Trait-mediated environmental filtering drives assembly at biogeographic transition zones

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Abstract. Abiotic filtering is a major driver of gradients in the structure and functioning of ecosystems from the tropics to the poles. It is thus likely that environmental filtering is an important assembly process at the transition of biogeographical zones where many species occur at their range limits. Shifts in species abundances and association patterns along environmental gradients can be indicative of environmental filtering, which is predicted to be stronger in areas of high abiotic stress and to promote increased similarity of ecological characteristics among co-occurring species. Here we test these hypotheses for scleractinian corals along a broad latitudinal gradient in high-latitude eastern Australia, where corals occur at the margins of their ranges and environmental tolerances. We quantify variation in taxonomic, zoogeographic, and functional patterns combined with null model approaches and demonstrate systematic spatial variation in community structure and significant covariance of species abundance distributions and functional characteristics along the latitudinal gradient. We describe a strong biogeographic transition zone, consistent with patterns expected under abiotic filtering, whereby species are sorted along the latitudinal gradient according to their tolerances for marginal reef conditions. High-latitude coastal reefs are typified by widely distributed, generalist, stress-tolerant coral species with massive and horizontally spreading morphologies and by diminishing influence of tropical taxa at higher latitudes and closer to the mainland. Higher degree of ecological similarity among co-occurring species than expected by chance supports the environmental filtering hypothesis. Among individual traits, the structural traits corallite size and colony morphology were filtered most strongly, suggesting that characteristics linked to energy acquisition and physical stability may be particularly important for coral survival in high-latitude environments. These findings highlight interspecific differences and species interactions with the environment as key drivers of community organization in biogeographic transition zones and support the hypothesis that environmental filters play a stronger role than biotic interactions in structuring ecological communities in areas of high abiotic stress.

Key words: *biogeography; community assembly; environmental filtering; functional traits; high-latitude reefs; latitudinal gradient; life-history strategy; range limit; scleractinian corals.*

INTRODUCTION

Theories of community assembly come from one of two broad paradigms, which differ fundamentally in their perspectives on the role of species' demographic characteristics. Stochastic theories propose that species are ecologically equivalent and that coexistence patterns are the consequence of random demographic processes, dispersal limitation, and ecological drift (Hubbell 2001). In contrast, deterministic niche-based theories explain variation of community structure based on interspecific trade-offs and stabilizing mechanisms that facilitate coexistence (Chase and Leibold

2003). While it is increasingly recognized that deterministic and stochastic processes occur simultaneously, their relative influence continues to fuel contemporary debate (Chase and Myers 2011). This question is particularly pertinent to ecosystems at the transition of biogeographical zones, as they have characteristics relevant to both processes. For example, transitional environments often support species at the edges of their ranges, where habitat conditions may fall outside their optimal requirements. Species range limits have been likened to the spatial manifestation of a species' ecological niche and are projected to shift in response to climate change (Sexton et al. 2009). Populations in marginal environments typically differ in their demographic characteristics from those in core habitats as they tend to be smaller, fragmented, may have diminished reproductive success, have varying demo-

graphic and genetic connectivity with those in core habitats, and frequently rely on immigration from core habitats for their long-term persistence (Kawecki 2008). These attributes render marginal populations more vulnerable to drift processes, such as environmental fluctuations, Allee effect, demographic stochasticity, and local extinction (Kawecki 2008), which can make it more difficult to detect the signature of niche-based processes (Chase and Myers 2011).

While it is likely that a combination of deterministic (i.e., environmental conditions, species interactions) and stochastic (i.e., chance colonization, ecological drift) mechanisms (Leibold and McPeek 2006, Chase and Myers 2011) explain organization of marginal communities, evidence suggests that environmental filtering is a major driver of gradients in the distribution of species and their functional characteristics from the tropics to the poles (e.g., Hillebrand 2004). The concept of environmental filtering proposes that species are sorted along environmental gradients based on their functional traits and their adaptations to prevailing environmental conditions (Chase and Leibold 2003). Whether or not species pass through these filters therefore depends on their functional traits. For example, plants that cannot tolerate frost are excluded from alpine regions (Körner 2003) and animals that cannot tolerate high temperatures move to higher elevations (e.g., Wilson et al. 2007). Trait-based approaches can provide insights into the mechanisms that drive community organization, ecosystem functioning, and species coexistence, and it is increasingly recognized that robust tests of community assembly need to incorporate information about the functional characteristics of species (e.g., McGill et al. 2006).

Environmental filtering and competitive interactions produce opposite expectations about the similarity of species traits within communities, which have given rise to tests of assembly processes based on the functional similarity of co-occurring species. Under environmental filtering, species that experience the same environmental conditions are expected to be more similar in their functional traits, whereas biotic interactions are thought to limit their similarity (Cavender-Bares et al. 2004). The favorability hypothesis predicts that environmental filtering is stronger in areas of high abiotic stress (Fischer 1960), which should thus promote increased similarity of ecological traits that affect how species at their range edges respond to marginal environmental conditions. While functionally based investigations of abiotic filtering in harsh environments have been conducted for plants (e.g., Cavender-Bares and Reich 2012), to our knowledge, this hypothesis has not been tested for coral reefs. Here, we use measures of co-occurrence and functional similarity of species to characterize assembly processes for high-latitude coral communities of eastern Australia, where scleractinian corals occur at the margins of their distribution. High-latitude reefs occur in close proximity to their environmental limits (i.e., temperature, light availability, aragonite saturation, nutrient availability) and are exposed to highly fluctuating conditions (Guinotte et al. 2003). Poleward transport of tropical waters by the East Australian Current (Roughan and Middleton 2004) facilitates predominantly non-reefal coral communities in pockets of suitable habitat. High-latitude reefs are projected to undergo multidimensional changes, both through altered environmental conditions (Hobday and Lough 2011) and shifts in the distribution of organisms (Greenstein and Pandolfi 2008, Yamano et al. 2011). Poleward range shifts of tropical corals have already been observed in this biogeographic transition zone (Baird et al. 2012), making high-latitude reefs good sentinels of environmental change.

We examine assembly mechanisms at the margins of coral species distribution in four ways. We initially investigate spatial variation in abundance patterns along a latitudinal gradient of six degrees: (1) among species, (2) zoogeographically, (3) among functional characteristics, and subsequently, (4) compare observed patterns against null models of random assembly. More specifically, we test whether species co-occurrence patterns along the latitudinal gradient are more similar than randomly expected, and compare measures of co-occurrence and ecological similarity of species to determine whether patterns are caused by a common response to abiotic conditions. We test the hypotheses that marginal environmental conditions impose a deterministic filter on community assembly and that community structure varies systematically along the latitudinal gradient. Consistent with the trait-based hypothesis of environmental filtering in harsh environments, we predict that co-occurring species are more similar in their functional characteristics than would be expected by chance. In combination, these approaches reveal how zoogeographic and functional patterns influence community organization along a latitudinal gradient to elucidate assembly processes at biogeographic transition zones.

METHODS

Data collection

We sampled the coastal subtropical coral communities of eastern Australia using five replicate 30 m long, 1 m wide photographic belt transects (see Sommer et al. [2011] for more details on survey method) at each of 17 locations along a latitudinal environmental gradient from 26°36′ S to 32°48′ S. Study sites were selected based on the known occurrence of scleractinian corals and were located on the semi-protected leeward side of headlands and islands, where corals mainly occur in these wave-exposed environments. Thus, the factors, wave and current exposure, were similar throughout the study sites. Surveys were conducted in a depth range of 8–12 m between August 2010 and August 2011. We quantified coral abundance using the software Coral

TABLE 1. Regressions between summary variables of eastern Australian high-latitude coral communities and the predictors latitude and distance from the mainland (conditional on latitude).

Variable	Latitude			Distance from mainland		
	r	R^2	P	r	R^2	P
Species richness						
Total	−0.765	0.585	**0.001**	0.167	0.028	0.179
Tropical	−0.717	0.514	**0.002**	0.276	0.076	0.089
Subtropical	−0.473	0.224	**0.045**	0.252	0.063	0.153
Cosmopolitan	−0.809	0.655	**0.001**	0.235	0.055	0.089
Species per genus	−0.660	0.435	**0.005**	0.288	0.083	0.089
Abundance						
Total	−0.280	0.078	0.155	0.139	0.019	0.297
Tropical	−0.674	0.455	**0.003**	0.674	0.455	**0.041**
Subtropical	0.371	0.138	0.089	−0.089	0.008	0.318
Cosmopolitan	0.129	0.017	0.297	−0.155	0.024	0.294
Relative abundance						
Tropical	−0.794	0.631	**0.001**	0.532	0.283	**0.001**
Subtropical	0.656	0.430	**0.005**	−0.087	0.008	0.297
Cosmopolitan	0.114	0.013	0.061	−0.452	0.204	0.297
Shannon diversity	−0.788	0.621	**0.001**	0.280	0.078	0.061
Dominance						
Simpson dominance	0.661	0.437	**0.005**	0.339	0.115	0.061
Relative dominance	0.636	0.404	**0.007**	0.465	0.216	**0.020**

Note: Significant false discovery rate adjusted P values ($P \leq 0.05$) are highlighted in boldface type.

Point Count with Excel extensions (Kohler and Gill 2006) and the random point count method (600 points per transect). We identified scleractinian corals to species level, except 30 *Acropora*, *Montipora*, and *Goniopora* colonies, which we coded to growth form and genus as we could not reliably identify them from photographs or skeletal samples.

Ecological characteristics of species

Coral zoogeography.—To investigate zoogeographical patterns of corals, we assigned all coral taxa to one of three zoogeographical groups based on the distributional information in Veron (1993, 2000): tropical for taxa classified as common or sometimes common in the tropics, and that occur in the tropics and are generally rare or uncommon; subtropical for taxa described as rare or uncommon in the tropics and common in high latitudes; cosmopolitan for taxa described as common in the tropics and especially common in high latitudes, common throughout their geographical distribution, and taxa that occur all around Australia (Appendix C).

Functional traits.—To examine functional patterns we characterized coral taxa based on six structural and reproductive traits, with a total of 19 character states: colony morphology, corallite formation, corallite size, reproductive mode, sexuality, and symbiont transmission (Appendix A). All traits were weighted equally in the analyses. While we acknowledge that other traits may also be important, previous studies indicate that the traits used provide robust indicators of coral functional strategies (Rachello-Dolmen and Cleary 2007, Darling et al. 2012).

Life-history strategies.—To evaluate life-history strategies of high-latitude coastal coral communities of eastern Australia in the context of the recently developed life-history framework for scleractinian corals by Darling et al. (2012), we classified the species recorded in our study as competitive, weedy, stress-tolerant, or generalist (Appendix B and Darling et al. [2012]).

Spatial patterns in community structure

To characterize spatial patterns in coral community structure, we tested associations between community summary variables (see Table 1 for a complete list of tests) and the latitudinal gradient. As previous localized surveys have identified cross-shelf gradients in benthic and fish communities within the study region (Harriott et al. 1994, Malcolm et al. 2011), we tested whether distance from the mainland explained additional variation in community structure, given that latitude had already been fitted in the model (i.e., conditional test). We performed nonparametric distance-based multiple regressions with P values obtained by permutation and thus not constrained by the assumptions of normality (Anderson 2001). We used R^2 values as the test statistic and adjusted P values using the false discovery rate procedure to control against errors from multiple comparisons (Pike 2011).

To test variation in multivariate coral community structure with spatial gradients, we performed canonical analysis of principal coordinates (CAP) on Bray-Curtis similarities from square-root-transformed data, using the trace test statistic, π (sum of canonical eigenvalues)

(Anderson and Willis 2003). To identify which taxa primarily discriminated coral communities along spatial gradients, we overlaid vectors based on correlations with canonical axes.

Tests of random assembly.—To examine whether spatial patterns in community structure differed from patterns expected at random, we used similarity profiles (Clarke et al. 2008) and tested the null hypotheses (1) that species co-occur randomly across the 17 locations and (2) that there is no multivariate structure among locations. We calculated Bray-Curtis similarities of abundance distributions between every pair of coral species for observed and simulated random communities (10 000 permutations), and plotted them against their ranks. We repeated the analysis for variation of coral communities among locations. If nonrandom processes prevail, observed similarity profiles should deviate significantly from random profiles, as measured by the summed absolute distances (π) between the real similarity profile and the simulated mean profile. Multiple regressions, CAP, and tests of random assembly were conducted using PRIMER v6 (Clarke and Gorley 2006) and PERMANOVA (Anderson et al. 2008).

Trait-based tests of environmental filtering

Ecological similarity of co-occurring species.—To test whether species co-occurrence patterns in the region reflect ecological similarity between species, we compared the relationship between the co-occurrence of pairs of coral species and their functional dissimilarity, and tested significance levels by comparing the observed correlations with correlations expected under a null model (Cavender-Bares et al. 2004). We used a standardized measure of co-occurrence (DO) that is robust to the abundances of species being compared and computed co-occurrence as $DO_{ij} = (P_{ij} - P_iP_j)/(P_iP_j)$, where P_i (and P_j) is the proportion of sites where coral species i (or j) occurs, and P_iP_j is the proportion of sites where both species i and j co-occur (Slingsby and Verboom 2006). We generated functional dendrograms (Petchey and Gaston 2002) using Ward's hierarchical clustering of Gower species distances and correlated trait differences of all species pairs and their corresponding degree of co-occurrence in the region. Significant negative correlation coefficients would indicate that species that are more similar in their functional traits (i.e., have less functional distance between them) have higher co-occurrence and would support the environmental filtering hypothesis. Significant positive correlations, on the other hand, would indicate that less similar species co-occur more, suggesting that competitive processes are dominant in structuring communities (Cavender-Bares et al. 2004). To determine whether specific traits were driving the observed patterns, we conducted these analyses for all six traits, individually and combined, and for coral zoogeography and life-history strategy (Darling et al. 2012).

Null model tests.—To test whether the observed degree of ecological similarity of co-occurring species was significantly greater than would be expected at random, we compared the strength of the observed correlations with the strength of correlations in 999 random datasets devoid of functional structure. If niche-based processes (i.e., abiotic filtering, biotic interactions) prevail, the observed correlations should be significantly stronger than would be expected by chance (Cavender-Bares et al. 2004). We generated null models using the independent swap algorithm (Gotelli 2000), which randomizes the community data matrix while maintaining species richness at the locations and occurrence frequency of species among locations. These assumptions are known to minimize Type I error and have high power to detect niche-based processes in situations where multiple traits are involved (Kembel 2009). We conducted all trait-based analyses using the picante package (Kembel et al. 2010) in R (R Development Core Team 2012).

RESULTS

Spatial patterns in community structure

We describe a strong biogeographic transition zone for high-latitude coral communities of eastern Australia. A total of 92 scleractinian coral taxa (75 tropical, 10 cosmopolitan, 7 subtropical) were recorded in this study. Most species were narrowly distributed and tropical, while cosmopolitan and subtropical species generally had widespread occurrence (Appendix D). The number of tropical, cosmopolitan, and subtropical species, as well as overall species richness declined significantly with increasing latitude (Table 1). In contrast to the strong contribution of tropical species to overall species richness, coral abundance was dominated by cosmopolitan and subtropical species at all except the four most northerly locations (Appendix D). Variation in overall coral cover was independent of latitude and distance from the mainland and dominance increased with increasing latitude (Table 1). Using a multivariate CAP model, latitude and distance from shore explained 94% of the variation in coral community structure (canonical correlations, $\delta_1 = 0.99$ and $\delta_2 = 0.95$; number of PCO axes, $m = 8$; $P = 0.0001$; Fig. 1a). Vectors illustrate that tropical genera were primarily responsible for discriminating coral communities along spatial gradients (Fig. 1b, Table 1).

Tests of random assembly of coral species abundances and communities.—Observed abundance distributions of species pairs across the 17 locations (Appendix E) were significantly more similar than would be expected by chance (summed absolute differences, $\pi = 11.011$, $P = 0.0001$; Fig. 2a). The similarity profile of observed coral communities at the locations also deviated significantly from random profiles ($\pi = 6.582$, $P = 0.0001$), with an excess of smaller and larger similarities among communities (i.e., locations) relative to the null expectation (Fig. 2b).

Trait-based tests of environmental filtering

Co-occurrence of coral species in the subtropical-to-temperate transition zone in eastern Australia is highly structured in terms of species zoogeography, functional characteristics, and life-history strategies. Zoogeography was the best predictor of species' co-occurrence in the study region. As for species functional characteristics, species that were most similar in their traits overall (all six traits combined), in their corallite size, colony morphology, reproductive mode, sexuality, and life-history strategy had the highest degree of co-occurrence in the study region, resulting in significant negative correlations between functional distance and species co-occurrence (Fig. 3, Table 2). Subsequent null model tests showed that the observed correlations for zoogeography, overall species traits, corallite size, colony morphology, corallite formation and life-history strategy were significantly greater than randomly expected (Table 2).

Structural traits.—The majority of species (54 species) had corallites of less than 3 mm diameter and only 19 species had corallites greater than 8 mm (Appendix A). Almost all species displayed horizontally spreading morphologies and had encrusting-to-massive (48 species), laminar (9 species), tabular/platy (9 species), and stout-branching-to-tabular (21 species) growth forms (Appendix A), comprising over 95% of mean coral abundance at the sampled locations. Only four species displayed tall, tree-like arborescent growth, and these were generally narrowly distributed and rare, except *Acropora intermedia*, which was most abundant at lower-latitude and offshore (26°59′ S, 153°29′ E) Flinders Reef (Fig. 1a). Corals with plocoid corallites (i.e., have their own walls) were prevalent throughout the region, followed by 29 species with cerioid corallites (i.e., share walls) and 7 meandroid species (i.e., form valleys; Appendix A).

Reproductive traits.—Even though species with similar reproductive traits were frequently encountered together, co-occurrence rates were not greater than randomly expected. The 83 broadcast spawning species dominated coral abundance at all but four locations, where brooding species were more abundant, most notably the endemic *Pocillopora aliciae* (Schmidt-Roach et al. 2013) at highest latitudes (Appendix A). Although 70 species were hermaphroditic, gonochores (mainly *Turbinaria*) were abundant at many high-latitude locations (Appendix A). Horizontal symbiont transmission (i.e., symbionts are not maternally transmitted to larvae) was dominant across the region, except at the highest latitude locations, where *P. aliciae* was dominant.

Life-history strategy.—The 32 stress-tolerant species made up the greatest component of coral cover at six locations, followed by 35 competitive, five weedy, and 12 generalist species at five, four, and two locations, respectively. Consistent with the brooding reproductive mode, weedy species had greatest relative abundance at the southernmost locations (Appendix B).

DISCUSSION

Biogeographic patterns in the subtropical-to-temperate transition zone

The latitudinal diversity gradient is one of the most enduring biogeographic patterns in ecology and is almost ubiquitous in both terrestrial and marine realms (Hillebrand 2004). The proposed mechanisms include biological (e.g., competition, predation, parasitism), abiotic (e.g., energy, temperature, available biome area) and evolutionary (e.g., speciation, extinction) drivers. However, the generality of the pattern supports the operation of very basic principles such as the relationship between species richness and temperature (reviewed in Hillebrand 2004). Latitude is a surrogate for many environmental gradients (e.g., temperature, productivity, seasonality, solar angle), and the favorability hypothesis highlights the potential that increased abiotic filtering from the tropics toward higher latitudes drives gradients in the diversity of biotas (Fischer 1960).

Here, we confirmed the latitudinal diversity gradient for high-latitude coastal coral communities of eastern Australia and recorded a decline in taxonomic richness and diversity with increasing latitude. A strong biogeographic transition zone was characterized by a gradual decline in occurrence and abundance of tropical species along the north to south gradient and closer to the mainland. These spatial gradients are consistent with regional oceanographic features. In addition to a general decline in sea surface temperature toward higher latitudes, stronger offshore influence of the East Australian Current leads to warmer, clearer waters offshore, whereas upwelling drives incursion of cooler, nutrient-enriched waters near the coast (e.g., Roughan and Middleton 2004, Malcolm et al. 2011). Gradients in coral species composition along light availability and turbidity gradients have also been observed on tropical coral reefs (e.g., Fabricius et al. 2005) and suggest that high-latitude corals respond to similar processes. For example, tropical species of the genus *Acropora* are known to thrive in clear, warm waters (Veron 2000) and to occupy a smaller turbidity–light niche than *Turbinaria mesenterina*, which maintained a positive energy balance in lower light and higher turbidity (Anthony and Connolly 2004). High association of abundance patterns of *Turbinaria* species and of tropical species with nearshore and offshore locations in this study, respectively, support these findings (Fig. 1b). Higher levels of sedimentation closer to the mainland (e.g., from rivers) are likely to also contribute to the observed cross-shelf gradients in community structure.

The climatic variability hypothesis predicts that, because high-latitude taxa experience greater climatic variation, they are likely to be better adapted to a greater range of environmental conditions and tend to be more generalized in their habitat use. Their broader ecological niches thus allow generalists to find suitable conditions over larger geographic areas (Stevens 1989). Our study corroborated
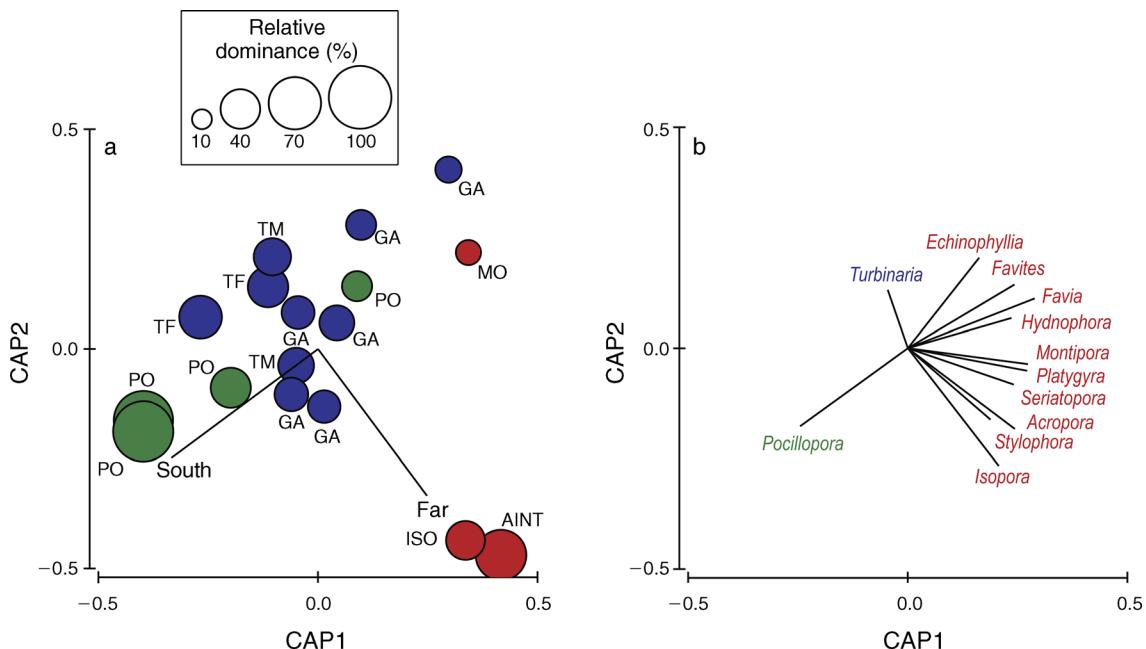
FIG. 1. (a) Canonical analysis of principal coordinates (CAP) revealing variation in coral community structure of subtropical eastern Australian reefs (bubbles) in relation to latitude (South) and distance from the mainland (Far). Letters adjacent to bubbles identify the dominant species at the locations and bubble colors denote their zoogeography: GA, *Goniastrea australensis*; PO, *Pocillopora aliciae*; TM, *Turbinaria mesenterina*; TF, *Turbinaria frondens*; ISO, *Isopora* sp.; MO, *Montipora* sp.; AINT, *Acropora intermedia*; red indicates tropical species; blue indicates cosmopolitan species; green indicates subtropical species. Bubble size indicates relative abundance of the most abundant species. (b) Vectors identify genera that primarily discriminate communities along spatial gradients and their zoogeography.

this hypothesis, as we found that cosmopolitan and subtropical species were widely distributed and abundant in the study region. In contrast, most tropical species were locally distributed and rare and tended to be more prevalent at lower latitudes and offshore, where abiotic conditions are more similar to those experienced in their core tropical range.

Nonrandom community assembly processes

Niche-based and stochastic theories make fundamentally different predictions about the assembly of species along environmental gradients. According to stochastic theories, species differences and species interactions with each other and with the environment are not relevant to community assembly (Hubbell 2001). In contrast, deterministic concepts predict that species are assembled along environmental gradients based on their functional characteristics, their tolerances for local conditions, and biotic interactions (Chase and Leibold 2003). Here, we found systematic spatial variation in community structure and significantly greater covariance of species abundance distributions relative to simulated randomly assembled communities (Fig. 2a). This suggests that coral communities in marginal environments are assembled nonrandomly
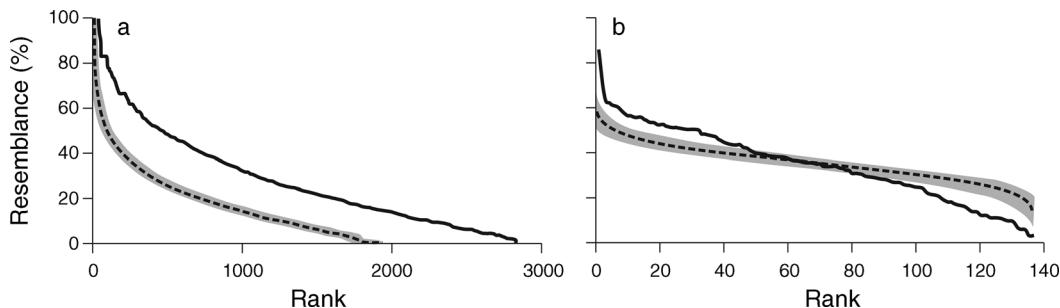

FIG. 2. Tests of random assembly of subtropical eastern Australian coral communities. Resemblance profiles for the observed real data (solid black line), the mean of 10 000 permuted simulated matrices (dashed black line), and 95% envelope for a further set of 10 000 matrices (gray area) for (a) resemblance of abundance distributions of coral species pairs and for (b) resemblance of community structure between location pairs, plotted against their ranks (from most to least similar).
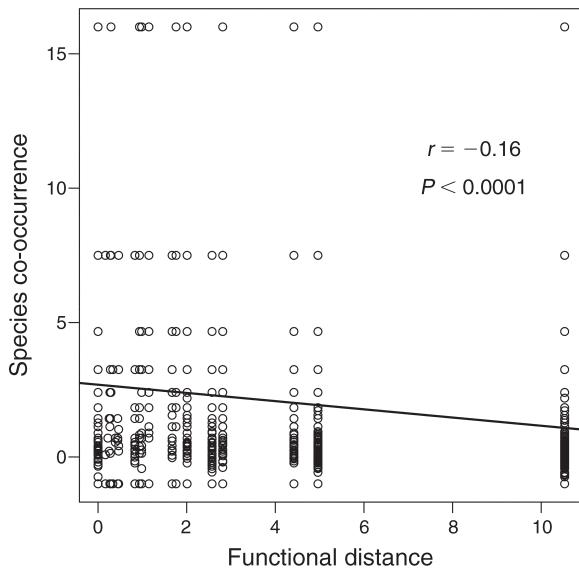
Fig. 3. The relationship between trait differences of species pairs and their co-occurrences in the tropical-to-temperate transition zone in eastern Australia. Species pairs with the least functional distance between them (i.e., pairs that are most similar in terms of their functional characteristics; see *Methods: Ecological similarity of co-occurring species: Trait-based tests of environmental filtering*) show the highest degree of co-occurrence, resulting in a significant negative correlation between functional distance and species co-occurrence.

and that the harsher environmental conditions impose a deterministic filter on community assembly. The high similarity of species abundance distributions (Fig. 2a; Appendix E) is consistent with strong species sorting processes (Chase and Leibold 2003) along the latitudinal gradient, which reduce the regional species pool to taxa whose functional traits are best suited to local environmental conditions. The excess of smaller and larger similarities among locations than randomly expected (Fig. 2b) is also consistent with deterministic processes and the tendency for local communities to experience different abiotic conditions along the latitudinal gradient. Communities exposed to similar conditions are likely to be

more similar than the null expectation (Chase and Myers 2011) and the observed greater similarity of some communities could thus be due to stronger filtering (Fischer 1960) and a common response to marginal conditions (Leibold and McPeek 2006) at the edges of coral distribution.

Trait-mediated environmental filtering

The co-occurrence of ecologically similar species has long been thought to be incompatible with the mechanism of niche differentiation; however, it is not unusual for ecologically similar species to coexist, particularly when their similarities are largely associated with characteristics that affect how they respond to the environment (Leibold and McPeek 2006). For example, species from the largest extant coral genus *Acropora* tend to display fast growth rates and similar life-history traits (Darling et al. 2012), and co-occur and dominate coral cover throughout Indo-Pacific reefs (Veron 2000). Our findings that species that are more similar in their functional characteristics have higher co-occurrence (Table 2) are likely related to the equalizing effect of marginal environmental conditions (Leibold and McPeek 2006) at high latitudes and suggest that in these harsh conditions abiotic filtering exerts a stronger influence on the structure of coral communities than biotic interactions. Consistent with the strong biogeographic transition we recorded, coral zoogeography was the best predictor of species co-occurrence patterns in the study region, followed by all six traits combined and life-history strategy. Among individual traits, structural characteristics (i.e., corallite size, colony morphology, corallite formation) were filtered most strongly (Table 2), suggesting that traits linked to energy acquisition and colony stability may be particularly important for coral survival in these marginal environments. For example, the high abundance of coral species with very small corallites (<3 mm) at most locations could be related to enhanced photosynthetic potential of corals with small and tightly packed corallites due to greater surface area available for endosymbionts (Houlbrèque and Ferrier-Pagès 2009). While larger corallites were previously deemed more favorable for heterotrophic

TABLE 2. Tests of the degree of functional overlap of co-occurring species for coral communities of subtropical eastern Australia.

Variable	r_{obs}	P_{obs}	$r_{obs} > r_{rand}$	$P_{obs\ vs.\ rand}$
Coral zoogeography	−0.202	**<0.001**	999	**0.001**
Traits				
All six traits combined	−0.163	**<0.001**	999	**0.001**
Corallite size	−0.209	**<0.001**	999	**0.001**
Morphology	−0.167	**<0.001**	999	**0.001**
Corallite formation	−0.039	**0.010**	964	**0.035**
Reproduction	−0.074	**<0.001**	910	0.089
Sexuality	−0.046	**0.003**	765	0.234
Symbiont transmission	0.008	0.606	422	0.577
Life-history strategy	−0.162	**<0.001**	999	**0.001**

Notes: Tests were conducted for species traits (individually and combined), coral zoogeography, and life-history strategy (Darling et al. 2012). Significant *P* values ($P \leq 0.05$) are highlighted in boldface type.

feeding, recent studies suggest that feeding rates are independent of polyp size, but increase with declining surface-to-volume ratio of colonies (i.e., mounding corals have higher feeding rates than branching corals [Houlbrèque and Ferrier-Pagès 2009]). Particle feeding is considered an important mechanism in sustaining reefs in impoverished conditions (e.g., turbid and deep reefs [Houlbrèque and Ferrier-Pagès 2009]), and it is plausible that it is an important source of energy replenishment in light reduced high-latitude environments. While we observed many corals with extended tentacles during the day, further work is required to quantify the relative occurrence of heterotrophic feeding with latitude.

Phenotypic plasticity can optimize photosynthetic energy acquisition in plants and corals (Falster and Westoby 2003, Hoogenboom et al. 2008) and might be particularly advantageous at niche boundaries (Hoogenboom et al. 2008). In our study, many species such as the dominants *Turbinaria mesenterina*, *Turbinaria frondens*, and *Goniastrea australensis*, had horizontally spreading laminar and encrusting-to-massive morphologies, a strategy that optimizes energy acquisition in light limited habitats (Hoogenboom et al. 2008). Moreover, flat growth forms close to the substratum confer physical stability in these highly wave-exposed environments. Consistent with strong filtering of morphological traits, the subtropical endemic *P. aliciae*, which was dominant at four locations in this study, has robust plate-like growth commonly displayed by deep-water morphs of pocilloporids (Schmidt-Roach et al. 2013). We hypothesize that in combination with small corallites and heterotrophic feeding, horizontally spreading morphologies may serve to maximize energy acquisition in these marginal environments.

The ability of species to adapt to marginal conditions in species-edge zones is important from an evolutionary perspective, as it may give rise to genetic innovation (Budd and Pandolfi 2010) and the evolution of species niches and ranges (Kawecki 2008). Local adaptations lead to greater abundance and persistence of peripheral populations, which can then become the source of colonists for higher latitude areas (Kawecki 2008). High coral abundance at some high-latitude locations recorded in this and other studies in Australia and elsewhere (see Table 2 in Thomson and Frisch 2010) corroborate these predictions and indicate that scleractinian corals can flourish in pockets of suitable habitat even at their range margins. The observed increase in dominance along the north to south gradient is consistent with increasing marginality of abiotic conditions for corals and fewer species thriving along this gradient of environmental severity.

Growing evidence points to a shift in life-history strategies on contemporary reefs impacted by anthropogenic and climatic stress, away from sensitive, fast-growing species (e.g., branching *Acropora* spp.) to morphologically simpler, more stress-tolerant species and to opportunistic species with good colonizing ability (Darling et al. 2012). The observed dominance of stress-tolerant and opportunistic species in our study (Appendix B) therefore also highlight the prominent role of deterministic factors in structuring high-latitude reefs.

Metacommunity considerations for peripheral populations

Metacommunity (e.g., Leibold et al. 2004) and neutral (Hubbell 2001) theories emphasize the role of dispersal in linking local communities with other local communities or external species pools. Marginal populations of some species, in particular, may rely on immigrants for their persistence when their intrinsic population growth is negative (Kawecki 2008). The occurrence of tropical coral species at southern locations in this study indicates that local communities are deriving propagules from regions to the north, and larval connections between the Great Barrier Reef and high-latitude reefs have been reported for the cosmopolitan species *Goniastrea australensis* (Miller and Ayre 2008). High-latitude corals of eastern Australia reproduce successfully, however, they tend to have less synchronous spawning patterns (Harrison 2011) and lower recruitment rates than corals in the tropics (Hughes et al. 2002). Combined with our findings of low abundance and narrow distribution of most tropical species, this points to diminished reproductive success of corals at their range margins and might suggest that high-latitude reefs are demographic sinks for tropical species outside their core habitats (Kawecki 2008).

Conclusion and outlook

Understanding how and why ecosystems at the transition of biogeographical zones vary along spatial and environmental gradients is critically important to predicting how they may respond to projected future change and for their management and conservation (Beger et al. 2011, Beger et al. accepted 2013). Our findings indicate that coral communities in marginal settings are strongly shaped by local environmental conditions and thus support ecological theory that recognizes species functional traits as key drivers of community structure (e.g., Bode et al. 2012). Our study suggests that traits linked to energy acquisition play an important role for survival of corals at their range edges. High-latitude coral communities of eastern Australia are dominated by generalist, stress-tolerant species that are seemingly well adapted to marginal environmental conditions. As generalist species have broader niches (Stevens 1989), these may be less likely to disappear because of climatic change. Nevertheless, recent coral bleaching events (Harrison et al. 2011) indicate that high-latitude corals are not immune to the impacts of climate change. Moreover, observed low taxonomic richness of many high-latitude reefs, as well as demographic characteristics of marginal populations in general (Kawecki 2008), might render them particularly vulnerable to projected future change.

Ecological responses of coral communities to changing environmental conditions are likely to be heterogeneous due to demographic differences among species (Pandolfi et al. 2011); however, we may see a general

shift in life-history strategies on tropical coral reefs away from sensitive to more stress-tolerant and opportunistic strategies, which may improve persistence in conditions of high abiotic stress (Darling et al. 2012) while reducing three-dimensional structure and recovery potential after disturbance. This supports the notion that coral communities in marginal environments may provide predictive models for potential future states of tropical coral reefs that may become marginal under climate change (Guinotte et al. 2003). Although this remains to be modeled in relation to observed and projected environmental parameters, it is plausible that additional tropical species might first establish on reefs offshore and at lower latitudes, where we observed them to be more prevalent. However, low abundances of tropical species at most high-latitude locations, fragmented habitats and likely dependence on tropical source populations further north, suggest that the capacity of high-latitude coral communities of eastern Australia to host abundant and self-sustaining populations of tropical coral species may be limited.

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SUPPLEMENTAL MATERIAL

Appendix A

The six functional traits and 19 character states used to characterize coral taxa recorded in our surveys of high-latitude coral communities of eastern Australia (*Ecological Archives* E095-084-A1).

Appendix B

The coral life-history framework by Darling et al. (2012) applied to high-latitude coral communities of eastern Australia (*Ecological Archives* E095-084-A2).

Appendix C

Zoogeography of the coral taxa recorded in surveys (*Ecological Archives* E095-084-A3).

Appendix D

Coral distribution and abundance at eastern Australian high-latitude reefs (*Ecological Archives* E095-084-A4).

Appendix E

Similarity profiles of coral species abundance distributions along a latitudinal gradient in subtropical eastern Australia (*Ecological Archives* E095-084-A5).