counts of colonies yielded almost identical results, so we present only the former here, as is conventional for sessile, clonal organisms. We used variance components analysis [49] to quantify the importance of scale by partitioning the overall variation in abundance of each taxon into components associated with regions, reefs, sites, and within sites, separately for the two habitats. Spatial variation in community structure of coral assemblages among habitat and regions was analyzed via multivariate analysis of variance followed by canonical discriminant analysis, based on percent cover of the 12 taxonomic categories.

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