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# Environmental tolerance governs the presence of reef corals at latitudes beyond reef growth

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## ABSTRACT

**Aim** Understanding mechanisms that enhance survival outside the usual range of a taxonomic group is key to understanding diversity gradients, how range boundaries operate and how environmental change might influence geographical distributions. Our aims were: (1) to identify species-level traits associated with reef-building coral species whose ranges extend into high-latitude, non-reefal habitats (i.e. 'beyond reef'), (2) determine if these patterns were consistent in different global regions, and (3) determine if traits associated with living beyond reef were related to enhanced dispersal or tolerance to harsher environmental conditions.

**Location** Three regions of the Central Indo-Pacific with tropical–temperate gradients from 35° N to 36° S.

**Methods** Scleractinian coral richness was collated and analysed as a function of latitude, region and whether or not reef accretion occurred. Species traits that are hypothesized to contribute to living beyond the environmental limits of carbonate reef accretion were compiled; these included traits associated with dispersal potential and environmental tolerance. The contribution of species traits to presence beyond reefs was then quantified using a binomial generalized linear mixed effects model.

**Results** In each region, coral species richness dropped by up to 73% where reef accretion ceased. Compared with corals restricted to coral reefs, the subset of species extending beyond reefs shared common traits related to environmental tolerance (larger depth ranges, more robust morphologies and tolerance of turbid water), but not to dispersal potential. Patterns were mostly consistent among regions.

**Main conclusions** We show for the first time that coral species living successfully in beyond-reef habitats share common characteristics that are consistent in three global regions. Environmental tolerance appears to play the dominant role in determining which species successfully establish beyond reefs. Our trait-based approach sheds light on how species assemblages and ranges might be altered by environmental change or loss of reef habitats.

## Keywords

Community assembly, coral traits, environmental filtering, Indo-Pacific, latitudinal gradient, non-reef communities.

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## INTRODUCTION

A decline in species richness of tropical marine organisms from the low-latitude centre of biodiversity in the Indo-Australian Archipelago (IAA) to higher latitudes is one of the most prominent patterns in biogeography (Stehli & Wells, 1971; Briggs, 1999). This latitudinal diversity gradient has been observed across varied taxa including reef fishes, snails, corals and lobsters (Roberts *et al.*, 2002). However, the drivers of this gradient are not well understood (Hillebrand, 2004; Mittelbach *et al.*, 2007). Latitude is a surrogate for a number of important environmental variables that interact and are correlated with each other, making it difficult to tease apart the main drivers of decreased diversity with latitude (McArthur *et al.*, 2010).

The IAA is the centre of diversity for reef-building scleractinian corals. This is where 76% of all coral species are found (Veron *et al.*, 2009) and from where species richness also attenuates to the north and south (Veron, 1993; Hoeksema, 2015). Many abiotic factors have been suggested as potential drivers of the correlation between declining coral diversity and increasing latitude, particularly decreasing temperature (Dana, 1843; Veron & Minchin, 1992; Veron, 1995), light (Wells, 1957) and carbonate saturation (Gattuso *et al.*, 1998), which affect coral growth, as well as patterns of surface currents (Veron, 1995; Hughes *et al.*, 2002) and hydrodynamic forces (Done, 1982; Massel & Done, 1993; Ferrario *et al.*, 2014), which influence recruitment and mortality.

While coral richness attenuates with latitude, there is a dramatic decline in diversity associated with the limits of coral reef accretion around the world (Veron & Minchin, 1992; Veron, 1995; Hoeksema, 2015). Beyond these boundaries globally, which occur at approximately 30° N and 30° S, corals fail to produce enough calcium carbonate to build a three-dimensional reef structure (Buddemeier & Smith, 1999). Nonetheless, a subset of the same corals that build tropical reef structures continues to exist in high-latitude non-reefal habitats, i.e. 'beyond reefs' (Harriott & Banks, 2002). While species assemblages on high-latitude coral reefs have been relatively well documented (Harriott *et al.*, 1995; Yamano *et al.*, 2001; Celliers & Schleyer, 2008), much less is known about beyond-reef assemblages (Harriott *et al.*, 1994; Nozawa *et al.*, 2008; Denis *et al.*, 2013). Therefore, we do not currently have a mechanistic understanding of why some species ranges successfully extend beyond reef while others do not.

The processes that structure beyond-reef assemblages have been difficult to generalize, because research has focused on species composition, which overlaps minimally in different regions around the world (Veron, 2000). For this reason, the current understanding of beyond-reef assemblages is limited; for example, in the Indo-Pacific, coral reef and beyond-reef assemblages have generally been differentiated based on coarse taxonomic groupings (e.g. dominance of Acroporidae, Poritidae, Faviidae) (Harriott & Banks, 2002; Nozawa *et al.*, 2008; Speed *et al.*, 2013). However, such patterns are not

consistent globally, and given the lack of species overlap across regions a new approach is required. Combining species assemblage data with species trait data provides a structured framework for understanding relationships between organisms and their environment at multiple spatial scales (Poff, 1997). For example, are assemblages near range edges where diversity is lower dominated by species with certain traits? If so, what can these traits tell us about community assembly rules (e.g. the relative importance of dispersal versus establishment; Keith *et al.*, 2015)?

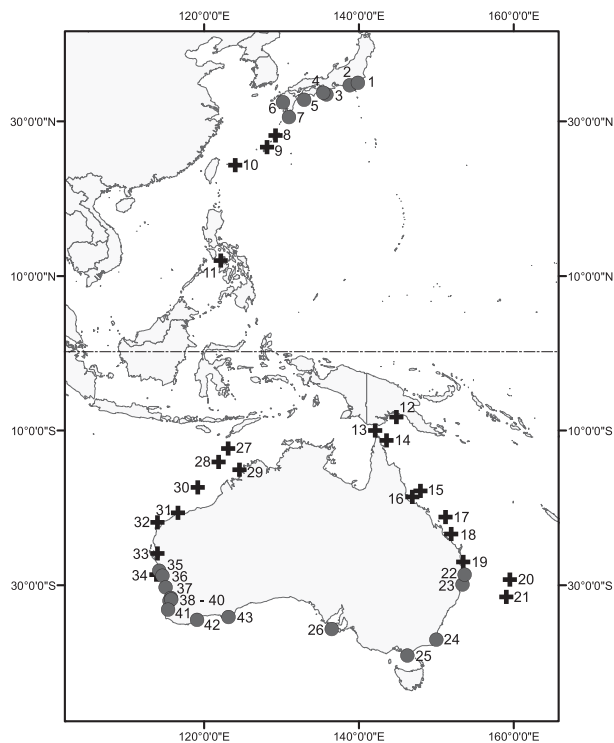
In this study, we first quantified the extent of loss of coral species diversity at the boundary between reef and beyond-reef habitats along three latitudinal gradients in the Indo-Pacific. We then tested whether or not the traits associated with beyond-reef species were a non-random subset of species on coral reefs, and subsequently if these trait patterns were consistent for the three latitudinal gradients. Finally, based on the traits that tended to be associated with beyond-reef species, we consider whether dispersal traits (e.g. those related to access of larvae to and time in ocean currents) or establishment traits (e.g. those related to environmental tolerance) best explain the capacity to live beyond reefs. Understanding the species traits associated with successfully living beyond reefs is an important step for predicting how species ranges might shift with environmental change or loss of reef habitats.

## METHODS

### Species occurrence data

We used biogeographical data from Veron (1993) that included species occurrences at 43 sites along three latitudinal gradients spanning 35° N to 36° S through the Central Indo-Pacific Ocean. No additional surveys were included, for consistency in survey effort within a temporally restricted period and to avoid differences in taxonomic opinion. In total, 535 species representing 74% of Indo-Pacific scleractinian corals were documented in at least one of the sites. Species names were updated using the World Register of Marine Species (WoRMS, 2015) and, where necessary, occurrence records representing synonymous species were combined (e.g. *Cycloseris erosa* revised to *Cycloseris tenuis*; see also Appendix S1 in Supporting Information). Any records not identified to species (9%) were retained for the species diversity analysis, but removed from species trait analysis.

Survey sites spanned from low-latitude tropical coral reefs to high-latitude coral assemblages accreting beyond reef along three latitudinally contiguous but geographically distinct regions of the Indo-Pacific. The North region (N) included 11 sites from the Philippines (12° N) to Tateyama, Japan (35° N); the Papua New Guinea and East Australia region (PNG-EA) included 15 sites from southern Papua New Guinea (8° S) to South Australia (36° S) and West Australia (WA) included 17 sites from Ashmore Reef (12° S) to Recherche Archipelago (34° S) (Fig. 1). Each of these regions has different environmental and geological settings where



**Figure 1** Survey locations throughout the Indo-Pacific (modified from Veron, 1993). Bold plus signs (+) indicate coral reef and solid circles (•) indicate high-latitude beyond-reef sites. Sites in the North (N): 1, Tateyama; 2, Izu; 3, Kushimoto; 4, Shirahama; 5, Tosashimizu; 6, Amakusa; 7, Tanegashima; 8, Amami Island; 9, Okinawa; 10, Yaeyama; 11, Philippines. Sites from Papua New Guinea to East Australia (EA): 12, southern Papua New Guinea; 13, Torres Strait; 14, north Great Barrier Reef (GBR); 15, Coral Sea; 16, central GBR; 17, Pompey and Swain Reefs; 18, Capricorn and Bunker Reefs; 19, Flinders Reef; 20, Elizabeth and Middleton Reefs; 21, Lord Howe Island; 22, north New South Wales (NSW); 23, Solitary Islands; 24, south NSW; 25, Victoria; 26, South Australia. Sites in West Australia (WA): 27, Ashmore Reef; 28, Scott Reef; 29, Kimberly coast; 30, Rowley shoals; 31, Dampier Archipelago; 32, Ningaloo Reef Tract; 33, Shark Bay; 34, Houtman; 35, Port Gregory; 36, Geraldton; 37, Jurian Bay; 38, Quinns Rock region; 39, Marmion; 40, Rottneest Island; 41, Geographe Bay; 42, SW coast; 43, Recherche Archipelago.

separate pole-ward surface currents transport tropical water to higher latitudes.

Each site was classified as ‘coral reef’ or ‘beyond reef’ (i.e. coral communities that do not accrete the three-dimensional carbonate reef structure) following Veron (1995). Accordingly, a species could be restricted to ‘coral reef’ or ‘beyond-reef’ habitats, or could occur in both. For this study we excluded high-latitude, beyond-reef endemic species (*c.* 3% of species), because our goal was to evaluate differences in coral traits between species restricted to coral reefs and those also found beyond reefs (Appendix S1). As such, beyond-reef corals were classified as species that occur both on coral reefs and beyond reefs within any of the regions.

## Species richness patterns

Negative binomial regression was used to model species richness as a function of the interactive effects of latitude (absolute), region (N, PNG-EA or WA) and reef accretion (coral reef or beyond reef). The regression was run with the `mod.nb` function from the ‘MASS’ package (Ripley *et al.*, 2002) using R statistical software (R Development Core Team, 2014). Best subset modelling was applied to find the model with the lowest Akaike information criterion (AIC) that best described the relationship between species richness and latitude, region, reef accretion and interactions of all factors.

## Coral traits associated with species in beyond-reef communities

Species-level trait data for corals were downloaded from the Coral Trait Database (CTDB; Madin *et al.*, 2016) (<https://coraltraits.org>; Appendix S2). We selected 10 traits that (1) were considered a priori to be of potential importance for living in high-latitude non-coral reef habitats and (2) had data available for at least 80% of the study species in order to maximize the number of species included. These traits capture reproductive and dispersal capacity, environmental tolerance of species, biomechanical vulnerability and family to account for phylogenetic relatedness among traits (Table 1).

Coral reproductive traits, including mode of larval development (brooder or broadcast spawner), sexual system (hermaphrodite or gonochore) and the presence of *Symbiodinium* species in propagules (present or absent), were hypothesized to contribute to successfully dispersing to and establishing at higher latitudes. A species’ depth range, preference for water clarity and preference for wave exposure conditions were selected as traits that represent measures of tolerance to potentially stressful environmental conditions. Depth range measurements (m, log transformed) were derived from differences in the lower and upper depth that each species has been observed to occupy. Water clarity and wave exposure preference are categorical traits that were transformed to binomial variables to represent tolerance or intolerance to environmental conditions. That is, original water clarity preference values (clear, turbid, both) were reduced so that species found primarily in turbid water (turbid) or occasionally in turbid or clear (both) were considered tolerant to turbidity and those that are only found in clear water (clear) were considered intolerant. Similarly, original wave exposure values (exposed, protected, broad) were represented as tolerant (either exposed or broad) or intolerant (protected).

The CTDB describes the most common growth form of each coral species globally, with a total of 15 growth forms represented among the species in this study. Growth forms with similar biomechanical vulnerabilities to dislodgement were combined into seven categories representing varying tolerances to hydrodynamic stress (Madin *et al.*, 2014) that may provide a survival advantage in higher-wave-energy environments (Table 1). Since a lack of available substrata may limit coral colonization beyond reef growth (Veron, 1995),

**Table 1** Coral traits hypothesized to affect the probability of persistence in beyond-reef assemblages including the possible values those traits can take after transforming or grouping.

| Trait category           | Coral trait                               | Possible trait values  |
|--------------------------|---|--|
| Dispersal                | Mode of larval development                | Brooder<br>Spawner   |
|                          | <i>Symbiodinium</i> species in propagules | 1 (present)<br>0 (absent)  |
|                          | Sexual system                             | Gonochoric<br>Hermaphroditic   |
| Environmental            | Depth range, log transformed              | 0.70–2.26 (4–150 m)  |
|                          | Water clarity tolerance                   | Tolerant (turbid, both)<br>Intolerant (clear)  |
|                          | Wave exposure tolerance                   | Tolerant (exposed, broad)<br>Intolerant (protected)  |
| Mechanical vulnerability | Growth form                               | Massive (massive, phaceloid, flabello-meandroid, columnar)<br>Tabular (tabular, branching-tabular)<br>Branching (branching, caespitose, hispidose, encrusting-branching)<br>Digitate (digitate, corymbose)<br>Encrusting<br>Foliaceous<br>Solitary   |
|                          |   | Substrate attachment   |
| Structural/physiological | Maximum corallite width, log transformed  | 0.146–2.779 (0.4–600 cm)   |
| Phylogenetic relatedness | Molecular family                          | Acroporidae<br>Agariciidae<br>Coscinaraeidae<br>Dendrophylliidae<br>Diploastraeidae<br>Euphylliidae<br>Fungiidae<br>Lobophyllidae<br>Merulinidae<br>Pachyseridae<br>Plesiastreidae<br>Pocilloporidae<br>Poritidae<br>Psammocoridae<br>Siderastreidae |

Original trait values are shown in parentheses.

substrate attachment was included as a trait to categorize species whose colonies are attached to a substratum (attached) or can be found unattached (either unattached or both). Large corallite sizes can increase the potential for heterotrophic feeding, especially in low-light conditions where the potential for photosynthesis is limited (Crabbe & Smith, 2006). Maximum corallite size (cm, log transformed) was included to evaluate the contribution of differences in energy gained through heterotrophic or autotrophic feeding to being found in assemblages beyond reef. Although some coral traits are more plastic than others, we used a single trait value for a species regardless of location to generalize differences in patterns between hundreds of species.

Trait information was incomplete for 127 of the 535 species included in this study, including the 48 records not

identified to species. These were excluded from the following analyses. To assess spatial variability in the distributions of traits, species presence was accounted for in each region (N, PNG-EA, WA), resulting in 1010 observations of the 408 remaining species. In total, 54% of species were found in all three regions while 28% were found in only one.

### Model and model selection

Collinearity among species traits was assessed visually and quantitatively with generalized variance inflation factors (GVIF). GVIF values were calculated using the “car” package and  $GVIF^{1/(2d.f.)}$  evaluated to account for factors with multiple degrees of freedom (Fox & Weisberg, 2016). Traits with large GVIF values relative to a cutoff of 2.5 were sequentially

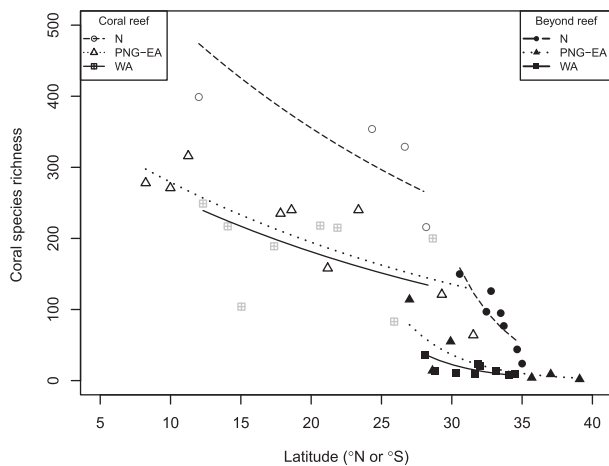
dropped from further analysis due to collinearity. All remaining traits were included in a generalized linear mixed effects model (GLMM) with a binomial response variable (beyond reef = 1, restricted to coral reef = 0) and logit link function, to describe species traits in assemblages beyond reef accretion.

Common traits shared among phylogenetically related species were accounted for by including species molecular family as a random factor with a model intercept offset. All remaining traits and biologically meaningful trait interactions were included as fixed effects. Region of occurrence (N, PNG-EA, WA) and region and trait interactions were also included as fixed effects to quantify any underlying differences between regions. Analyses were performed using the `glmer` function from the 'lme4' package (Bates *et al.*, 2014). Model selection was conducted with a best subset modelling approach by comparing AIC values of all possible candidate models. The final reduced model with the lowest AIC described coral traits that best characterize beyond-reef species. The independent contribution of each trait to the final model total variance explained was quantified with the 'hier.part' function and package (Walsh & Mac Nally, 2013).

## RESULTS

### Species richness

Overall, coral species richness is greatest in the N region (459 total species) compared with PNG-EA (395 species) and WA (351 species). Species richness patterns varied by latitude, region and reef accretion (Fig. 2, Table 2). The latitudinal attenuation of corals was greater beyond reef compared with coral reefs (Table 2, reef  $\times$  lat interaction) and richness beyond reefs in PNG-EA and WA were significantly less than richness beyond reefs in N (Table 2, reef  $\times$  region interaction)



**Figure 2** Coral species richness per site (coral reef or beyond reef) with fitted model predictions through the Indo-Pacific by latitude and region. Latitude is measured as the absolute value of the centre latitude of the sites surveyed (Fig. 1) in the North (N), Papua New Guinea to East Australia (PNG-EA) and West Australia (WA).

**Table 2** Results of the negative binomial regression capturing species richness gradients in three regions in relation to latitude (lat) and reef accretion (coral reef or beyond reef).

| Coefficients                | Estimate | SE    | z-value | P(> z ) |
|-----------------------------|----------|-------|---------|---------|
| Intercept                   | 6.594    | 0.298 | 22.160  | <0.001  |
| Reef                        |          |       |         |         |
| Coral reef                  |          |       |         |         |
| Beyond reef                 | 6.302    | 1.139 | 5.532   | <0.001  |
| Latitude                    | -0.036   | 0.011 | -3.321  | 0.001   |
| Region                      |          |       |         |         |
| N                           |          |       |         |         |
| PNG-EA                      | -0.602   | 0.204 | -2.953  | 0.003   |
| WA                          | -0.673   | 0.207 | -3.256  | 0.001   |
| Reef $\times$ lat           |          |       |         |         |
| Coral reef $\times$ lat     |          |       |         |         |
| Beyond reef $\times$ lat    | -0.220   | 0.035 | -6.353  | <0.001  |
| Reef $\times$ region        |          |       |         |         |
| Beyond reef $\times$ PNG-EA | -1.016   | 0.304 | -3.343  | 0.001   |
| Beyond reef $\times$ WA     | -1.422   | 0.289 | -4.916  | <0.001  |

Interaction terms are indicated by  $\times$ .

where richness declined between 35% and 73% in all regions beyond the coral reef boundary.

### Coral traits

Substrate attachment and corallite size had the largest GVIF values, indicating collinearity, and were consecutively removed from the model (Table 3A–C, Appendix S3). Traits included in the GLMM were mode of larval development, *Symbiodinium* species present in propagules, sexual system, depth range, water clarity tolerance, wave exposure tolerance and growth form.

Species traits associated with reef corals beyond reefs include region, depth range, water clarity tolerance and growth form (Table 4). Within each region, the proportion of species found on coral reefs with ranges that extended beyond reefs varied. Along the N gradient, 43% of species were found beyond reefs, 33% in PNG-EA and 15% in WA. Depth range was the only trait that had a significant interaction with region. Beyond-reef species in N and PNG-EA had a larger depth range on average than coral species restricted to reefs. The opposite pattern was found in WA. Species beyond reefs also tended to be more tolerant of turbid water conditions. Encrusting, tabular and massive growth forms were more likely to occur beyond reefs, while branching and solitary growth forms were least likely. Region had the greatest independent contribution to the explained model variation (49%), followed by growth form (40%), depth range (8%) and tolerance to water clarity (3%) (Table 4). Total model variance explained by fixed factors (marginal  $R^2$ ) was 18.6% and by fixed and random factors (conditional  $R^2$ ) was 31.1%. Mode of larval development, *Symbiodinium* species in propagules and sexual system were not included in the final

**Table 3** Calculated generalized variance inflation factors (GVIF) for each coral trait with degrees of freedom (d.f.);  $GVIF^{1/(2d.f.)}$  provides relative GVIF for factors with more than 1 d.f.

| Trait                      | GVIF  | d.f. | $GVIF^{1/(2d.f.)}$ |
|----------------------------|-------|------|--------------------|
| <b>A</b>                   |       |      |                    |
| Mode of larval development | 1.250 | 1    | 1.119              |
| Symbiont transmission      | 1.897 | 1    | 1.377              |
| Sexual system              | 1.571 | 1    | 1.253              |
| Depth range                | 1.193 | 1    | 1.092              |
| Water clarity tolerance    | 1.072 | 1    | 1.035              |
| Wave exposure tolerance    | 1.186 | 1    | 1.089              |
| Growth form                | 9.180 | 6    | 1.203              |
| Substrate attachment       | 3.710 | 1    | 1.926              |
| Corallite size             | 2.654 | 1    | 1.629              |
| <b>B</b>                   |       |      |                    |
| Mode of larval development | 1.251 | 1    | 1.119              |
| Symbiont transmission      | 1.895 | 1    | 1.377              |
| Sexual system              | 1.555 | 1    | 1.247              |
| Depth range                | 1.192 | 1    | 1.092              |
| Water clarity tolerance    | 1.071 | 1    | 1.035              |
| Wave exposure tolerance    | 1.183 | 1    | 1.088              |
| Growth form                | 3.874 | 6    | 1.119              |
| Corallite size             | 2.661 | 1    | 1.631              |
| <b>C</b>                   |       |      |                    |
| Mode of larval development | 1.231 | 1    | 1.109              |
| Symbiont transmission      | 1.310 | 1    | 1.145              |
| Sexual system              | 1.410 | 1    | 1.188              |
| Depth range                | 1.191 | 1    | 1.091              |
| Water clarity tolerance    | 1.074 | 1    | 1.036              |
| Wave exposure tolerance    | 1.150 | 1    | 1.073              |
| Growth form                | 1.994 | 6    | 1.059              |

A, all traits evaluated for collinearity; B, remaining traits evaluated for collinearity after 'substrate attachment' was removed; C, remaining traits evaluated for collinearity after 'corallite size' was removed.

model as none were significantly associated with an increased probability of being found beyond reefs.

## DISCUSSION

While reef-building corals displayed the well-known diversity declines over each of the three main Indo-Pacific latitudinal gradients, we quantified these declines and found a decrease in richness of between 35% (N) and 73% (WA) associated with the cessation of carbonate reef accretion in each region (Fig. 2). Despite regional differences in diversity loss at the reef boundary, the probability of being found beyond reefs was strongly associated with traits related to environmental tolerance (Table 4). In contrast, none of the traits related either to reproduction or dispersal potential were found to be important, suggesting that environmental filtering plays the dominant role in structuring beyond-reef coral assemblages.

Despite little overlap in beyond-reef species in all regions (< 7%), these species share traits that are likely to enhance survival beyond reefs, including more robust morphologies, a

higher tolerance to turbid water and the capacity to survive at a greater range of depths, reflecting similar trait patterns of high-latitude assemblages in East Australia (Sommer *et al.*, 2014). In areas where shallow-water reef structures do not dissipate wave energy, massive and encrusting growth forms are less likely to be damaged, dislodged or killed compared with the more vulnerable branching or unattached, solitary species (Dao-ru *et al.*, 2013). Corals tolerant to turbid water may be better adapted to low-light conditions or more effective at sediment rejection (Loya, 1976; Veron *et al.*, 2009). Depth range is generally considered a proxy for environmental tolerance, because colonies of species with broad depth ranges can live in a greater range of temperature and light conditions. Exceptions to these large-scale patterns can result from the influence of variation in local conditions.

Traits shared by beyond-reef species were generally consistent; however, there was a three-fold difference in the proportion of species diversity lost among regions (15–43%). Differences among regions have likely been affected by bathymetry, sea level fluctuations and the direction, strength and seasonality of poleward currents. For instance, the greatest diversity of corals was found in the N region, where 43% of coral reef species were also found beyond reefs (Appendix S2). In this region, bathymetric continuity that enabled coral assemblages to shift with past sea level changes would have been less disruptive to population persistence compared with the other regions that were submerged and re-emerged (Veron, 1995). Additionally, the Kuroshio Current moves the greatest volume of water to the highest absolute latitude of the Western Boundary Currents (Tomczak & Godfrey, 2003) and is strongest during the summer when coral spawning occurs. This northern transport of warm water, stronger than other boundary currents in the IAA, likely contributes to the regional differences in coral diversity and may be responsible for the higher proportion of reef species observed beyond reefs. Conversely, the weakest poleward flowing current is the shallow Leeuwin Current (LC) in WA which sits atop a strong equatorward undercurrent (Tomczak & Godfrey, 2003). In this region only 15% of species were found beyond reefs (Appendix S2), and this subset had a smaller average depth range than species restricted to reefs. A potential explanation for this pattern is that two of the four species with the largest depth ranges (*Leptoseris hawaiiensis* and *Echinophyllia aspera*; Appendix S2) were found beyond reefs in the N and PNG-EA regions but not in WA. This may be due to differences in oceanographic conditions, environmental filters that have not been accounted for, an artefact of fewer total species present in WA therefore a lower probability of occurrence beyond reefs or that species with larger depth ranges may have been present but were not observed by Veron (1993). Variable hydrodynamic forces, seasonal fluctuations and poleward extent of major currents likely dominate differences in overall diversity and the proportion of species beyond reefs in all regions, regardless of species traits.

Successful establishment beyond reefs could additionally be influenced by traits not included in these analyses. For

**Table 4** Results of the generalized linear mixed effects model for describing coral traits for corals in communities beyond reef compared with on coral reefs and the independent contribution of each factor to the model total variance explained.

| Random factor                 | Variance | SD     |         |  |
|-------------------------------|----------|--------|---------|--|
| Family intercept ( $n = 15$ ) | 0.596    | 0.772  |         |  |
| Fixed factors                 | Estimate | SE     | z-value | Contribution of total explained variance |
| Intercept                     | -2.925   | 0.781  | -3.748  |  |
| Region                        |          |        |         | 48.8%                                    |
| N                             |          |        |         |  |
| PNG-EA                        | 0.986    | 0.9856 | 1.000   |  |
| WA                            | 1.9934   | 1.159  | 1.720   |  |
| Growth form                   |          |        |         | 39.8%                                    |
| Massive                       |          |        |         |  |
| Tabular                       | 0.157    | 0.427  | 0.367   |  |
| Encrusting                    | 0.101    | 0.268  | 0.377   |  |
| Digitate                      | -0.190   | 0.334  | -0.570  |  |
| Foliaceous                    | -0.588   | 0.259  | -2.272  |  |
| Solitary                      | -0.986   | 0.459  | -2.148  |  |
| Branching                     | -1.394   | 0.295  | -4.728  |  |
| Depth range (logged)          | 0.949    | 0.223  | 4.259   | 8.3%                                     |
| Water clarity tolerance       |          |        |         | 3.1%                                     |
| Intolerant                    |          |        |         |  |
| Tolerant                      | 0.254    | 0.182  | 1.397   |  |
| Region $\times$ depth range   |          |        |         |  |
| N $\times$ depth range        |          |        |         |  |
| PNG-EA $\times$ depth range   | -0.466   | 0.300  | -1.551  |  |
| WA $\times$ depth range       | -1.122   | 0.355  | -3.158  |  |

All coral traits and region of occurrence (N, PNG-EA, WA) were included as fixed effects and coral family ( $n = 15$ ) was included as a random effect. Interactions of terms are indicated by  $\times$ .

example, evaluating the contribution of growth rate, generation time or skeletal density to successful establishment beyond reef can suggest whether faster growth, faster reproduction or additional skeletal strength is advantageous in these environments. However, limited trait information available for a large number of species prohibited further investigation of these traits in this study. Another potential limitation of our analyses was that we included global estimates of species traits, which are assumed to be true of all individuals for each species throughout the Central Indo-Pacific. Trait plasticity that varies from global estimates can provide an advantage to individuals in different environments (Todd, 2008). Colonies of many species develop more robust morphologies in subtropical environments to better cope with physical stress of wave energy (Veron *et al.*, 2009). For example, many species with a tabular morphology in the tropics, such as *Acropora hyacinthus*, form side-attached plates in the subtropics (Veron, 1995) supporting the results that tabular corals are the most likely growth forms to be found beyond reefs (Appendix S2).

Biotic and abiotic processes acting at scales smaller than these regions can also result in exceptions to the patterns in traits observed. The environment varies greatly within these regions, influencing the local species assemblage. For example, while traits associated with dispersal were not

associated with beyond-reef coral species they can be important biogeographically. For instance, coral assemblage structure on Lord Howe Island is dominated by brooding corals, possibly because the rapid development of larvae is the key to successful population establishment on this isolated coral reef (Keith *et al.*, 2015). In contrast, the distances between reefs along the latitudinal gradient we examined are not sufficient to provide a barrier to dispersal in species, such as coral, that have long-lived larvae (Graham *et al.*, 2008). Additionally, biotic interactions such as varied predator distributions or competition for space, especially with macroalgae, shape communities not captured by the regional patterns we evaluated (Johannes *et al.*, 1983). While these analyses capture coral traits for over 400 species, additional detail provided by species abundance rather than presence-absence data, in addition to spatial climate velocities (Burrows *et al.*, 2014), more specific environment-trait relationships (Jamil *et al.*, 2013) and biotic interactions (Wisiz *et al.*, 2013) would also increase our understanding of these patterns among traits and their relative influence.

As sea surface temperatures increase poleward, higher latitudes may become more favourable for corals, and have been suggested as a refuge from increased temperatures in the tropics (Glynn, 1996). However, a simultaneous decrease in

aragonite saturation is projected to result in less overall reef accretion (Kleypas *et al.*, 2001; Guinotte *et al.*, 2003). Given these anticipated changes, more coral assemblages are likely to become non-reefal. Whether corals expand their ranges into higher latitudes where reefs do not accrete or net accretion decreases in the tropics, those corals with traits that enhance environmental tolerance will be more likely to persist and dominate the assemblages. These results highlight that the subset of corals found at high latitudes and that show beyond-reef growth are a non-random subset of those on coral reefs that share characteristics promoting environmental tolerance. As complex environmental changes occur, evaluating species traits associated with corals beyond reefs globally provides a deeper understanding of the processes shaping assemblages near range edges and how they may be affected with environmental change.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Coral occurrence records.

**Appendix S2** Coral traits from Coral Trait Database.

**Appendix S3** Pairwise plot of coral traits to evaluate collinearity.

## BIOSKETCH

**Toni Mizerek's** research interests include macroecological patterns in marine systems and the use of those patterns to understand threats to species persistence. Ongoing projects focus on using species traits to evaluate species distribution and threats to persistence.

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