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Local and regional controls of phylogenetic structure at the high-latitude range limits of corals

Sommer Brigitte *[1], Eugenia M. Sampayo [1], Maria Beger [2, 3], Peter L. Harrison [4], Russ C. Babcock [5], John M. Pandolfi [1]

[1] Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, Brisbane QLD 4072 Australia

[2] Australian Research Council Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, Brisbane QLD 4072 Australia

[3] School of Biology, Faculty of Biological Sciences, University of Leeds, LS2 9JT, UK

[4] Marine Ecology Research Centre, Southern Cross University, Lismore NSW 2480 Australia

[5] CSIRO Marine and Atmospheric Research, Dutton Park QLD 4102 Australia

Key words: range limit, phylogenetic structure, niche conservatism, environmental filtering, coral, trait

Abstract

Understanding how range edge populations will respond to climate change is an urgent research priority. Here we used a phylogenetic community ecology approach to examine how ecological and evolutionary processes shape biodiversity patterns of scleractinian corals at their high-latitude range limits in eastern Australia. We estimated phylogenetic signal in seven ecologically important functional traits and conducted tests of phylogenetic structure at local and regional scales using the net relatedness (NRI) and nearest taxon indices (NTI) for presence/absence and abundance data. Regional tests showed light phylogenetic clustering, indicating that coral species found in this subtropical-to-temperate transition zone are more closely related to each other than are species on the nearby, more northerly Great Barrier Reef. Local tests revealed variable patterns of phylogenetic clustering and overdispersion and higher than expected phylogenetic turnover among sites. In combination, these results are broadly consistent with the hierarchical filtering model, whereby species pass through a regional climatic filter based on their tolerances for marginal conditions and subsequently segregate into local assemblages according to the relative strength of habitat filtering and species interactions. Conservatism of tested traits suggests that corals will likely track their niches with climate change. Nevertheless, high turnover of lineages among sites indicates that range shifts will probably vary among species and highlights the vulnerability and conservation significance of high-latitude reefs.

INTRODUCTION

Understanding local and regional controls on biodiversity is fundamental to understanding species range dynamics and how they may be affected by global change. Ecological community structure arises from a combination of processes that operate at different spatial and temporal scales. Species may occur in the same communities by occupying different niches (i.e. limiting similarity) and / or because they have specialised traits that allow them to persist locally (i.e. environmental filtering) [1]. Classical ecological theory predicts that the relative importance of these processes in driving biodiversity patterns varies systematically along stress-gradients, with abiotic factors predominant at high elevation, high latitude, and other abiotically stressful regions, and biotic interactions relatively more important in abiotically more benign regions [2, 3]. Moreover, a growing body of literature suggests that biotic and abiotic filters operate at different spatial scales, with environmental conditions often found to be the dominant process at regional scales and biotic interactions relatively more important at local scales [4, 5]. Quantifying the relative strength of these processes at multiple spatial scales is necessary to accurately predict species range shifts in response to climate change [3]. For instance, when biotic interactions are important in setting species range limits, models solely based on climatic influences could overestimate species range shifts in response to climate change [3].

Phylogenies are increasingly used to investigate ecological and evolutionary drivers of biodiversity patterns. The central idea is that patterns of phylogenetic community structure differ depending on whether environmental filtering or competition is the dominant assembly process [6]. This is based on the premise that closely related species have similar traits [i.e. trait conservatism; 7] and consequently require similar environmental conditions and resources to persist. Close relatives therefore compete more intensely for the same resources, which is thought to limit coexistence and to drive trait and niche difference [2]. Environmental filtering, on the other hand, can prevent species with unsuitable traits from occurring locally. Under classical ecological theory, competition is therefore generally expected to limit the similarity of co-occurring species, leading to phylogenetic overdispersion, while environmental filtering is thought to drive the co-occurrence of closely related species, leading to phylogenetic clustering [6]. For example, seminal work by Cavender-Bares et al. [8] found that co-occurring oak trees in Florida were phylogenetically overdispersed, suggesting that competition restricts close relatives from inhabiting the same areas. Recent advances in coexistence theory challenge the universality of this pattern, highlighting that competition can also lead to the co-occurrence of similar species, if the traits in question are associated with competitive dominance [9].

Gradients in phylogenetic alpha and beta diversity and tests for phylogenetic structure have been used to infer the dominant assembly processes operating in local and regional assemblages [6]. This work indicates that biotic and abiotic filters often operate at different spatial scales, such that local assemblages are embedded in regional assemblages and species sequentially pass through historical, abiotic and biotic filters [4, 10]. For example, regional climate might initially filter species with certain traits (e.g. cold tolerance) into large patches of homogeneous habitat (e.g. alpine mountains) that are further partitioned at finer scales (e.g. soil type). Species then segregate into local assemblages based on the relative strength of habitat filtering versus competition [4, 6]. These processes can be detected by spatially nesting analyses [6] and by combining metrics of phylogenetic alpha and beta diversity [4]. For example, environmental filtering at local scales combined with high turnover of habitat types in the region is expected to manifest in local phylogenetic clustering and high phylogenetic beta diversity among sites [4].

While studies of phylogenetic community ecology are well established in terrestrial ecosystems, this approach is underrepresented in marine ecosystems [reviewed in 11, but see 12, 13]. Due to their ecological diversity, eco-morphological plasticity and habitat sensitivity, scleractinian corals are especially suited to examining the role of evolutionary history in shaping extant communities. In eastern Australia, diverse coral assemblages extend into high latitudes (32°48’S) south of the Great Barrier Reef [14-16], where various coral species occur at the edges of their ranges and experience cooler, darker and more seasonal and variable conditions than their tropical counterparts [17]. These high-latitude reefs represent ideal systems in which to investigate how evolutionary stability of species traits and phylogenetic relatedness may influence biodiversity patterns in marginal and changing environments. A recent study found that these range-edge coral assemblages are shaped by trait-mediated environmental filtering, with similar species co-occurring in the region [15] along strong environmental gradients [17]. As phylogenetic relatedness does not predict species’ ecological similarity per se [18], investigating the evolutionary stability of ecological traits in these physiologically challenging environments is a critical next step in predicting species responses to climate change. For instance, if species’ climatic tolerances are stable over time (i.e. conserved), they will probably only expand their ranges to environments that are similar to their core ranges, and be constrained in their evolutionary responses to novel environmental conditions [7].

In this study, we take a hierarchical approach (Fig. 1) to disentangle the relative importance of regional to local processes in generating biodiversity patterns of corals in the subtropical-to-temperate transition zone (26°36’S to 32°48’S) along the eastern Australian coast. To investigate evolutionary stability of species traits, we initially estimate phylogenetic signal in ecologically important functional traits. Under niche conservatism we expect closely related species to be more similar in their functional traits than distantly related species, implying that there has been limited evolutionary change since species have diverged from a common ancestor [7]. We subsequently combine analyses of phylogenetic alpha and beta diversity and of phylogenetic structure at multiple spatial scales to evaluate how evolutionary and ecological processes shape the distribution of corals in this biogeographic transition zone (Fig.1). To examine the shared history of high-latitude coral assemblages with the Great Barrier Reef (GBR; situated to the north of the study region), we test whether species found on eastern Australian high-latitude reefs are a random subset of the GBR species pool in terms of their phylogenetic relatedness (Fig. 1A, B). Consistent with stronger influence of environmental filtering at the high-latitude margins of species ranges [19], we expect that the species within the high-latitude species pool are more closely related to one another than are the species within the Great Barrier Reef species pool. We then perform site-level tests of phylogenetic structure to investigate whether local assemblages are phylogenetically clustered or overdispersed (Fig. 1C) and whether patterns vary with latitude. Due to increasingly marginal environmental conditions for corals towards higher latitudes, we expect coral species to be more closely related to each other at higher latitude sites and high turnover of lineages (i.e. high phylogenetic beta diversity; Fig. 1C) among sites in this biogeographic transition zone.

MATERIALS AND METHODS

Ecological data

Coral species abundances

We determined species abundance distributions of scleractinian corals at 17 locations (Supplementary Fig. S1) along a latitudinal gradient (26°36’S to 32°48’S) in the subtropical-to-temperate transition zone in coastal eastern Australia [15]. We quantified percent cover of 85 coral species from photographic belt transects using the random point count method [600 points per transect, total of 51,000 points; see 15].

Coral functional traits and phylogeny

To examine functional strategies of corals, we characterised each species based on seven traits known to influence the ecology of corals [20]. We included the three structural traits colony morphology, corallite formation, and corallite size, as they undergo strong environmental filtering at high-latitudes [15], as well as reproductive mode, sexual pattern, larval development rate and symbiont transmission mode to characterise reproductive strategies [21-23]. Following Keith et al. [24] egg size was used as a proxy for larval development rate, because small eggs develop more rapidly [25]. The character states of all categorical traits were expressed as separate binary traits, where '1' indicates that the species displays the trait and '0' that it does not. For example, reproductive mode was classified as two separate binary traits: brooding and spawning (see supplementary material for more information on traits). Due to the known variation with latitude in other traits [e.g. growth rate; 26], and our inability to quantify this variation due to data deficiency, we did not include more traits in our analyses. We used the coral 'supertree' of Huang and Roy [13] to construct phylogenies of the 85 coral species recorded in our surveys and of the 412 species from the GBR species pool obtained from the Atlas of Living Australia [27].

Statistical analyses

Tests for phylogenetic signal in traits

We tested for phylogenetic signal in traits using the D statistic [28] for binary traits (i.e. colony morphology, corallite formation, reproductive mode, sexual pattern and symbiont transmission), and Pagel's λ [29] for the traits corallite size and larval development rate. Lower D values indicate stronger phylogenetic signal (i.e. more conserved trait evolution), whereby a value of 0 equates to a Brownian model (i.e. conserved trait evolution) and a value of 1 to random phylogenetic structure (i.e. no signal). Negative D values indicate that traits are extremely clumped (i.e. more conserved than under Brownian motion) and D values greater than 1 indicate phylogenetic overdispersion [28]. Conversely, higher values of Pagel's λ indicate stronger phylogenetic signal, where λ equal to zero means no phylogenetic signal and λ equal to 1 indicates trait evolution consistent with Brownian motion. P values indicate departure from random phylogenetic structure and from Brownian structure (i.e. non-significant P values for Brownian motion indicate conserved trait evolution).

Patterns in phylogenetic diversity and tests for phylogenetic structure

We quantified phylogenetic diversity patterns of corals using two metrics that are sensitive to patterns at different depths of the phylogeny and identify processes operating at different evolutionary time-scales [6], mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). MPD represents the average phylogenetic distance between all species in an assemblage and is sensitive to tree-wide (i.e. more ancestral) patterns. MNTD represents the average distance between each species and its closest relative and is thus sensitive to patterns at the tips of the phylogeny (i.e. more recent events). In comparative analyses, MPD and MNTD values can be affected by differences in species richness among sites. At our study sites, coral species richness ranged between 52 and 2 species; we therefore standardised the observed MPD and MNTD values with respect to expected values calculated under a null model that controls for coincidental gradients in species richness. More specifically, we calculated the net relatedness index (NRI) and the nearest taxon index (NTI) to test whether species in local assemblages were phylogenetically clustered or overdispersed i.e. relatively more closely or distantly related than randomly expected, respectively [6, 30]. We compared the observed MPD and MNTD values to null distributions generated by shuffling the species names across the tips of the phylogeny (1000 times). This null model randomises the relatedness of species to one another, but leaves the abundance distributions and species richness of local assemblages unchanged. In addition to these site level tests, we also conducted a regional test to determine whether coral species found in the subtropical-to-temperate transition zone (i.e. all species that we recorded at the 17 study sites; Fig. 1B) are more closely or distantly related than the species in the GBR phylogeny (Fig. 1A). For both local and regional tests, positive NRI/NTI values indicate phylogenetic clustering while negative values indicate phylogenetic overdispersion [30] (Fig. 1C). We performed nonparametric multidimensional scaling ordination to visualise the relationships among patterns in phylogenetic structure, community-weighted trait means, and coral community structure at the study sites.

Phylogenetic beta diversity was calculated in a way analogous to the NRI and NTI metrics, by comparing the observed phylogenetic beta diversities to the patterns expected under a null model that randomly shuffles the species names across the GBR phylogeny. Positive values of beta_NRI and beta_NTI indicate higher than randomly expected phylogenetic turnover of species in pairs of local assemblages; negative values indicate lower than expected phylogenetic turnover. As the coral supertree contains a number of polytomies, we conducted all analyses for 1000 fully resolved trees [13] and report results as the means over the 1000 trees. We calculated all metrics using both presence/absence and abundance data, with respective results identified by the letters 'pa' and 'ab' (e.g. beta_NRIpa, beta_NRIab). When used with abundance data the interpretation of metrics changes from phylogenetic distances among taxa to distances among individuals. We used generalised additive models to evaluate the relationships between phylogenetic alpha diversity metrics and latitude. We selected smoothness using restricted maximum likelihood and specified smoothness with up to three effective degrees of freedom. We used Procrustes analysis to test the association of phylogenetic beta diversity patterns and geographic distance (in degrees latitude) and visualised site-level beta diversities using boxplots. All analyses were conducted using the packages 'picante' [31], 'caper' [32], 'vegan' [33], and 'mgcv' [34] in R [35].

RESULTS

Tests for phylogenetic signal in traits

We found a phylogenetic signal for all tested functional traits, as their phylogenetic structures were significantly different from random and not significantly different from Brownian motion (Table 1). Indeed, six of the binary traits (sexual pattern, symbiont transmission, laminar growth, meandroid corallites, encrusting-to-massive and branching-to-tabular growth) had negative D values, indicating that they were more phylogenetically conserved than under a Brownian model [28]. Arborescent growth had the weakest signal and showed modest clumping (Table 1).

Patterns in phylogenetic diversity and tests for phylogenetic structure

Overall, the regional test for phylogenetic structure indicates that the coral species present on high-latitude reefs (the high-latitude species pool) are more closely related to one another than are the species in the GBR species pool. Phylogenetic structure for NRI (NRI = 0.842) and NTI (NTI = 1.289; Table S1 in supplementary material) was related to a clustering pattern, although values calculated for 1000 phylogenetic trees were only significantly clustered for approximately 25% of trees (third quartile: NRI = 1.193, NTI = 1.516). Site level tests of phylogenetic structure revealed contrasting patterns for NRI and NTI, except for northern- and southernmost sites where both metrics were positive (Fig. 2). Phylogenetic structure for most sites was clustered at the tips of the phylogeny (NTI > 0) and overdispersed or close to random when measured at deep levels in the phylogeny (NRI < 0), with NRI and NTI metrics generally showing both low positive and negative values. NRIpa showed a concave relationship with latitude (R^2 = 0.549, deviance explained = 60.5, p = 0.002), but NRIab (R^2 = 0.162, DE = 25.5, p = 0.192), NTIpa (R^2 = 0.006, DE = 6.12, p = 0.356), and NTIab (R^2 = 0.028, DE = 9.240, p = 0.252) were independent of latitude (Fig. 2).

Assemblages that showed basal and terminal clustering (red circles in Fig. 3) were characterised by species with branching-to-tabular morphology, large corallites, fast development rates, hermaphroditic sexual pattern, brooding reproduction, and vertical symbiont transmission (e.g. Pocillopora, Stylophora, Acanthastrea). This pattern was seen across sites except at Black Rock, which had high abundance of laminar species that were gonochoric broadcast spawners and transmit their symbionts horizontally (e.g. Turbinaria spp.). Assemblages that showed contrasting patterns for NRI and NTI (green diamonds and blue triangles in Fig. 3) generally showed large variation in species traits, except for Flinders Reef (orange square in Fig. 3), which associated strongly with arborescent morphology, spawning reproduction and horizontal symbiont transmission (e.g. *Acropora* spp.). Note that vectors represent associations of community-weighted trait means with the nMDS axes and that individual species don't necessarily possess the trait combinations listed above.

Analyses of phylogenetic betadiversity showed that most sites showed higher than expected phylogenetic turnover at both basal and terminal levels (beta_NRI and beta_NTI > 0), and that this pattern was stronger when abundance information was used (Fig. 4). With the exception of beta_NRIpa (Procrustes correlation t = 0.48; p = 0.015), phylogenetic turnover patterns were independent of geographic distance (Fig. 4). Indeed, some geographically close site pairs (within 0-3 degrees latitude of each other) had high terminal phylogenetic beta diversity (beta_NTIab), indicating high turnover of abundant species from site to site (Fig. 4). Beta_NRIpa and beta_NTIpa were positively correlated with each other (Procrustes correlation t = 0.67, p = 0.001), indicating that site pairs with high basal turnover tended to also have high terminal turnover (beta_NTI > 0). This relationship was not significant (t = 0.21, p = 0.929) when species abundances were considered.

DISCUSSION

Phylogenetic niche conservatism of corals

Understanding species range dynamics and how they may be affected by global change requires the consideration of multiple ecological and evolutionary processes [36]. Our results suggest that coral species attenuate at higher latitudes in response to habitat filtering that is mediated by conserved ecological niches. Niche conservatism has been invoked to explain large-scale biogeographic gradients, such as the latitudinal diversity gradient [reviewed in 7]. This is based on the premise that many groups originated in the tropics and are limited from colonising temperate regions by niche conservatism (such as lack of adaptations to survive cold winter temperatures). Conversely, recent studies have found multimodality of latitudinal gradients in species distributions and thermal affinities of marine species [e.g. 37] and linked these patterns to adaptations of ‘bridge species’ at the edges of the tropics and subsequent colonisation of temperate regions [i.e. the out of the tropics hypothesis'; 38]. While rigorous tests of these hypotheses require data for entire species ranges, our results indicate trait conservatism for corals at their high-latitude range limits and we find phylogenetic diversity patterns that are consistent with species sorting in these marginal environments. These findings are consistent with a recent study of habitat affinities of marine invertebrates over geological time - niche conservatism was common in the oceans, but variable among clades, with coral and sponges among the most conservative [39].

We found a phylogenetic signal in all tested species traits (Table 1). Larval development rate, corallite size, sexual patterns and symbiont transmission showed the strongest conservatism among the tested traits. Indeed, six of the binary traits (sexual pattern, symbiont transmission, laminar growth, meandroid corallites, encrusting-to-massive and branching-to-tabular growth) were more phylogenetically conserved than under a Brownian model [28]. Structural traits such as corallite size and colony morphology undergo strong filtering in this region, whereby coral species with similar trait expressions frequently co-occur at the same sites [15]. Corallite size has been linked with energy storage and reproductive investment [40], and colony shape with light interception [41] and it is plausible that these traits enhance energy acquisition [15] in these colder and light-limited environments [17]. This is also consistent with the observation that corals on high-latitude reefs in Australia and Japan share traits relevant to environmental tolerance [42].

Faster larval development rates and larger depth ranges were recently found to increase the likelihood that coral species traverse faunal breaks [24]. Indeed, in our study species with relatively fast development rates, including Paragoniastrea australensis, Turbinaria spp., Acanthastrea spp. and Pocillopora spp., were abundant and widely distributed across the high latitude study region [15]. Larval developmental time has important ecological implications for marine organisms because it affects dispersal distance and connectivity [22, 25]. For instance, high relative abundance of brooding corals, whose larvae are ready to settle upon release [25], is thought to be important for population establishment and persistence on Lord Howe Island, the world's southernmost coral reef [43, 44]. In our study, the strong association of brooding reproduction and fast development rates with coral assemblages that were phylogenetically clustered (red circles in Fig. 3) also support the hypothesis that the capacity to derive new recruits from local populations is important in these marginal habitats [43].

Phylogenetic community ecology of high-latitude coral assemblages

Overall, regional tests revealed phylogenetic clustering of coral assemblages, indicating that coral species on high-latitude reefs are on average more closely related with one another than are species in the GBR species pool. While this is generally consistent with regional filtering, NRI and NTI values only showed significant clustering for approximately 25% of the 1000 phylogenetic trees. Site level results (Fig. 2) support the role of local filtering, indicating that patterns of phylogenetic clustering and overdispersion vary among sites and at ancestral and more recent temporal scales. This is consistent with other studies that found closely related or functionally similar species co-occurring at larger spatial scales and more distantly related or dissimilar species co-occurring locally. For example, local tree frog assemblages in the Americas were generally overdispersed, while regional assemblages were frequently clustered in their body sizes [10]. Moreover, the authors found that regional processes tend to be stronger in temperate than in tropical zones, such that antagonistic regional and local filtering can substantially mask variation in trait dispersion [10].

We found that most assemblages contained species that were distributed randomly or slightly overdispersed with respect to the entire tree (NRI < 0), but were clustered towards the tips of the tree (NTI > 0). Thus, although local assemblages support numerous lineages that are widely spread across the entire phylogeny, they harbour many close relatives within those lineages. Such evenness in tree-wide phylogenetic structure (NRI) of local assemblages indicates that a diverse range of lineages has been able to disperse to and establish on many high-latitude reefs, including many species in the Acroporidae family that are the predominant reef builders on tropical coral reefs [45]. Nevertheless, the presence of close relatives within those lineages indicates the co-occurrence of species with similar traits and tolerances for marginal conditions. Branch tips represent more recent divergences, where new species have formed. Species that are closely related at the tips of the phylogeny are therefore generally expected to occupy more similar niches and to have similar resource needs when species traits are conserved [6]. The traits branching-to-tabular morphology, large corallite sizes, hermaphroditic sexual pattern, brooding reproductive mode, fast development rates, and vertical symbiont transmission were most strongly associated with phylogenetically clustered assemblages (red circles in Fig. 3) that included Pocillopora, Stylophora, Acanthastrea and Micromussa species. Moreover, gonochoric sexual pattern, broadcast spawning reproduction, horizontal symbiont transmission and laminar growth also appear to be advantageous at sites that were phylogenetically clustered (green diamonds in Fig. 3). In particular, these sites had high abundance of several Turbinaria species that tend to do well in marginal environments [15, 46].

Contrary to our expectation, species at higher latitudes were not phylogenetically more related to each other than those at lower latitudes. NRIpa even showed a convex relationship with latitude, indicating that phylogenetic clustering was strongest at opposite ends of the study region (Fig. 2). Indeed, Mudjimba Island, the northernmost site in our study, contained species that were phylogenetically clustered at deep and shallow levels of the phylogeny. In particular, Mudjimba comprised many lineages from the robust clade (e.g. genera Acanthastrea, Paragoniastrea,

Goniastrea, Dipsastrea, Favites, Pocillopora and Stylophora) and contained several species within most genera. Moreover, several abundant species (e.g. Acanthastrea) were clustered in those lineages, leading to higher NRIab than NRIpa values (Fig. 2). Our study was restricted to subtropical and temperate latitudes and future work that examines these patterns across the entire tropical-to-temperate gradient is needed to assess the importance of climatic niche conservatism in shaping phylogenetic structure of coral assemblages throughout core and marginal species ranges.

Species interactions and tolerances for local environmental conditions both influence species abundances. Abundance information can therefore considerably improve inferences from community phylogenetic studies and improve the power to detect limiting-similarity competition [47]. In our study, phylogenetic structure for several sites (i.e. Flinders Reef, Flat Rock and Cook Island) changed from clustered to overdispersed when abundance information was used in the analysis, highlighting the influence of biotic interactions at these sites and the importance of using abundance data. For example, Flinders Reef, the most speciose of our survey sites, had the highest occurrence of species from the Acroporidae family of all sites, leading to phylogenetic clustering for both NRI and NTI when presence/absence data were used. However, high dominance of the arborescent species Acropora intermedia, which occupied a large patch of the reef in a mono-specific stand (site F and photo in Fig. 3), resulted in weak overdispersion at the tips of the tree when species abundances were considered (NTIab < 0), pointing to the influence of biotic interactions. This example highlights that abundance-weighted metrics more accurately reflect assembly processes, particularly where there is high dominance of particular species with unusual traits (arborescent growth was absent or rare at other sites; Fig. 3).

Phylogenetic beta diversity measures the phylogenetic distance among local assemblages and allows us to connect local and regional processes [48]. Our phylogenetic betadiversity analyses show that most site pairs had higher than expected phylogenetic turnover at both basal and terminal levels (Fig. 4). These patterns were stronger when species abundances were considered, consistent with species present at many sites but only abundant at certain sites [48]. Site pairs with high basal turnover (beta_NRIpa) generally also had high terminal turnover (beta_NTIpa), but this relationship was not significant for abundance-weighted data. Except for beta_NRIpa, which was greater for geographically distant sites, we found no relationship between patterns in phylogenetic turnover and geographic distance. Indeed, beta_NTIab was particularly high among site pairs that were geographically close (within 0-3 degrees latitude or 0-300 km of each other), indicating high turnover of abundant species among these sites (Fig. 4 e and f). In particular, site pairs in the Solitary Islands region (30° southern latitude; Fig. S1 in supplementary material) were phylogenetically most dissimilar from each other at the branch tips (Fig. 4f), even though closely related species co-occurred locally (Fig. 2). These patterns of local phylogenetic clustering (Fig. 2) and higher than randomly expected phylogenetic turnover (Fig. 4f) are consistent with high spatial and temporal variability in environmental conditions and biological communities in this region, where assemblages range from kelp- to coral-dominated [14, 16, 17].

Conclusions and caveats

In combination, patterns in phylogenetic alpha and beta diversity are broadly consistent with the hierarchical filtering model of community assembly operating on high-latitude reefs (Fig. 1); that is regional filtering of the high-latitude species pool relative to the GBR species pool (Fig. 1A-B), segregation of species into local assemblages depending on the relative strength of biotic and abiotic processes, and high phylogenetic turnover in this biogeographic transition zone (Fig. 1C). Recent advances in coexistence theory suggest that patterns of phylogenetic clustering in observational data alone can be insufficient to clearly establish the role of environmental filtering [9, 49, 50]. While experiments are therefore needed to tease apart the relative strength of niche and competitive fitness differences among coral species, our results are consistent with findings that environmental tolerance is important in structuring high-latitude coral assemblages [15, 17, 42, 43]. More specifically, we hypothesise that the colder, light limited and more variable environmental conditions that govern coral biodiversity patterns in this region [17] impose abiotic filters at the high-latitude range limits for corals. Nevertheless, our local scale analyses revealed the signature of competitive processes at some sites, particularly for abundance-weighted data, highlighting the importance of using abundance data when investigating assembly processes. Conservatism of tested traits suggests that coral distributions will likely shift with climate change. While this is consistent with recent observations of coral range expansion on high-latitude reefs in Japan [51] and Australia [52], the higher than expected phylogenetic beta diversity between most site pairs recorded in this study and species-specific relationships with environmental parameters [17, 53], suggest that coral range shifts will likely vary among species. High phylogenetic turnover among sites highlights the vulnerability and conservation significance of high-latitude reefs [14] and the need to protect a substantial proportion of reefs to preserve the breadth of phylogenetic diversity in the region.

Ethics: Methods were approved under the University of Queensland ethics guidelines (193/10).

Data accessibility: Supporting data are freely available as electronic supplementary material.

Authors' contributions: BS, ES, MB and JMP designed the study; BS and MB collected the field data; BS identified corals, performed data analysis and led the writing; all authors contributed to writing the manuscript.

Competing interests: We declare we have no competing interests.

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Table 1. Phylogenetic signal in ecological traits of corals in the subtropical-to-temperate transition zone in eastern Australia using Pagel's λ or D as the test statistic. P (random) and P (Brownian) indicate significance levels of departure from random and from Brownian phylogenetic structure, respectively ($P < 0.05$). Not significant departure from Brownian structure indicates conserved trait evolution.

Trait	**Test statistic**	**P (random)**	**P (Brownian)**
Larval development rate	$\lambda = 0.997$	< 0.001	n.s.
Corallite size	$\lambda = 0.980$	< 0.001	n.s.
Sexual pattern (hermaphroditic / gonochoric)	$D = -0.522$	< 0.001	n.s.
Symbiont transmission	$D = -0.513$	< 0.001	n.s.
Laminar morphology	$D = -0.340$	< 0.001	n.s.
Meandroid corallite formation	$D = -0.128$	< 0.001	n.s.
Encrusting-to-massive morphology	$D = -0.160$	< 0.001	n.s.
Branching-to-tabular morphology	$D = -0.093$	< 0.001	n.s.
Reproductive mode (brood / spawn)	$D = 0.009$	< 0.001	n.s.
Cerioid corallite formation	$D = 0.033$	< 0.001	n.s.
Plocoid corallite formation	$D = 0.058$	< 0.001	n.s.
Tabular morphology	$D = 0.146$	< 0.001	n.s.
Arborescent morphology	$D = 0.554$	0.04	n.s.

Figure captions:

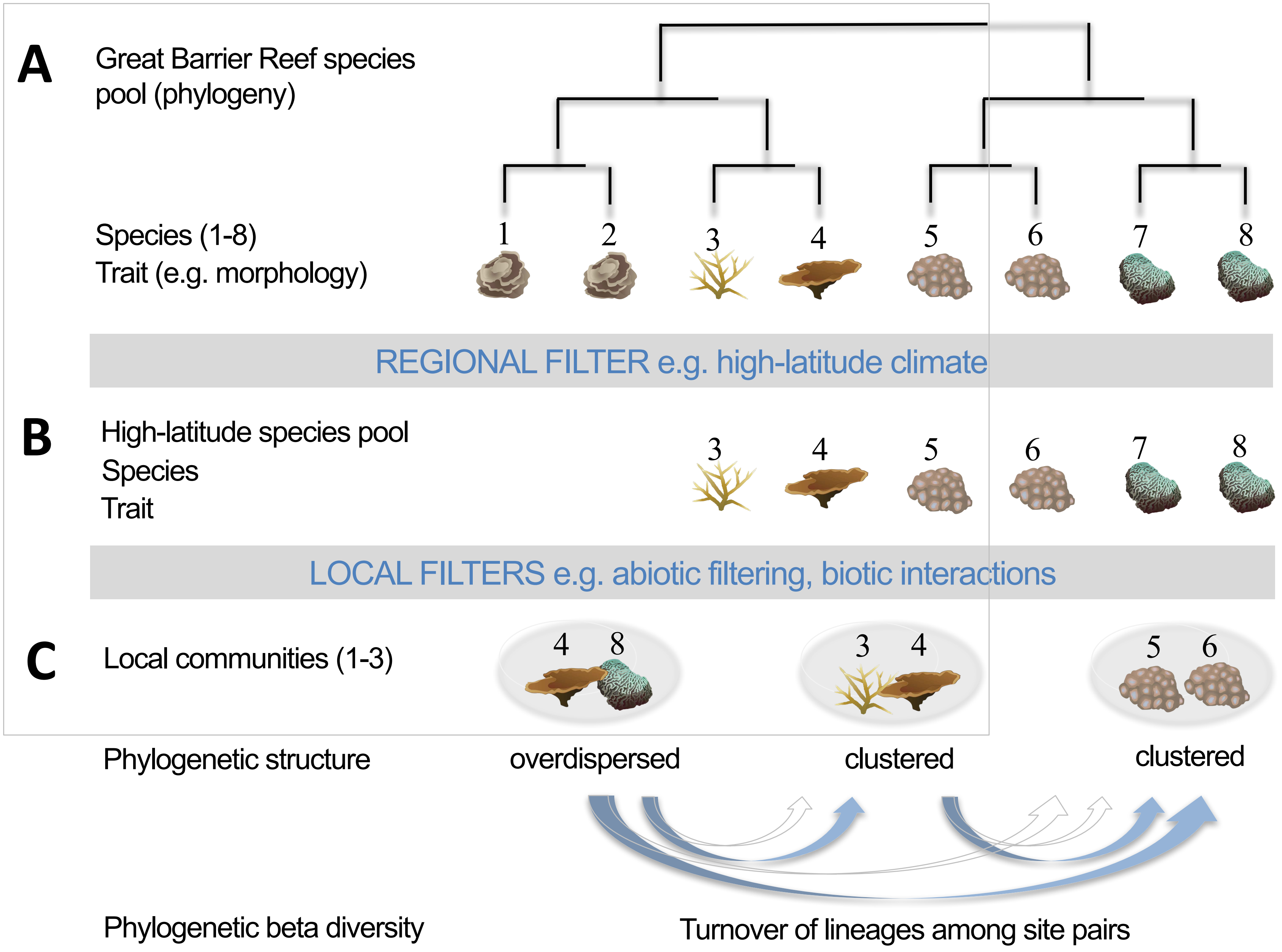
Figure 1. Conceptual representation of the hierarchical filtering assembly model tested for high-latitude reefs of eastern Australia. Coral species from the Great Barrier Reef species pool (A) pass through a regional filter e.g. based on species tolerances for marginal reef conditions (i.e. regional high-latitude species pool) (B), and subsequently segregate into local assemblages according to local biotic and/or abiotic filters that lead to clustered (more closely related) or overdispersed (more distantly related than expected) phylogenetic structure (C). There is substantial turnover of lineages from site to site (phylogenetic beta diversity) due to environmental gradients in the region (C).

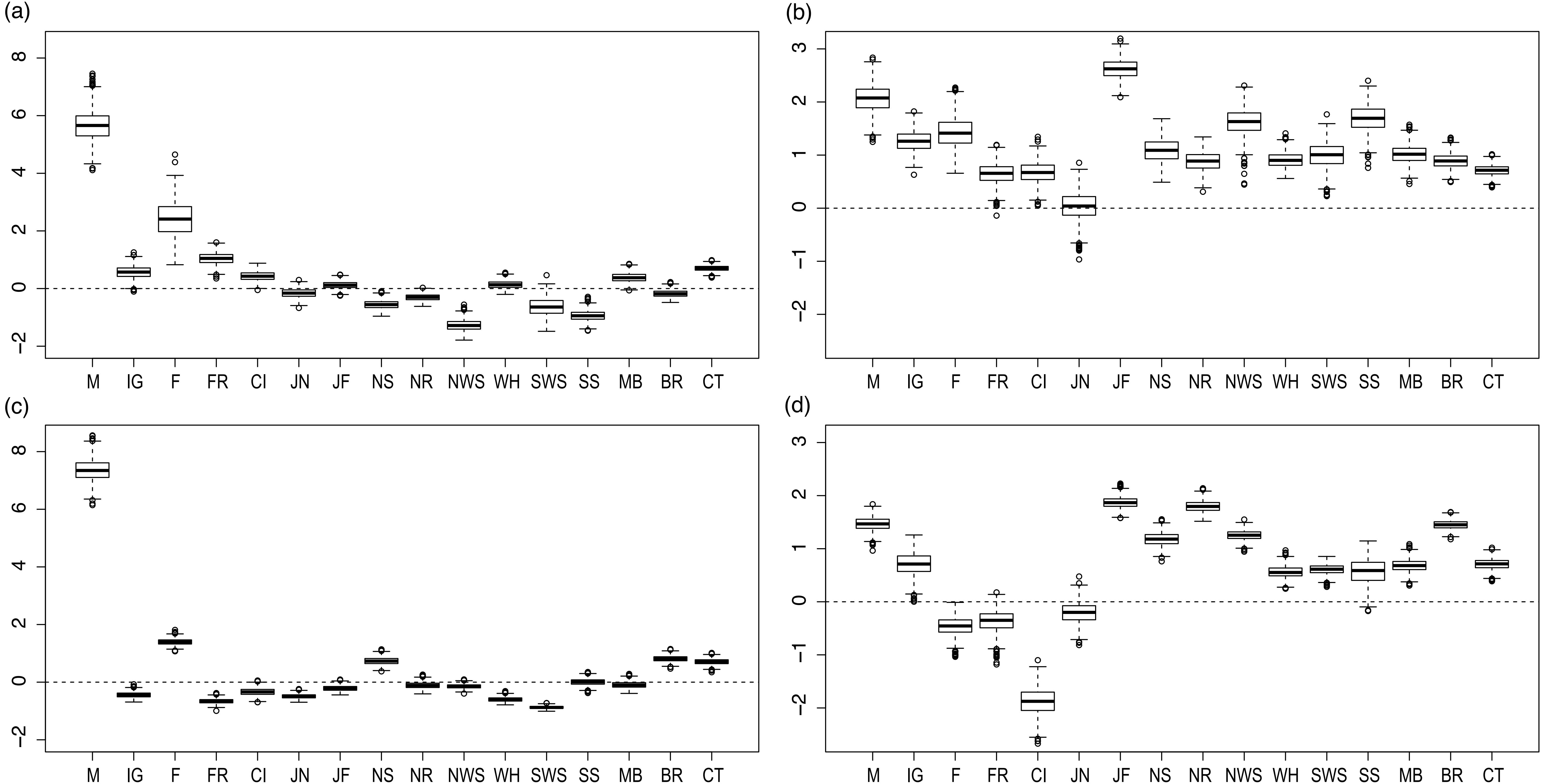
Figure 2. Local tests for phylogenetic structure of coral assemblages arrayed along the subtropical-to-temperate transition in eastern Australia, showing net relatedness index (NRI, a and c) and nearest related taxon index (NTI, b and d) values using presence/absence (a and b) and abundance data (c and d). Positive values indicate phylogenetic clustering and negative values reflect phylogenetic overdispersion. Abbreviations for site names, with latitude increasing left to right: M = Mudjimba; IG = Inner Gneerings; F = Flinders; FR = Flat Rock; CI = Cook Island; JN = Julian Rocks Nursery; JF = Julian Rocks False Trench; NS = North Solitary Island; NR = North Rock; NWS = North West Solitary Island; WH = Woolgoolga; SWS = South West Solitary Island; SS = South Solitary Island; MB = Muttonbird Island; BR = Black Rock; CT = Cabbage Tree Island.

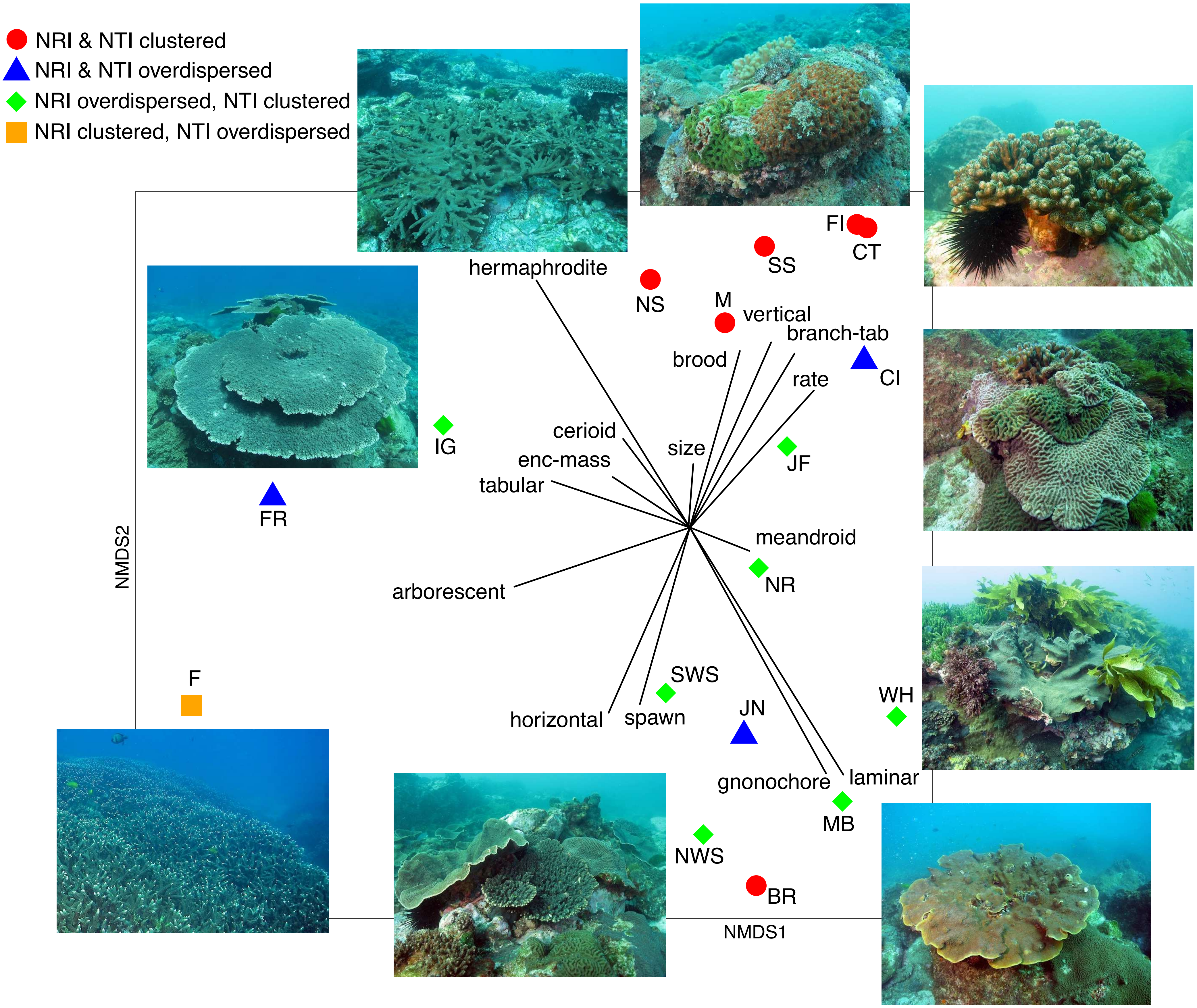
Figure 3. Non-parametric multidimensional scaling ordination of phylogenetic diversity patterns of corals on high-latitude reefs in eastern Australia. The ordination is based on the abundance-weighted net relatedness index (NRIab) and symbols represent patterns in phylogenetic structure at the study sites as indicated in the legend; see Fig. 2 for abbreviations of site names. Vectors identify traits that primarily discriminate assemblages: enc-mass = encrusting-to-massive morphology; branch-tab = branching-to-tabular morphology; rate = larval development rate; size = corallite size.

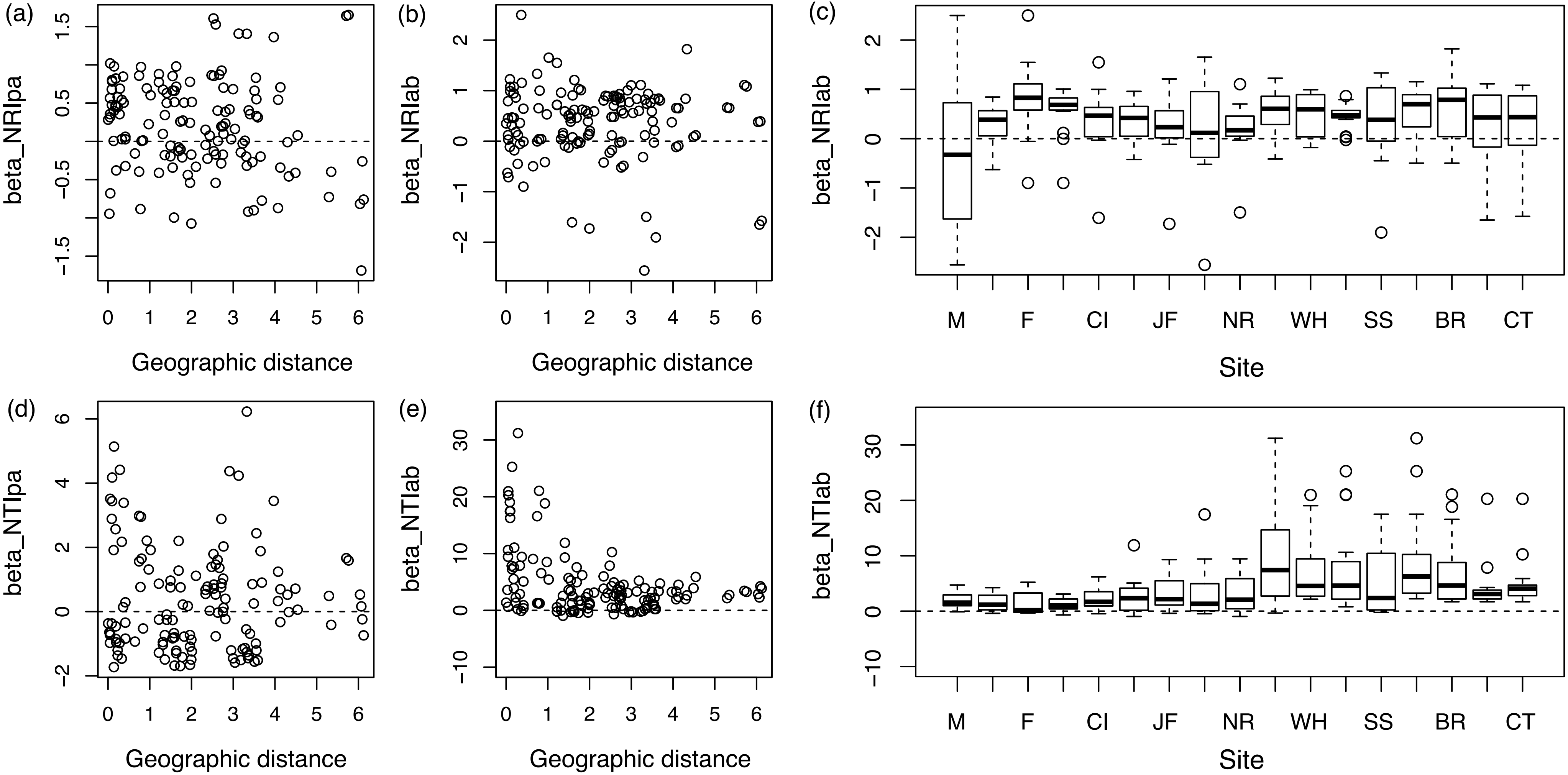
Photos portray assemblage types at the study sites. All photos by B. Sommer.

Figure 4. Phylogenetic betadiversity patterns of corals in the subtropical-to-temperate transition zone in eastern Australia. Standardised effect sizes for beta_NRI (a-c) and beta_NTI (d-f) using presence/absence (a, d) and abundance (b-c, e-f) data; pairwise turnover values plotted versus geographic distance (in degrees latitude; a-b, d-e) and boxplots for site level turnover patterns (c, f). The dashed line represents the expectation under a null model of random shuffling of taxa across the tips of the phylogeny. Positive values indicate higher than expected turnover of species in pairs of local assemblages, negative values indicate lower turnover than expected. See Fig. 2 for abbreviations of site names.


A
Great Barrier Reef species pool (phylogeny)
Species (1-8)
Trait (e.g. morphology)
1
2
3
4
5
6
7
8
REGIONAL FILTER e.g. high-latitude climate
B
High-latitude species pool
Species
Trait
3
4
5
6
7
8
LOCAL FILTERS e.g. abiotic filtering, biotic interactions
C
Local communities (1-3)
4
8
3
4
5
6
Phylogenetic structure
overdispersed
clustered
clustered
Phylogenetic beta diversity
Turnover of lineages among site pairs


(a)
(b)
(c)
(d)
8
6
4
2
0
−2
3
2
1
0
−1
−2
M
IG
F
FR
CI
JN
JF
NS
NR
NWS
WH
SWS
SS
MB
BR
CT


● NRI & NTI clustered
▲ NRI & NTI overdispersed
◆ NRI overdispersed, NTI clustered
■ NRI clustered, NTI overdispersed
FI
CT
SS
NS
M
hermaphrodite
vertical
branch-tab
brood
rate
CI
IG
cerioid
enc-mass
tabular
size
JF
FR
meandroid
NR
arborescent
NMDS2
F
SWS
horizontal
spawn
JN
WH
gnonochore
laminar
MB
NWS
BR
NMDS1



(a)
beta_NRIpa
1.5
0.5
−0.5
−1.5
0 1 2 3 4 5 6
Geographic distance
(b)
beta_NRIab
2
1
0
−1
−2
0 1 2 3 4 5 6
Geographic distance
(c)
beta_NRIab
2
1
0
−1
−2
M F CI JF NR WH SS BR CT
Site
(d)
beta_NTIpa
6
4
2
0
−2
0 1 2 3 4 5 6
Geographic distance
(e)
beta_NTIab
30
20
10
0
−10
0 1 2 3 4 5 6
Geographic distance
(f)
beta_NTIab
30
20
10
0
−10
M F CI JF NR WH SS BR CT
Site