

Differential establishment potential of species predicts a shift in coral assemblage structure across a biogeographic barrier

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Biogeographic breaks are locations where multiple species reach range limits simultaneously. Numerous breaks have been identified; however, the mechanisms that generate and maintain these breaks are largely unresolved. One break of particular interest lies between the subtropical Lord Howe Island off the east coast of Australia and the Great Barrier Reef 1000 km to the north, because of the potential for Lord Howe Island to serve as a refuge from climate change. Our aim was to quantitatively disentangle the mechanisms proposed to explain this break. To do so, we combined species abundance and trait data to test the hypotheses that dispersal limitation, environmental tolerance, competitive ability or evolutionary processes maintain the break. Specifically, we used multiple linear regression to analyse the extent to which species traits could predict the location of species along a non-metric multidimensional scaling axis, which was representative of assemblage change across the break. Three of the twelve species traits considered – reproductive mode, upper depth and depth range – contributed significantly to the averaged model. The higher relative abundance of species that brood larvae on Lord Howe Island supports the hypothesis that local retention of larvae is critical for population establishment at this location. In addition, abundant species on Lord Howe Island were disproportionately associated with global depth distributions that encompass deep water, which might indicate that these species are better able to tolerate sub-optimal environmental conditions, such as low light levels in the sub-tropics. Therefore, we conclude that the biogeographic break between the Great Barrier Reef and Lord Howe Island is maintained primarily by the ability of species to establish populations upon arrival. More broadly, our work adds to a growing body of evidence that suggests, over large temporal scales, establishment is more important than dispersal for the maintenance of biogeographic breaks in the oceans.

Biogeographic breaks are regions where multiple species reach their range limits simultaneously, leading to abrupt transitions in species composition and potentially in species richness. Breaks have been identified for many taxa in both the terrestrial and marine realms (Lohman et al. 2011, Carstensen et al. 2012, Holt et al. 2013). However, moving beyond pattern characterisation to determine the mechanisms that prevent species geographical ranges from expanding indefinitely has proven more difficult. A recent study that explored the role of environment, habitat limitation and history of biogeographic breaks found that scleractinian corals in the Indo-Pacific are arranged as eleven biogeographic provinces (Keith et al. 2013). The large-scale biogeographic breaks between those provinces were coincident with tectonic plates and mantle plume tracks, suggestive of a strong role for geological history in their generation and maintenance – a mechanism consistent with earlier analyses of coral distributions (Pandolfi 1992b).

However, some coral assemblages do not fit into this general scheme of Indo-Pacific coral provinces and instead

have a unique assemblage structure. For these assemblages, an alternative explanation might be more appropriately sought at a smaller spatial scale to match the reduced geographical extent of these idiosyncratic reefs relative to a coherent province (Rahbek 2005, Fenberg et al. 2014). Coral assemblages located in marginal areas, such as those at higher latitudes, are of particular interest because of their potential to provide a refuge during climate change (Beger et al. 2014, Makino et al. 2014, Sommer et al. 2014): coral distributions have shifted towards the poles during both past and current periods of climate change (Precht and Aronson 2004, Greenstein and Pandolfi 2008, Yamano et al. 2011, Baird et al. 2012). Therefore, understanding the relative importance of different underlying processes, such as tolerance of environmental conditions and dispersal limitation, for influencing the assemblage composition of these reefs will help determine their potential suitability as a refuge in the future (Beger et al. 2014). For instance, a reef with an assemblage determined by environmental conditions could serve as a good candidate for protection as a future refuge, whilst

one that is dispersal limited would have negligible potential to act as a refuge even if environmental conditions become suitable (Makino et al. 2014).

One reef with the potential to act as a subtropical refuge is Lord Howe Island (31.5°S, 159.1°E) off the east coast of Australia, separated by > 1000 km from the Great Barrier Reef (GBR). Lord Howe Island is a marginal coral reef at the southernmost limit of coral reef growth (Anderson and Pratchett 2014) with approximately 63 species, compared with a regional pool of more than 350 species on the GBR (Veron 1993). Evidence suggests that the break between the GBR and Lord Howe Island coincides with a marked break in population genetic connectivity (Ayre and Hughes 2004, Noreen et al. 2009) and a semi-permeable hydrodynamic barrier (Wood et al. 2014), which implicates dispersal limitation as an explanation. However, given that Lord Howe Island is estimated to be 6.7 million yr old (McDougall et al. 1981), it is likely there has been ample time for species to successfully disperse to the Island through infrequent long distance dispersal across the semi-permeable hydrodynamic barrier, particularly as the East Australian Current periodically swings close to Lord Howe Island and could deliver coral larvae during these episodes (DeVantier and Deacon 1990). The assemblage structure of corals on Lord Howe Island has long been recognized as distinct from the GBR (Veron and Done 1979, Harriott et al. 1995). However, quantitative analyses that can tease apart potential drivers of this difference are lacking and, as a result, the underlying mechanisms remain elusive.

Coral species richness is positively correlated with various environmental variables including sea surface temperatures, habitat area, proximity to the centre of the domain, and proximity to other reefs (Bellwood and Hughes 2001, Hughes et al. 2002, Connolly et al. 2003, Bellwood et al. 2005). All of these variables are proxies for multiple hypothesised processes that could be invoked to explain this biogeographic break, and many were included in a qualitative model to explain different assemblage structures in subtropical reef assemblages such as Lord Howe Island (Harriott and Banks 2002). However, their relative importance is not easily disentangled. For instance, the isolation of Lord Howe Island infers dispersal limitation as a plausible explanation, whilst lower temperatures could infer multiple hypotheses, such as the metabolic theory of ecology (Brown et al. 2004) or the energy limitation hypothesis (Hurlbert and Stegen 2014). Moreover, in marine environments, environmental conditions are rarely abrupt and dispersal barriers are often semi-permeable (Steele 1991, Keith et al. 2011). Subsequently, more subtle switches in relative abundance rather than complete species replacements are likely to provide a more sensitive test of underlying processes. Presence–absence is particularly problematic for understanding biogeographic breaks at smaller spatial scales because a shift in species composition could be the result of the presence of unusual species in very low abundance, which could distort the signal. Therefore, a new approach is required to help reveal the dominant processes that maintain this barrier.

Here, we use a trait-based approach to detect the underlying drivers of the biogeographic break between the GBR and Lord Howe Island. Traits offer a way to generalise beyond individual species (Cadotte et al. 2011), which is

particularly useful in high diversity ecosystems such as coral reefs, and can be used as proxies for hypothesized processes (Keith et al. 2009, Luiz et al. 2012). Valuable information can be gained by knowing not only how many species are present, but also the characteristics of those species. For instance, the mode of larval development (often referred to as reproductive mode) is considered a proxy for dispersal ability: coral species that reproduce through broadcast spawning have an obligate pre-competent period of between two and four days and therefore are expected to be transported further by ocean currents than species that reproduce through the release of brooded larvae, which are ready to settle on release (Baird et al. 2009). From such information, we can predict that if dispersal limitation is the underlying process maintaining the GBR – Lord Howe Island biogeographic break, species that spawn will have a higher relative abundance on Lord Howe Island because they are more likely to disperse from upstream reefs on the southern GBR. Coral traits are also available as surrogates for a species' environmental tolerance, competitive ability, and evolutionary processes (expanded upon in Material and methods). Our trait-based approach is enhanced by high-resolution species abundance data, which enables identification of subtle shifts in relative abundance of species that might be associated with semi-permeable dispersal barriers and gradual shifts in environmental conditions. We test whether the trait composition across the GBR to Lord Howe Island biogeographic barrier is consistent with the qualitative model of Harriott and Banks (2002), which broadly hypothesises that depauperate subtropical reef assemblages could be maintained by 1) dispersal limitation, 2) physiological tolerance of marginal environmental conditions, or 3) competition. We also test the additional hypothesis that the break is associated with 4) evolutionary processes. Specifically, our quantitative approach tests the contribution of species with particular traits to the assemblages on either side of the break.

Material and methods

All analyses were conducted in R ver. 3.1.1 (R Development Core Team) with packages *vegan* (Oksanen et al. 2011), *lme4* (Bates et al. 2011), *MuMIn* (Barton 2012), and *effects* (Fox 2003).

Coral abundance data

Coral assemblage structure was quantified using line intercept transects at Lizard Island in the northern GBR in November 2011, One Tree Island in the southern GBR in March 2012, and Lord Howe Island in January 2012 (Fig. 1). At each location, we used a hierarchical survey design. Six sites were surveyed per island: three lagoon sites and three crest sites. Within each site, we conducted 12 × 10 m line intercept transects (Loya 1972) at 1–2 m depth, except in the crest habitat for One Tree where at two sites we surveyed 8 × 10 m transects and at one site surveyed 6 × 10 m transects due to poor weather conditions. The intercepts of coral colonies ≥ 5 cm maximum diameter were measured to the nearest 1 cm, and the total length of the

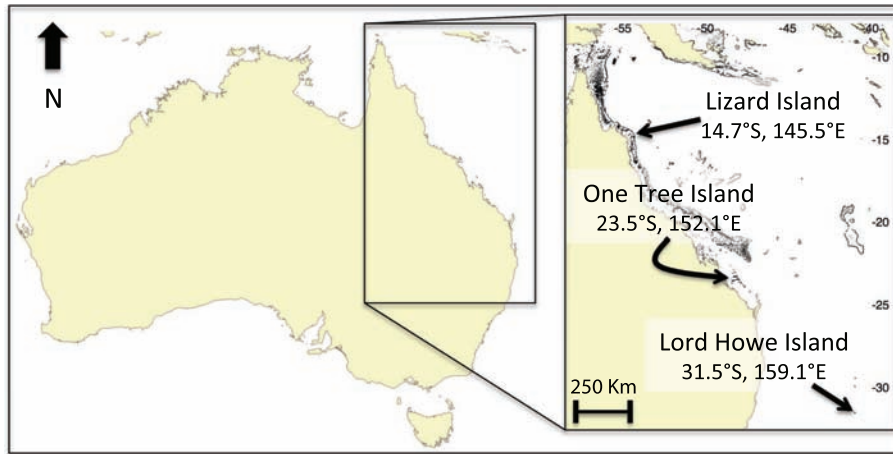


Figure 1. Location of three surveyed islands off the east coast of Australia. Land is shown in yellow, coral reefs are shown in black. Latitude and longitude (WGS84) markings are provided in the inset.

transect that was intersected by a given species was used as a measure of its relative abundance. Colonies were identified to species in the field or ex situ using photographic images captured in the field, following Wallace (1999) and Veron (1993, 2000).

Difference in assemblage relative abundance

To ensure the biogeographic boundary was robust to our abundance data, we used analysis of similarity (ANOSIM) to test for significant differences in the assemblages (sensu Diaz et al. 2013). ANOSIM was based on a Chao similarity matrix for relative abundance data (Chao et al. 2005) and generated a global R statistic, which indicates similarity amongst assemblages, and ranges from zero (assemblages identical) to one (assemblages share no species). The Chao measure of similarity was chosen because it is robust to variation in sampling effort (Chao et al. 2005). Significant difference of the R statistic from that expected through chance is determined by comparison of observed data with the distribution of R statistics from 1000 permutations of the observed matrix. Data were visualised using non-metric multidimensional scaling (NMDS) based on the same Chao similarity matrix. NMDS is non-linear and uses rank similarity, which makes it more robust to ecological community data than linear ordination techniques such as principal components analysis (Minchin 1987, Diaz et al. 2013). We also used ANOSIM to determine whether the difference between lagoon and crest habitats was greater than the difference between islands, which would indicate that small scale environmental filtering was more important than larger scale spatial factors.

Species trait data

We downloaded twelve species traits from the Coral Traits database (Coral Trait Database Consortium 2014) to test whether any of these traits were associated with the relative abundance of species in the GBR or Lord Howe Island assemblages. Lord Howe Island is hydrodynamically isolated

(Wood et al. 2014), and therefore, we would expect certain dispersal and reproductive modes to be better able to disperse to, and establish on, the island. To test this assumption, we included three traits related to reproduction: reproductive mode (brooder or spawner), larval nutritional mode (autotrophic or lecithotrophic), and sexuality (gonochore or hermaphrodite). The difference in time to settlement suggests that spawning species have a dispersal advantage because more larvae will escape the reef of origin, whereas brooding species are more likely to be retained on the reef of origin (Figueiredo et al. 2013). Nutritional mode is also expected to influence dispersal ability, because autotrophic species are capable of generating their own energy and therefore are likely to be able to survive for longer in the open ocean (Richmond 1987, Marshall and Keough 2003). Hermaphroditic species are expected to have enhanced capacity for establishment compared with gonochores, because one individual can produce both male and female gametes, which means there is the potential for breeding with the arrival of a single individual (Paulay and Meyer 2002).

If alternatively the assemblage structure at Lord Howe Island is driven by the capacity of species to tolerate marginal conditions, we would expect traits indicative of physiological tolerance to be more informative predictors. Therefore, we included six traits related to habitat preference. Three of these traits were related to the vertical distribution of species: depth range, lower depth, and upper depth. Depth traits are global estimates from Carpenter et al. (2008). Specifically, we assume that a broad depth range infers broad environmental tolerance, whilst deeper placements (indicated by lower/upper depth) infer greater tolerance of reduced light and temperature. An additional indication of high environmental tolerance is whether species tend to be tolerant of, and found within, habitats that experience high wave exposure and turbid water. We also included colony growth form as a species trait because particular forms are better able to withstand high wave energy environments (Madin et al. 2014), and colony shape can influence energy acquisition owing to capture of photosynthetically available radiation (Hoogenboom et al. 2008). In general, given the marginal location of Lord Howe Island, we would expect the species

that are most abundant to have relatively high tolerance of sub-optimal conditions.

Ecological theory and empirical evidence suggests that competitive ability is less important in marginal environments as physiological tolerance becomes increasingly important for maintenance (Callaway et al. 2002). Therefore, we predict competitive species to be less abundant on Lord Howe Island than on the GBR. Corallite size has been linked to competitive ability in adult corals (Lang 1973, Lang and Chornesky 1990) and is strongly filtered at high latitudes (Sommer et al. 2014), and is therefore included in our trait list. Finally, the taxon cycle hypothesis suggests that species geographic ranges transition through different states, where ranges initially increase in area with time before beginning to shrink in size as a species progresses towards extinction (Ricklefs and Cox 1972). Therefore, in general we expect older species to have larger range sizes. Consistent with this idea, genus age was shown to be a significant predictor of whether coral species crossed faunal breaks in the Indo-Pacific, indicative of a widespread range (Keith et al. 2013) and was therefore the last trait included in our analysis.

Species traits associated with assemblage shift

We used a linear regression model to test the extent to which species traits could predict assemblage structure across the islands. To achieve this, it was first necessary to collapse spatial changes in relative abundance of species into a tractable response variable. NMMDS generates axis scores for both samples and species. Sample scores, in this case for transects, are weighted averages of the species scores, determined by relative abundance (Oksanen et al. 2011). Therefore, species were positioned in multi-dimensional space such that they were placed optimally amongst transects in which they were most abundant, and closest to the transect in which they had the highest abundance. Because NMMDS axis one captured the difference in assemblage structure across the biogeographic break, species scores along this axis represent the change in relative abundance of species across this break. Lower NMMDS axis one species scores indicated higher relative abundance in the GBR assemblages, whilst higher NMMDS axis one species scores indicated higher relative abundance in Lord Howe Island assemblages. The model was therefore designed to predict the position of a species along the NMMDS axis according to its traits.

Traits measured on a continuous scale were centred at zero and scaled to have a standard deviation of one to simplify interpretation of regression coefficients for non-linear relationships. Categorical traits were added to the model as factors. As appropriate, Pearson and Spearman correlations were used a priori to test for collinearity of predictor variables and were considered problematic if $r > 0.6$ (Bolker 2008). Pearson correlations collapse to point biserial correlations in the case of dichotomous variables, which are appropriate for these kinds of data. In the event of collinearity, the trait chosen for inclusion in the model was the trait with the clearest biological meaning. Colony growth form is a multinomial categorical variable and therefore is not suitable for the above tests. Instead, we tested for non-random associations between growth form and other

categorical traits with Fisher's exact test – using a p value of < 0.05 as an indicator of strong association. Categorical and numeric traits were also visually assessed for association with growth form. All traits were tested for linear or quadratic relationships, with the latter selected if it was $> 3 \Delta AICc$ (Akaike information criterion corrected for small sample size) lower than the linear fit. In the full model, we included all trait interactions that were biologically plausible: all combinations of sexuality, reproductive mode, and nutritional mode; upper depth \times depth range; wave exposure \times water clarity.

Phylogenetic signals in trait values can obscure or mislead relationships in linear regression models owing to non-independence (Freckleton 2009). Therefore, we included genus (more robust and specific phylogenetic information is unavailable for corals) as a random effect within a mixed model (Zuur et al. 2009). The variance explained by genera within the mixed effect model was determined with the variance partition coefficient (variance across genera/(variance across genera + 3.29); Goldstein et al. 2002) and visually with a caterpillar plot, where overlapping 95% confidence intervals for the estimated intercept across genera indicate the random effect is weak. If the variance was low, the random effect was removed from subsequent models to prevent over-inflation of the variance explained owing to a high number of parameters (Zuur et al. 2009).

To find the best predictive model, we used model selection and averaged the model set within $3 \Delta AICc$ of the best model. We calculated 95% confidence intervals for the model-averaged coefficients and traits were deemed as significantly contributing to the predictive model if their confidence intervals did not overlap zero (i.e. we could be confident of a directional relationship).

Results

Assemblage abundance structure

The difference in relative abundance of species in assemblages between the GBR and Lord Howe Island, all combinations of islands, and between habitats were all significant at $p < 0.001$. However, as ANOSIM has a high type 1 error rate, we focus here on effect size as indicated by the global R , where a larger value indicates a lower similarity between assemblages. The relative abundance of species within the assemblages across the three islands were only slightly more different from each other (ANOSIM, $R = 0.37$, NMMDS Fig. 2–3) than the difference with Lord Howe Island when the GBR islands were pooled ($R = 0.34$), indicating that Lord Howe Island accounts for the majority of the difference (i.e. difference was maintained after pooling of the GBR sites). The differences between both Lord Howe Island and Lizard ($R = 0.44$), and Lord Howe Island and One Tree ($R = 0.49$) were larger (i.e. higher effect sizes) than the difference between the two GBR sites ($R = 0.16$, Fig. 3). The disparity between lagoon and crest sites across all islands was much less than the difference between islands or regions ($R = 0.10$). Species recorded during our surveys are listed for each island in Supplementary material Appendix 1, Table A1.

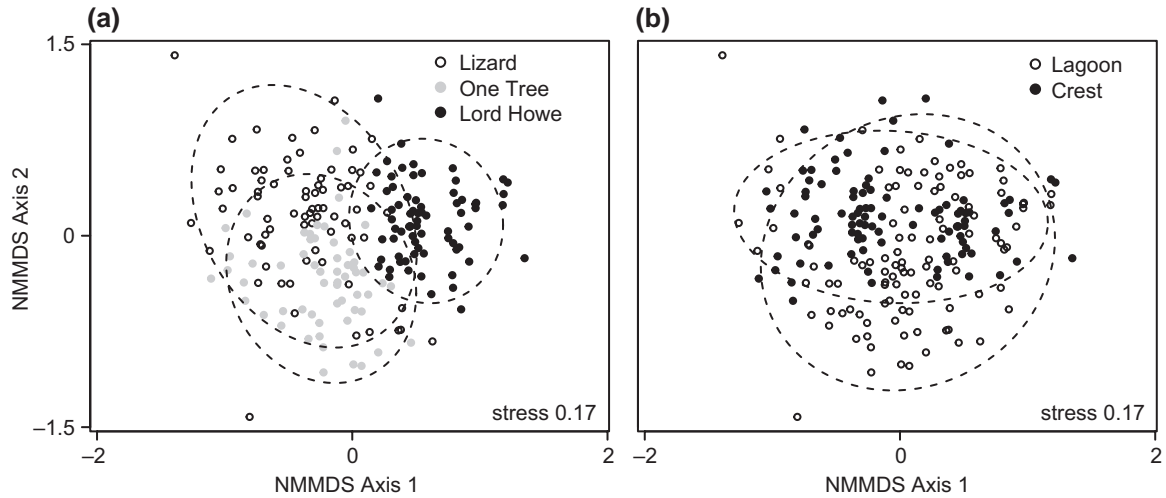


Figure 2. Similarity in relative abundance of species in the assemblages of three islands off the east coast of Australia (Lizard Island and One Tree Island are part of the Great Barrier Reef, GBR; Lord Howe Island is isolated). Each point represents one transect survey on one island; island is indicated by circular symbols (no fill = Lizard; grey fill = One Tree; black fill = Lord Howe). Similarities are calculated using the Chao similarity metric and visualized with non-metric multidimensional scaling (NMMDS), such that distance between sites is representative of the similarity between assemblage: closer points (transects) are more similar. Dashed lines outline bivariate standard deviational ellipses for axes one and two at a confidence interval of 95% for each island. 2D stress: 0.17.

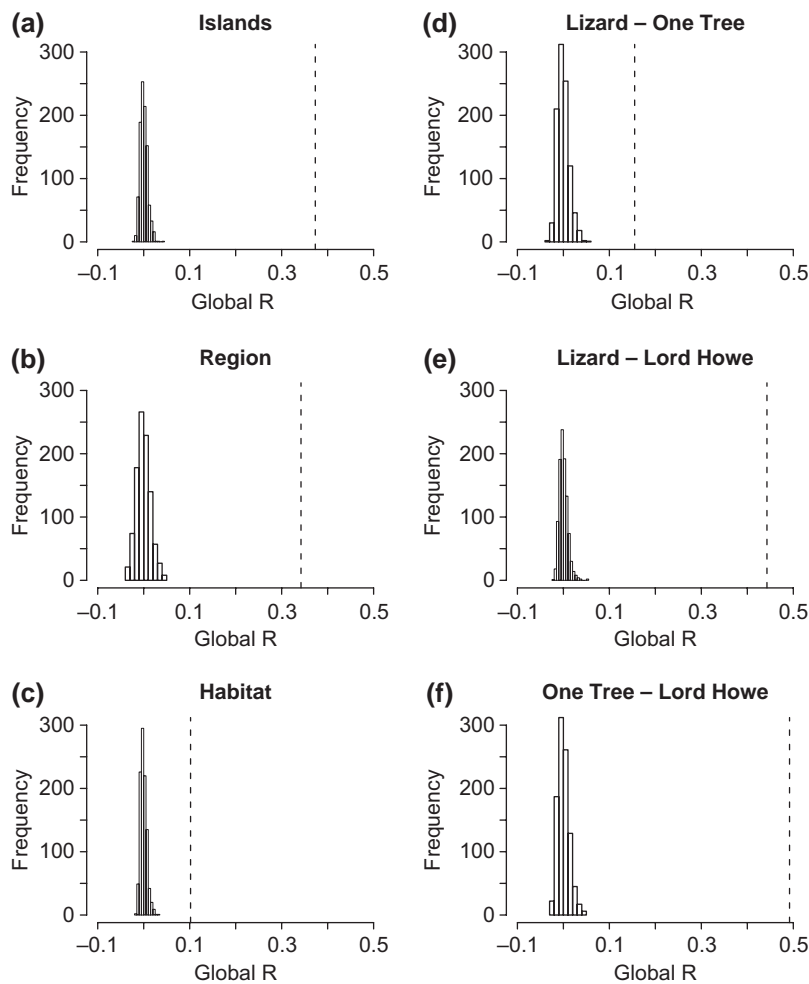


Figure 3. Analysis of Similarity (ANOSIM) between (a) all islands, (b) Great Barrier Reef region and Lord Howe Island, (c) lagoon and crest habitats, (d) Lizard Island and One Tree Island, (e) Lizard Island and Lord Howe Island, (f) One Tree Island and Lord Howe Island. Histograms show the global R statistics generated by 1000 permutations, dashed line shows the observed global R statistic. The observed value is significantly different from random if it lies outside the frequency histogram of simulated values.

Species traits across the biogeographic boundary

Genus accounted for <1% of the variation in NMMDS axis one species score and therefore a mixed effects model was not required. Two variables were correlated above the recommended threshold (Supplementary material Appendix 1, Table A2, lower depth and depth range $r = 0.99$). Lower depth was subsequently removed from further analyses. Colony growth form was significantly non-randomly associated with sexuality ($p < 0.001$, Supplementary material Appendix 1, Table A2, Fig. A1c), nutritional mode ($p = 0.006$, Supplementary material Appendix 1, Table A2, Fig. A1a) and wave exposure ($p = 0.037$, Supplementary material Appendix 1, Table A2, Fig. A1e), and boxplots suggested this trait was non-randomly distributed across the numeric traits (Supplementary material Appendix 1, Fig. A1f–j). Therefore, colony growth form was removed from further analysis. Prior to model averaging, interactions and higher order terms (quadratic term for corallite valley size) that were not significant were removed to make the model as simple as possible. The full model that underwent selection and averaging included corallite valley size, depth range, upper depth, wave exposure, water clarity, genus age, sexual mode, reproductive mode, nutritional mode and the interaction of depth range and upper depth.

Species that were strongly associated with Lord Howe Island were significantly more likely to be brooders compared with those in the GBR assemblage (Fig. 4a; Table 1). The dominance of brooding species on Lord Howe Island is driven by the high relative abundance of a small number of species (Fig. 5c). In particular, *Isopora cuneata* and *Porites heronensis* are highly abundant on Lord Howe Island, but are not present on the other two islands (Fig. 5a–c). In contrast, the spawning species that dominate at Lizard Island, such as *Acropora hyacinthus* and *A. muricata*, are either absent from

Table 1. Model-averaged coefficients and 95% confidence intervals for all traits selected. Coefficients for the traits in bold have 95% confidence intervals that did not overlap zero and are therefore considered to contribute significantly to the predictive model. *indicates variable was included in the best model.

CI	Coefficient	Lower 95% CI	Upper 95%
(Intercept)	0.42	0.01	0.82
Reproductive mode*	-0.66	-1.04	-0.28
Upper depth*	-0.16	-0.27	-0.04
Depth range × Upper depth*	-0.21	-0.35	-0.08
Depth range*	-0.07	-0.18	0.04
Wave exposure (exposed)	0.19	0.41	0.03
Wave exposure (protected)	0.14	-0.07	0.36
Nutritional mode	-0.13	-0.35	0.10
Sexuality	-0.13	-0.39	0.13
Valley size	0.04	-0.06	0.14

Lord Howe Island or occur at a much lower relative abundance (Fig. 5a–c). Lord Howe Island also has fewer species in the assemblage overall due to lower species richness than the GBR islands ($n_{LordHowe} = 30$; $n_{Lizard} = 85$; $n_{OneTree} = 63$). The other three reproductive traits, corallite size and genus age were either not included in, or were not significant in, the best model or the model-averaged results (i.e. 95% CIs for the coefficient overlapped zero; Table 1, Supplementary material Appendix 1, Table A3).

For the environmental traits, depth distribution of species significantly contributed to the model of assemblage structure through an interaction between depth range placement (indicated by upper depth) and the depth range associated with each coral species (Fig. 4b; Table 1). Species that have depth traits that indicate they can tolerate deep water conditions (i.e. either deep range placements or very broad depth distributions) are more likely to occur on Lord

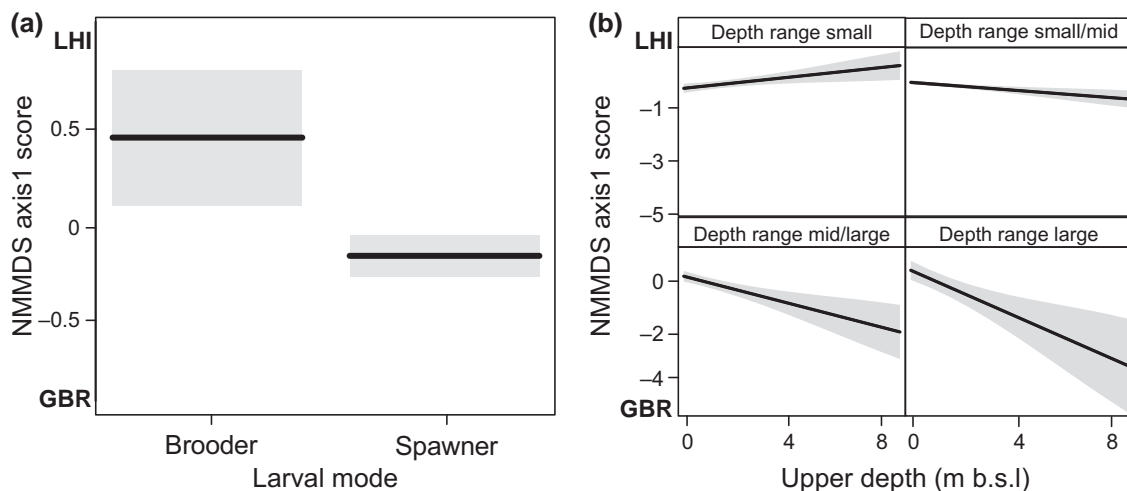


Figure 4. Contribution of individual species traits to the prediction of non-metric multidimensional scaling (NMMDS) axis 1 species score in a multiple linear regression model. Higher axis values are associated with Lord Howe Island (Lord Howe Island) assemblages, lower axis scores are associated with Great Barrier Reef (GBR) assemblages. Partial coefficients (black line) with 95% confidence intervals (grey shading) for traits that contributed significantly to the best model (and to model-averaged output): (a) reproductive mode, (b) interaction between upper depth and depth range. Plots are based on evaluation of upper depth when depth range is held constant at four different values spanning the range of possible values for the purpose of visualizing the interaction (small = 4.12 m, small/mid = 23.46 m, mid/large = 53.54 m, large = 78.26 m). Trait values for upper depth shown on a scale of meters below sea level (m b.s.l.) are back-transformed for the plot from the centered and scaled value used in the model ((trait value – mean)/standard deviation).

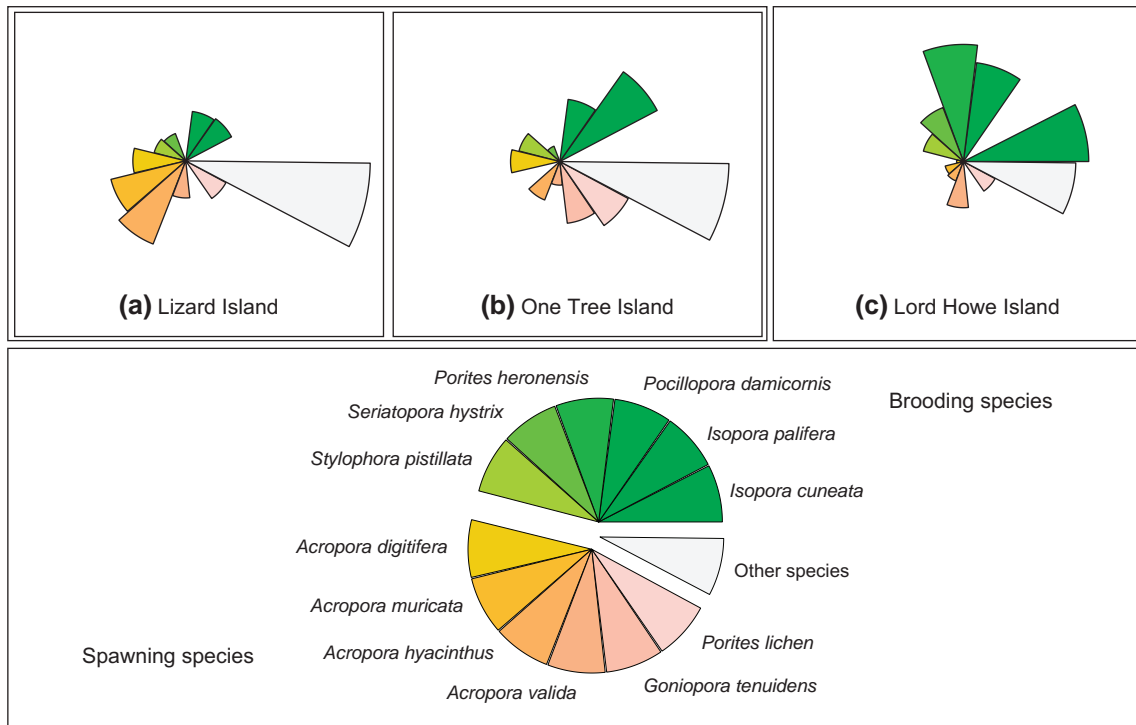


Figure 5. Star plots of relative abundance for the twelve species with the highest mean relative abundance across all islands. ‘Other species’ includes one brooder on all islands plus a varying number of species with a spawning reproductive mode. Size of the segment represents the mean relative abundance of a given species. Green segments are brooding species, yellow to pink segments are spawning species, and the white segments represent all other species observed in our surveys. Specific species for each segment are labeled in the key at the bottom of the panel. Lizard Island (a) has a high relative abundance of spawning species and other species, the latter indicating its high diversity relative to the other two islands.

Howe Island than species that are restricted to shallow water environments (Fig. 4b; Table 1). The variation in species axis score explained by traits in the best model was relatively low at 13% (adjusted $R^2 = 0.13$, $p < 0.001$).

Discussion

The biogeographic break between the Great Barrier Reef and Lord Howe Island off the east coast of Australia is characterised, not only by a loss of species as range limits are reached south of One Tree Island, but also by the gain of subtropical species and a change in the relative abundance of the species that remain. The change in abundance for some species implies that a mechanism other than, or in addition to, dispersal limitation maintains the differences in the Lord Howe Island assemblage. Species traits analysis suggests that the most important mechanism maintaining the biogeographic break is not the inability of species to disperse to Lord Howe Island, but rather the ability of a species to establish a viable population after successful dispersal. Specifically, the ability to successfully colonise the subtropical Lord Howe Island reefs depends on reproductive mode and tolerance of low light and temperature conditions. Our results are broadly consistent with previous analyses that also identified establishment, rather than dispersal, as the key process in the maintenance of biogeographic breaks in the marine environment at much larger spatial scales (Pandolfi 1992a, Luiz et al. 2012, Mora et al. 2012, Keith et al. 2013)

and therefore contributes to a broader understanding of processes that determine biogeographic patterns in the oceans.

The effect size of the difference between assemblage structures across the GBR and Lord Howe Island is much larger in comparison with the difference between the two islands in the GBR region (Fig. 3), which are separated by a geographic distance similar to that between the GBR and Lord Howe Island. Also, the fact that assemblages on One Tree Island and Lord Howe Island differ by a magnitude similar to Lizard Island and Lord Howe Island demonstrates that assemblage shifts are relatively abrupt, as we would expect at a biogeographic break, and do not occur gradually over the latitudinal gradient. Assemblages in crest and lagoon habitats also differed but much less so than the regional difference (Fig. 3), indicating that more variation is driven by island location than by habitat. Our results support the existence of a significant biogeographic break and are consistent with previous research (Veron and Done 1979, Harriott et al. 1995, Harriott and Banks 2002). In particular, the shift in species dominance suggests that the underlying processes may be more subtle or nuanced than the dispersal limitation or post-settlement mortality owing to subtropical environmental conditions.

Three species traits contributed significantly to the predictive model for assemblage structure: reproductive mode, upper depth, and depth range (the latter two traits together describe depth distribution). The higher relative abundance of species on the southern side of the biogeographic

break that reproduce via brooded larvae was consistent with observations of high numbers of brooded recruits found on artificial settlement tiles placed at Lord Howe Island (Harriott 1992). The shift in the abundance of species with this trait (12% on Lizard Island, 30% on One Tree Island, 73% on Lord Howe Island) is particularly striking because less than 5% of species present on the GBR reproduce through brooded larvae (Baird et al. 2009). Therefore, species with brooded larvae appear to have an advantage over spawning species at Lord Howe Island, which fits with the hypothesis that geographic and hydrodynamic isolation of Lord Howe Island leads to high dependence on local recruitment for population persistence (Harriott 1992), as demonstrated for reef fishes using genetic evidence (van der Meer et al. 2013). Larvae released by corals on the southern GBR will be transported southwards by the East Australian Current, but are highly likely to pass by, and subsequently settle on, other reefs before reaching Lord Howe Island (Bode et al. 2006). Moreover, larvae that do manage to reach Lord Howe Island may have a higher chance of a mismatch between the larval phenotype and the local environment (Crean et al. 2010). Therefore, there is strong evidence that high local recruitment is fundamental to population persistence on Lord Howe Island.

Specifically, we hypothesise that the mechanism that leads to higher local recruitment of brooders in comparison with spawners, conferring an advantage to the former, is linked strongly to development rate. Brooded larvae are able to settle immediately on release (Figueiredo et al. 2013). In contrast, spawned larvae are unable to settle for at least two to three days following release from the parent colony and, therefore, have an increased chance of being flushed out of the lagoon before settlement (Figueiredo et al. 2013). Moreover, the colder temperatures on Lord Howe Island (Veron and Done 1979) would be expected to slow larval development, further increasing the chance that spawned larvae are flushed from the lagoon and off the reef before larvae are competent to settle. Finally, low larval survivorship (Woolsey et al. 2015) and settlement rates of broadcast spawning species (Harriott 1992) observed at Lord Howe Island further suggest that spawning is a sub-optimal reproductive strategy at this location. Therefore, Lord Howe Island is unlikely to provide a suitable refuge for spawning corals as geographic distributions shift towards the poles. Conversely, larval development rate is predicted to accelerate as climate change leads to higher ocean temperatures (O'Connor et al. 2007), which will increase local retention (Figueiredo et al. 2014). In such a scenario, the potential for successful colonization of Lord Howe Island by spawning species could be improved substantially. Irrespective of the consequences for spawners, Lord Howe Island is likely to provide a stronghold for brooding species.

The ability of a species to tolerate environmental conditions can also influence its ability to establish a viable population after successful dispersal. For instance, the occurrence pattern of orchids across the islands of Samoa was more closely tied to environmental conditions, altitude in particular, than to the relative isolation of islands (Wagner 2011). This mechanism appears to play a role in the maintenance of the biogeographic break at Lord Howe Island. Species with depth traits that infer tolerance of deeper water conditions

(i.e. deep placement or broad depth range) were more likely to be abundant on Lord Howe Island than species associated with only shallow water environments (i.e. shallow water specialists). The most parsimonious explanation for this observation is that environmental suitability for species associated with shallow water is reduced on Lord Howe Island as light and temperature availability decreases at high latitude (Kleypas et al. 1999). The slower growth of many coral species on Lord Howe Island compared with the GBR supports the proposition that these factors are limiting (Harriott 1999). Therefore, our observations support the hypothesis that species that are tolerant of sub-optimal conditions are generally more abundant on Lord Howe Island. Interestingly, depth range was also found to be an important trait for predicting species presence across biogeographic breaks at the much larger scale of the entire Indo-Pacific (Keith et al. 2013), suggesting that the ability of a coral species to tolerate a range of environmental conditions is an important predictor of its geographical distribution at a range of spatial scales.

While our model indicates the importance of local processes (e.g. retention of larvae, environmental tolerance) in maintaining the biogeographic break and is consistent with previous analyses, the overall predictive ability is rather low, explaining only 13% of the variation in assemblage structure. Two limitations of trait-based analyses can offer potential reasons for the model performance: 1) the selected traits were not reliable proxies for the processes we hypothesised they reflected, and/or 2) additional processes that were not captured in our chosen traits influence the maintenance of the biogeographic break. For example, traits that relate more directly to the ability of corals to tolerate relatively low temperatures might explain more of the underlying variation in the data and reveal a clearer role for physiological limitation, but unfortunately such information is not currently available. An additional caveat for trait-based approaches at the biogeographical scale is that trait expression can be context-dependent; that is, the measured value of a species trait varies depending on the biotic and abiotic setting (Bolnick et al. 2011). For example, we could reasonably expect depth range to vary depending on geomorphology and light attenuation at a given reef. Therefore, some trait values may be expressed differently at Lord Howe Island compared with the location of data collection for traits in the database. Whilst large-scale quantification of intraspecific trait variation has begun, coverage over a large taxonomic and geographic extent will not be available for some time. However, as long as we recognise these caveats, traits offer an excellent opportunity to generalise across multiple species in high diversity systems and a more direct assessment of potential mechanisms than correlations with environmental factors (Cadotte et al. 2011).

More broadly, a recent proliferation of research in opposition to the traditional paradigm that marine systems are open and species can disperse everywhere has forced us to revise our view to one of relatively closed systems (Gaylord and Gaines 2000, Tremblay et al. 2008, Wood et al. 2014). However, whilst this is likely true over annual and decadal time scales (Keith et al. 2011), our analysis and previous analyses suggest that over longer time scales, dispersal limitation might not be the most important factor driving

biogeographic patterns in the marine environment. At larger spatial scales, biogeographic breaks for corals throughout the Indo-Pacific were better explained by traits that are indicative of establishment, than by those thought to be proxies for dispersal potential (Keith et al. 2013).

Furthermore, such conclusions are not restricted to corals. The importance of establishment over dispersal as a driving mechanism was demonstrated for maintenance of biogeographic breaks in the Atlantic Ocean for marine fishes, particularly linked to large body size and wide latitudinal range: traits that are hypothesised to confer a greater environmental tolerance to the adults (Luiz et al. 2012). Global models of hydrodynamics have also demonstrated that the vast majority of reef fish species are capable of dispersing between all coral reefs of the world given enough time, and therefore, assemblages of these fishes are unlikely to be determined by dispersal limitation (Mora et al. 2012). Whilst evidence suggests that establishment ability is also an important determinant of species geographic range limits in terrestrial biomes (Paulay and Meyer 2002), marine species tend to disperse further and more diffusely than terrestrial species, and therefore, local environmental (Wagner 2011) or biotic (Zimmerman 1948) conditions might provide a better explanation for terrestrial breaks (Paulay and Meyer 2002, Cornell and Harrison 2012). In conclusion, our results add to a growing body of evidence that establishment limited by propagule retention as a mechanism to maintain biogeographic breaks is pervasive in the marine environment and applies across multiple taxa.

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Supplementary material (Appendix ECOG-01437 at <www.ecography.org/appendix/ecog-01437>). Appendix 1.