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Differential response to abiotic stress controls species distributions at biogeographic transition zones

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Abstract

Understanding range limits is critical to predicting species responses to climate change. Subtropical environments, where many species overlap at their range margins, are cooler, more light-limited and variable than tropical environments. It is thus likely that species respond variably to these multi-stressor regimes and that factors other than mean climatic conditions drive biodiversity patterns. Here, we tested these hypotheses for scleractinian corals at their high-latitude range limits in eastern Australia and investigated the role of mean climatic conditions and of parameters linked to abiotic stress in explaining the distribution and abundance of different groups of species. We found that environmental drivers varied among taxa and were predominantly linked to abiotic stress. The distribution and abundance of tropical species and gradients in species richness (alpha diversity) and turnover (beta diversity) were best explained by light limitation, whereas minimum temperatures and temperature fluctuations best explained gradients in subtropical species, species nestedness and functional diversity. Variation in community structure (considering species composition and abundance) was most closely linked to the combined thermal and light regime. Our study demonstrates the role of abiotic stress in controlling the distribution of species towards their high-latitude range limits and suggests that, at biogeographic transition zones, robust predictions of the impacts of climate change require approaches that account for various aspects of physiological stress and for species abundances and characteristics. These findings support the hypothesis that abiotic stress controls high-latitude range limits and caution that projections solely based on mean temperature could underestimate species' vulnerabilities to climate change.

INTRODUCTION

Species range shifts are increasingly observed at biogeographic transition zones as the imprint of global environmental change on natural systems intensifies worldwide (Poloczanska et al. 2013). It is thus important to understand the environmental determinants of species distributions. Gradients in available energy have been invoked to explain many macroecological patterns including the latitudinal diversity gradient (Willig et al. 2003). Energy is experienced by organisms in many forms, including radiation, thermal and chemical energy (reviewed by Clarke and Gaston 2006), and energy hypotheses propose that species distributions are affected not only by mean conditions, but also by the extremes of energy regimes and their variability (Willig et al. 2003). As many environmental parameters co-vary with latitude, a central tenet of species-energy hypotheses is that environments at high latitudes are less favourable than those at low latitudes and, depending on the physiological tolerances of species, this affects their ecological performance and limits diversity at higher latitudes (Willig et al. 2003). For example, light is an important resource for photosynthetic organisms and varies with latitude due to the shallower solar angle and greater light scattering at higher latitudes (Clarke and Gaston 2006). Temperature governs the physiology and biogeography of many organisms and also declines with increasing latitude. Warmer environments are considered easier places to live in than colder ones and to support a greater diversity of species (Clarke and Gaston 2006). Moreover, regions with low fluctuations and narrow ranges of environmental conditions are thought to allow more specialisation and smaller ecological niches, and therefore greater diversity (Pianka 1966). Nonetheless, we know little about how greater seasonality and more variable environmental conditions at higher latitudes will affect the capacity of tropical species to expand their ranges poleward.

Many studies have highlighted the central role of temperature in influencing species ranges, with marine species, in particular, closely tracking thermal conditions (Poloczanska et al. 2013, Sunday et al. 2012, Tittensor et al. 2010). It is of note, however, that in a meta-analysis of the responses of marine organisms to climate change (96% of records based on temperature), changes in the distribution, phenology, community composition, abundance, demography and calcification at subtropical latitudes were least consistent with climate change predictions (see Fig. 4b in Poloczanska et al. 2013). This might indicate that factors other than temperature are important in explaining climate change responses of taxa in biogeographic transition zones, or that responses are species-specific.

Indeed, terrestrial studies have shown that the form and relative strength of species-energy relationships vary with the energy metric used and with the ecological characteristics of the species tested (Evans et al. 2006). It is thus likely that at subtropical latitudes, where tropical and temperate taxa overlap at their range margins, the distribution and abundance of different constituent species may respond variably to a range of different environmental drivers or show contrasting responses to the same environmental conditions. For example, at biogeographic transition zones, warmer ocean temperatures can drive the range expansion of tropical species (Baird et al. 2012, Poloczanska et al. 2013, Yamano et al. 2011), but also lead to the range contraction of temperate taxa (Smale and Wernberg 2013, Wernberg et al. 2016), and while tropical species may establish at higher latitudes during warm periods, they may not be able to survive over winter when temperatures drop below their physiological thresholds (Feary et al. 2014, Figueira and Booth 2010).

Moreover, at species' range boundaries, extreme climatic events can cause abrupt ecological change as exemplified by the range contraction of a temperate seaweed in response to a marine heatwave in Western Australia (Smale and Wernberg 2013). These species responses illustrate the likelihood that altered environmental conditions will fundamentally alter ecosystems at the transition of biogeographical zones in the coming decades. Increased understanding of the relationships between biota and their environment contributes to a predictive framework for how ecosystems are affected by global change, and thus to their ongoing management and conservation (Beger et al. 2011, Beger et al. 2014).

Classical hypotheses highlight the role of abiotic factors in controlling high-latitude distributional boundaries of species (Pianka 1966), and terrestrial studies underscore the importance of environmental stress in setting species range limits (e.g. minimum temperature; Normand et al. 2009). Subtropical environments experience harsher environmental regimes than their tropical counterparts, as they are cooler, receive less light and are exposed to greater variability and seasonality (Willig et al. 2003), providing powerful testing grounds of the role of abiotic stress in setting species range limits. They harbour a unique biogeographical overlap of tropical, subtropical and temperate taxa with different physiological requirements, and we currently only have a cursory understanding of the environmental conditions that govern their distribution.

Here, we investigate the role of abiotic stress in driving the distribution of scleractinian corals at their high-latitude range margins in the subtropical-to-temperate transition zone in eastern Australia, where environmental filtering is the dominant process in structuring coral communities (Sommer et al. 2014). It is widely accepted that temperature, light availability and carbonate chemistry are essential to physiological processes in corals and associated dinoflagellate symbionts, and that these environmental variables influence their latitudinal distribution (Harriott and Banks 2002, Kleypas et al. 1999, Wicks et al. 2010). Moreover, work on mesophotic (Kahng et al. 2010) and turbid (Butler et al. 2013, Butler et al. 2015) reefs highlights optical water quality as a determinant of coral distribution in marginal habitats. Nevertheless, we know little about the relative importance of these and other parameters in structuring marginal coral communities.

Here we evaluate these questions by using a comprehensive latitudinal species abundance dataset to test the extent to which light limitation, optical water quality, carbonate availability, cold stress, and short-term and seasonal temperature variability predict patterns in coral species richness (alpha diversity), species composition (beta diversity), Shannon diversity and functional diversity at their leading edge. To investigate whether the distribution of different groups of species may be governed by different environmental parameters, we also conduct these tests for the number and abundance of tropical and subtropical species. Our study highlights the role of abiotic stress in controlling higher latitudinal range limits of species and suggests that robust predictions of the impacts of climate change at biogeographic transition zones require approaches that account for climatic extremes and temporal fluctuations, and for species abundances and characteristics. Our research shows that the high-latitude range limit determinants of corals vary among taxa, as the distribution and abundance of tropical corals is best explained by light limitation, whereas minimum temperatures and temperature fluctuations limit subtropical species. This has broad implications for the prediction and management of species range shifts at biogeographic transition zones, as these approaches commonly rely on projections of mean temperature alone and could therefore lead to inaccurate assessments of species vulnerabilities to climate change.

MATERIALS AND METHODS

Spatial patterns in coral community structure and life-history strategies

We determined species abundance distributions of scleractinian corals at 17 locations along a latitudinal environmental gradient (26°36’S to 32°48’S) in the subtropical-to-temperate transition zone in eastern Australia (Sommer et al. 2014). In this region, coral assemblages are spatially restricted to pockets of suitable rocky habitat. To capture the breadth of coral biodiversity in the region and known gradients in community structure at local scales (e.g. in the Coffs Harbour region; Harriott et al. 1994, Malcolm et al. 2010) we sampled almost all known high-latitude reefs along the eastern Australian coast. At each location, we surveyed coral assemblages along five replicate 30 m long, 1 m wide photographic belt transects that were a minimum of 10 m apart from each other and were placed at 8-12 m depth along the leeward side of islands and headlands. At most locations, transects spanned the entire coral habitat, which tends to be small (i.e. hundreds of meters) in these marginal environments. The percent cover of 92 coral species was then quantified from photographic belt transects using the random point count method (600 points per transect, total of 51,000 points; Sommer et al. 2014). To examine zoogeographic patterns in this zone of biogeographical overlap, we characterised each of the 92 species as tropical (predominantly occur in the tropics), subtropical (common at high latitudes and uncommon in the tropics) or cosmopolitan (common in the tropics and at high latitudes). We also compiled information on six structural and reproductive traits (colony morphology, corallite formation, corallite size, reproductive mode, sexuality, and symbiont transmission) for each of the species recorded in our surveys (Madin et al. 2016b, Sommer et al. 2014).

Environmental parameters

To examine environmental conditions at the study sites we initially obtained data on four primary environmental variables that are considered important for the biology and ecology of scleractinian corals; sea surface temperature (SST), photosynthetically active radiation (PAR, a proxy for light availability), diffuse attenuation coefficient (KD490, a proxy for turbidity) and ocean acidity (pH, a proxy for carbonate availability). See Appendix Table S1 in Supporting Information for more details on environmental parameters. We obtained monthly mean PAR and KD490 from the Global Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua Satellite (Parkinson 2003) at a 5 km spatial resolution for the period July 2002 to December 2013. To examine the role of short-term environmental variability we obtained daily SST data for the period January 1993 to December

2007 from the Bluelink Reanalysis model (BRAN; Oke et al. 2008), which hindcasts mesoscale circulation around Australia at 10km spatial resolution. We obtained pH data from Bio-ORACLE (Tyberghein et al. 2012) at a 9.2 km spatial and monthly mean resolution.

To examine hypotheses about environmental stress we calculated the mean annual minima for PAR and SST to represent light limitation and cold stress, respectively. To investigate the importance of long-term environmental stability we calculated the standard deviation of the daily mean SST for the entire period. Intense short-period SST anomalies characterise the region (Malcolm et al. 2011), so we also calculated the standard deviation of daily SSTs over weekly periods to examine the role of short-term variability in driving biodiversity patterns. We checked for multicollinearity of environmental predictors using Spearman's correlation coefficient with a cut-off of $r > 0.7$ (see Appendix Table S2) and visually inspected the data to verify that there were no nonlinear relationships. We used SST_Min, PAR_Min, KD490, and the long-term (VAR_Long) and short-term standard deviation (VAR_Short) of temperature in all generalised linear multiple regression models, in order to test how cold stress, light limitation, optical water quality, and environmental variability limit the distribution of scleractinian corals at their latitudinal range limits. In an alternative approach we performed nested pre-selection of SST and PAR parameters (among means and minima) and used the SST and PAR parameters with the highest explanatory power, together with KD490, VAR_Long and VAR_Short in multiple regression models. As we found no qualitative difference in the results, these complementary analyses are contained in the Appendix (see Supplementary Analyses in the Appendix).

Modelling and analysis

Relationships between coral diversity patterns (alpha diversity) and environmental conditions.

We used generalised linear models (GLMs) with Gaussian error structure to determine the relative importance of environmental variables in driving gradients in alpha diversity. The models evaluated the associations between univariate coral community summary metrics (species richness, the number of tropical and subtropical species, Shannon diversity, the abundance of tropical and subtropical species, and functional dispersion) and the chosen environmental predictors. Functional dispersion (FDis; Laliberte and Legendre 2010), a multidimensional functional diversity index (here calculated using the species traits colony morphology, corallite size, corallite formation, reproductive mode, sexual pattern, and symbiont transmission), takes into account relative abundances of species and is unaffected by species richness. For each coral community summary metric, multiple regression models included SST_Min, PAR_Min, KD490, VAR_Long and VAR_Short as potential predictors. To contextualise our findings about environmental stress (from multiple regression models) with the explanatory power of mean climatic conditions, we also ran univariate GLMs for long-term mean values of SST (SST_Mean), PAR (PAR_Mean), KD490 and pH.

We examined the distribution of model residuals to check assumptions of linear regression and, where necessary, we fourth-root transformed the response variable (species richness, tropical richness and abundance, subtropical richness and abundance) to linearise and normalise relationships (see Table 1). We constructed a set of candidate models that contained all combinations of environmental predictors (SST_Min, PAR_Min, KD490, VAR_Long and VAR_Short) and used Akaike information criterion values corrected for small sample sizes (AICc) and Akaike weights to rank models from the best to the worst fitting model (i.e. from lowest to highest AICc value). To account for model selection uncertainty we selected the subset of candidate models with ΔAICc < 4 in relation to the best model and performed model averaging (Burnham and Anderson 2002). We ranked the explanatory variables based on the sum of their average Akaike weights, with larger values denoting greater relative variable importance (RVI; Burnham and Anderson 2002).

Relationships between gradients in species composition (beta diversity) and environmental conditions.

We quantified beta diversity using three measures that emphasise different aspects of variation in community structure. We calculated the turnover (beta_jtu) and nestedness (beta_jne) components of the Jaccard dissimilarity index from presence/absence data following (Baselga and Orme 2012). This allowed us to separate the contributions of species replacement (i.e. different species occurring at different sites) and of nested species loss (i.e. where sites with fewer species are subsets of species found at richer sites) to beta diversity patterns. To consider the effects of both species composition and species' relative abundances on variation in coral community structure we also calculated Bray Curtis dissimilarity (beta_bray) from species abundance data.

We used Mantel tests (9999 permutations) to examine whether differences in community structure were related to spatial distance (i.e. whether sites that were more distant from each other along the latitudinal gradient had higher beta diversity) following Anderson et al. (2011). We then conducted distance based redundancy analysis (Legendre and Anderson 1999) and backward model selection using permutation tests to identify the environmental predictors that contributed significantly to explaining beta diversity patterns of high-latitude coral assemblages. We performed all analyses using the packages betapart (Baselga and Orme 2012), MuMIn (Barton 2013), vegan (Oksanan et al. 2012) and FD (Laliberte and Legendre 2010) in R (R Core Team 2012).

RESULTS

Environmental parameters

As expected, mean and minimum SST and PAR declined with increasing latitude, with the 15-year SST_Mean and 12-year PAR_Mean at low-latitude sites up to 3°C and 4 Einstein/m^2, respectively, higher than at high-latitude sites. Daily SST in the region ranged between 15.0°C (at Fingal Island, 32°48'S) and 27.8°C (at Flinders Reef, 26°58'S) over the 15 year period (Fig. 2a), and SST_Mean ranged between 19.8°C and 22.8°C at the same locations. The absolute temperature range recorded at any given location over the 15-year period spanned 9.2°C (at Julian Rocks, 28°36'S) to 11.4°C (at Mudjimba Island, 26°36'S). Mean monthly PAR values in the region ranged between 16.1 (at Fingal Island, 32°48'S) and 62.3 Einstein/m^2 (at Flinders Reef, 26°58') over the 12-year period, with long-term mean (PAR_Mean) values between 36.2 and 40.6 Einstein/m^2, and mean annual minima (PAR_Min) between 18.1 and 23.2 Einstein/m^2 at the same locations (Fig. 2b).

Relationship between coral diversity patterns and environmental conditions

Patterns in coral species richness were positively correlated with gradients in light availability, with greater numbers of species in areas of higher PAR_Min (Table 1). Shannon diversity, on the other hand, was best predicted by gradients in thermal energy and declined as SST_Min became colder and as VAR_Short increased (Table 1, Fig. 3c). Functional dispersion (FDis) was the only response where the best model was clearly superior to the next best model (ΔAICc of next best model = 4.12) and model averaging was not required. FDis was tightly coupled with SST_Min and both VAR_Long and VAR_Short, with higher FDis in warmer and more thermally stable environments (Table 1, Fig. 4).

The importance of PAR_Min and SST_Min as determinants of coral species distribution at their southern range limit varied with zoogeography. The distribution of tropical coral species (species richness and abundance; Table 1, Fig. 3a) was consistently more closely and positively correlated

(RVI = 0.88 to 1) with PAR_Min than with any of the temperature variables (Table 1). In contrast, subtropical species richness and abundance responded most strongly to SST_Min and Var_Short (Table 1). Surprisingly, subtropical species richness and abundance metrics differed in the direction of their relationships with SST_Min, with subtropical species richness declining as temperatures decreased and abundance increased in colder environments. Subtropical species richness and abundance both showed a negative relationship with VAR_Short (Table 1, Fig. 3b). The attenuation of light with depth (KD490) had relatively low predictive power in all models (highest RVI of 0.40 for tropical species richness) and showed a negative relationship in models where it was included (Table 1).

Comparison of the results of multiple regression models of parameters of abiotic stress (Table 1) with univariate regression models of the role of mean climatic conditions (Table 2) in shaping biodiversity patterns showed that for most responses (species richness, subtropical species richness and abundance, Shannon diversity, functional dispersion) parameters of environmental stress had higher explanatory power (i.e. lower AICc values; Burnham and Anderson 2002) than SST_Mean or PAR_Mean alone (Table 2). Patterns in tropical coral species distribution (tropical species richness; tropical abundance) were better described by PAR_Mean than by PAR_Min models, and PAR parameters for these three metrics consistently outperformed SST parameters (Tables 1 and 2).

Species turnover (beta_jtu) increased with geographic distance among sites (Fig. 1b) and was best explained by gradients in PAR_Min (Table 3). In contrast, nestedness patterns were independent of geographic distance (Fig. 1c) and were most closely related to the local thermal regime, a combination of SST_Min, VAR_Short and VAR_Long (Table 3). Abundance-based beta diversity (beta_bray) increased with spatial distance (Fig. 1d) and was best explained by gradients in PAR_Min, SST_Min and VAR_Short (Table 3).

DISCUSSION

Environmental determinants of coral species distributions

Our ability to predict and manage species range shifts in response to global change relies on understanding the specific environmental factors that limit the distribution of species at their range edges. A growing body of literature suggests that the importance of specific climatic variables in driving biodiversity patterns varies among taxa and with spatial scale (e.g. Evans et al. 2006, Keith et al. 2014) and that parameters in relation to environmental stress are important in determining high-latitude range limits (e.g. minimum temperatures; Normand et al. 2009). Here, we investigated the extent to which gradients in light limitation, cold stress, and temperature variability predict alpha and beta diversity patterns of scleractinian corals at their high-latitude range limits and we found that abiotic stress is likely to be a key factor in structuring coral assemblages in this zone of biogeographical overlap.

Moreover, the relative importance of environmental parameters differed for the biodiversity measures tested and for groups of species that varied in their zoogeographic distribution. Gradients in species turnover (beta_jtu) and in species richness were most closely related to light availability, whereas gradients in species nestedness (beta_jne), Shannon diversity and functional dispersion were mostly related to cold stress and temperature variability. Consistent with the distinct distributional patterns of tropical and subtropical species in the region (Sommer et al. 2014), species of different zoogeography also varied in their relationships with environmental gradients. The distribution and abundance of tropical species was consistently linked with light availability, whereby the number and abundance of tropical taxa declined as light attenuated with latitude. Gradients in subtropical species, on the other hand, were more closely related to minimum temperature and short-term temperature variability. This suggests that light availability is a key factor in limiting the distribution of tropical coral species towards their high latitude range margins, but that high-latitude light environments may be less limiting for subtropical species. Thus, corals expanding to higher latitudes with global warming are likely to produce different community composition to their natal coral communities on reefs at lower latitudes, with potentially novel combinations of species and their abundances (Graham et al. 2014, Greenstein and Pandolfi 2008).

Light limitation

The ecology of phototrophic organisms is influenced by their ability to regulate the acquisition and utilisation of light. Shade-acclimated plants in the forest understorey, for example, typically occur under light conditions of around 1% of full sunlight but are exposed to high irradiance levels from sun flecks or tree-fall gaps (Krause et al. 2012). In aquatic environments, the light field is further altered by water and suspended particles, requiring phototrophic organisms to optimise the collection and utilisation of solar energy. Corals and their algal symbionts are masters of photo-acclimation and adaptation (reviewed in Dubinsky and Falkowski 2011). Indeed, owing to light enhancing properties of coral skeletons and tissues (Wangpraseurt et al. 2014), symbiotic corals are among the most efficient light collectors in nature.

Corals that live in low-light conditions harvest close to 100% of incident light, contrary to <10% absorbed by corals in high-light environments (Dubinsky and Falkowski 2011). These corals are also more efficient in using the absorbed light due to photoacclimative adjustments and metabolic changes, including reduced dark respiration, increased concentration of photosynthetic pigments, and thinning and widening of skeleton and tissue perpendicular to the direction of irradiance (Anthony and Hoegh-Guldberg 2003, Dubinsky and Falkowski 2011). The coral *Turbinaria mesenterina*, for example, is one of the most widely distributed and abundant species in the study region (Sommer et al. 2014), and has the capacity to photoacclimate faster than higher plants and to buffer variations in energy balance in highly variable light environments (Anthony and Hoegh-Guldberg 2003).

Shorter day-length in winter, high seasonality, and lower light intensity and greater reflectance due to shallower angle of entry into the water make for difficult light environments for phototrophic organisms at higher latitudes. This is especially the case in winter, when PAR at 30° latitude is 40% lower than at 10° latitude (Campbell and Aarup 1989). Winter irradiance was found to drive depth-specific distribution patterns of some staghorn corals (Muir et al. 2015), but these relationships are likely to be species-specific (Madin et al. 2016a). It is thus plausible that species-specific abilities to photoacclimate to varying and low light conditions influences their distribution and abundance. For example, Anthony and Connolly (2004) identified species-specific physiological niche boundaries along light and turbidity gradients for the corals *Acropora valida* and *Turbinaria mesenterina,* which were primarily related to a steeper increase in respiration of *Acropora valida*. Higher respiration in turn reduces the available energy budget for survival, growth and reproduction (Anthony and Connolly 2004), with likely effects on the distribution and abundance of species. We thus hypothesise that narrower light niches and a steep light availability gradient (see Appendix Table S2) explain the primary role of PAR_Min in governing the distribution of tropical species in this biogeographic transition zone (Fig 4b). It is interesting that KD490 (proxy for turbidity) had relatively lower predictive power in our models than PAR, which suggests that the overall latitudinal light regime is more influential in driving coral distributional patterns at high latitudes than gradients in optical water quality, which tend to be more locally influenced (e.g. by terrestrial run-off, local oceanography, substrata).

Cold stress and temperature variability

Marine ectotherms are more closely in equilibrium with their thermal niches at both leading and trailing range boundaries than terrestrial ectotherms (Sunday et al. 2012) and sea surface temperature is deemed a primary determinant of the latitudinal distribution of reef building corals (Fraser and Currie 1996, Harriott and Banks 2002, Kleypas et al. 1999). Although some corals can survive much colder temperatures (e.g. 11.5°C in the Arabian Gulf; Coles and Fadlallah 1991), 18°C annual minimum SST is considered the threshold for coral reef formation (Kleypas et al. 1999). Severe cold stress can negatively affect photosynthetic efficiency, lead to photodamage, coral bleaching and mortality (Coles and Fadlallah 1991, Saxby et al. 2003). In our study, the number of subtropical species, Shannon diversity and functional dispersion were higher in warmer environments and when VAR_Short was lower, highlighting that cold stress and temperature variability can act in concert to limit species distributions at high latitudes.

Gradients in mean thermal conditions can mask seasonal extremes and short-term temperature fluctuations, which are more indicative of abiotic stress, particularly at subtropical latitudes. At higher latitudes, seasonal differences in environmental conditions at the same location can be as great or greater than differences observed in mean conditions over the scale of thousands of kilometres (Fig. 2). It was thus unexpected that short-term temperature variability (at a scale of one week) was a more influential predictor of biodiversity gradients than seasonal fluctuations (Table 1). In highly variable environments, organisms must continually acclimate to changing conditions, which likely imposes high energetic costs, particularly in habitats where short-term variability is high and minimum temperatures are already close to their lower thermal thresholds.

While previous correlative studies have mainly considered the influence of seasonal variation on the distribution of organisms (e.g. Fraser and Currie 1996, Keith et al. 2014, Tittensor et al. 2010), our results highlight that short-term fluctuations are also important drivers, particularly in areas where oceanographic conditions are highly variable (e.g. East Australian Current; Malcolm et al. 2011).

Fraser and Currie (1996) used annual variation in salinity and cloud cover as proxies for environmental variability and found no significant correlation with coral generic richness. Here, we found that long-term fluctuations in SST generally had low explanatory power, except for gradients in functional dispersion (Fig. 4) and species nestedness (beta_jne, Table 3). Functional dispersion was highest where SST_Min was higher, and where the thermal environment was more stable (i.e. where seasonal and short-term temperature fluctuations were less pronounced). These results are consistent with strong trait-mediated environmental filtering processes at the transition of biogeographical zones (Sommer et al. 2014), and suggest that high abiotic stress limits the number of successful strategies at high-latitudes.

Moreover, our results show that multiple drivers of abiotic stress can jointly act to create environmentally harsh conditions and limit the distribution of species at biogeographic transition zones. This is further supported by the results of distance based redundancy analysis, which showed that variation in multivariate community structure, reflecting both species composition and species abundances (beta_bray), was best explained by a combination of PAR_Min, SST_Min and VAR_Short.

At geographic range limits, asymmetric and non-linear responses of demographic parameters (i.e. births, deaths, immigration, emigration) to environmental gradients are not unusual (reviewed in Gaston 2009). In our study this is exemplified by opposite responses of the number and abundance of subtropical species to gradients in minimum temperature (Fig. 3). Despite a decline in the number of subtropical species with colder minimum temperatures, the abundance of subtropical species was greater in colder environments (Table 1; Fig. 3). This suggests that fewer subtropical species persist as SST_Min approaches the lower thermal thresholds of corals, but that the ones that do occur, can reach high abundances [e.g. the subtropical endemic *Pocillopora aliciae* (Sommer et al. 2014)]. Moreover, the distribution of subtropical taxa extended to the highest latitudes in our surveys (32°48’S), where daily temperatures and mean annual minimum temperatures reached 15.0° and 16.5°C, respectively, much below the expected lower thermal limit of 18°C (Kleypas et al. 1999). These opposite responses to gradients in SST_Min highlight the importance of considering abundance distributions when investigating the range limit determinants of species (Mair et al. 2014).

Mechanisms underlying coral environment relationships

The results of our study support the classical hypothesis that abiotic factors are important range limit determinants at high latitudes (Pianka 1966). Our research shows that the environmental drivers of coral distributions towards their high-latitude range limits vary among taxa. This supports the role of species-specific tolerances in limiting the distribution of individual species and in driving biodiversity patterns (e.g. physiological tolerance hypothesis; Currie et al. 2004). Our incidence-based analyses show that variation in species composition is caused by a combination of nested species loss (beta_jne) and species replacement (beta_jtu), and that these are governed by different environmental parameters. While species replacement increased with spatial distance, nested species loss did not. This suggests that species don’t disappear sequentially from assemblages along the latitudinal gradient. Our finding that light availability drives species turnover is consistent with the notion that steeper ecological gradients cause stronger habitat filtering and the replacement of some species by others from site to site (Hortal et al. 2011). Conversely, cold and fluctuating temperatures better explained more ordered patterns of species loss (i.e. nestedness patterns).

Our findings suggest that, at biogeographic transition zones, more coral species with tolerances for different sets of climatic conditions can survive in relatively warmer, well-lit and more stable environments. This agrees with experimental studies and field observations that found species-specific physiological niche boundaries and sensitivities of corals to thermal and light conditions (Anthony and Connolly 2004). The results of our abundance-based analyses further support this, as abundance patterns of tropical and subtropical corals were significantly correlated with PAR_Min and SST_Min, respectively, and patterns in beta diversity (beta_bray) were best explained by the combined light and thermal regime (PAR_Min, SST_Min, VAR_Short).

Moreover, our findings demonstrate that at biogeographic transition zones, parameters related to environmental stress (i.e. environmental extremes, variability) may better explain species distributions than long-term trends in mean climatic conditions. This corroborates the results of terrestrial studies which showed that climatic extremes such as cold temperatures and minimum length of growing season are important in setting species range limits (e.g. Normand et al. 2009). Focus on mean climatic conditions alone therefore has the potential to underestimate species climatic vulnerability at biogeographic transition zones. While this may seem intuitive, it does not appear to find application in the published climate change modelling literature.

Conclusions and implications for global change predictions

Predicting the effects of global change on ecosystems at the transition of biogeographical zones requires improved understanding of the specific environmental factors that drive the distribution and abundance of species with different ecological requirements and tolerances. While mean sea surface temperature plays a dominant role in driving global gradients in marine organisms, including corals (e.g. Fraser and Currie 1996, Tittensor et al. 2010), we have shown that parameters that induce abiotic stress, such as light limitation, cold stress and temperature variability are key drivers of coral patterns on subtropical-to-temperate transitional reefs. These findings have bearing on studies investigating potential species range shifts and their implications for conservation decision-making, which have mainly relied on projections of mean sea surface temperature (e.g.

Makino et al. 2014), and may thus mask potential vulnerability to climate change. Instead, our results indicate that, if we are to more accurately predict climate change responses at biogeographic transition zones, we need to consider parameters that correspond to various aspects of physiological stress (e.g. SST, light availability, extremes, variability), the relative importance of which likely varies among species (e.g. tropical, subtropical). While our study does not address the role of biotic interactions in shaping the observed patterns, it is plausible that distributional and abundance shifts in response to novel environmental regimes may alter biotic interactions, with potential implications for community structure and ecosystem function (Beger et al. 2014, Vergés et al. 2016, Wernberg et al. 2016).

While our results indicate that coral species sensitive to minimum temperatures may perform better in warming oceans, coral species inhibited by light limitation at high latitudes (i.e. tropical species) may not benefit from increases in temperature to the same extent. Based on their observations for staghorn corals, Muir et al. (2015) argue that winter irradiance limits the scope for latitudinal range extension of reef corals. This, however, is contrary to the historical record of corals at high latitudes at times of elevated SST (Greenstein and Pandolfi 2008), and to the rapid poleward range expansion of tropical coral species in Japan (Yamano et al. 2011), including increasing abundance at some high-latitude locations (e.g. Kochi, 33ºN; Mezaki and Kubota 2012) in recent decades. While some recent range extensions of tropical coral species into higher latitudes have also been reported in Australia (Baird et al. 2012) high-latitude coral communities in Australia have remained comparatively stable in recent decades (Dalton and Roff 2013, Speed et al. 2013).

Studies into the role of abiotic stress in shaping physiological responses and distributional patterns of organisms highlight that altered environmental conditions can lead to unexpected changes in the relative importance of environmental forcing agents and to non-linear responses in the distribution of organisms (e.g. Byrne and Przeslawski 2013, Figueira and Booth 2010, Gaston 2009). For example, higher SSTs ameliorate some of the adverse effects of acidification on the development of benthic invertebrates (i.e. antagonistic effects; reviewed in Byrne and Przeslawski 2013), and winter temperatures above survival thresholds allow overwinter survival of some tropical fishes in temperate Australian waters (Figueira and Booth 2010). Moreover, regionally distinct patterns of complex oceanic change can lead to distinctive responses of organisms to interactive multi-stressor regimes (Boyd et al. 2015). Northern Hemisphere ocean temperatures have warmed more than Southern Hemisphere temperatures (Sen Gupta et al. 2013) and we hypothesise that antagonistic (e.g. warming mitigating the effects of light limitation) or threshold-like relationships (between physiological tolerances and abiotic conditions) may have led to greater tropicalisation of reefs in Japan. These examples from the literature and the species-specific responses to abiotic stress reported here underscore the need to consider the biology, physiology and ecology of species (Feary et al. 2014, Kearney and Porter 2009), as well as regionally distinct multi-stressor patterns (Boyd et al. 2015) when projecting potential climate change impacts. This is particularly important at biogeographic transition zones, where most species occur close to their physiological tolerance limits and where antagonistic and threshold-like relationships likely operate.

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Table 1. Multiple regression models explaining the role of environmental stress in shaping patterns in coral community structure at species southern range margins. The model coefficients associated with each variable are shown for the multimodel average (model average; numerals in brackets denote the number of models with ΔAICc < 4 in the set), and for the most parsimonious model with the lowest AICc (best model). Relative variable importance (RVI) ranks all explanatory variables from high to low importance, based on the model set used for model averaging. Bold values indicate explanatory variables with high RVI that provided a significant individual contribution ($P \leq 0.05$) to the model average. Akaike weights (Weight) indicate the relative likelihood of the best model, given the set of models considered for model averaging. Model average AICc values represent the range of AICc values across the averaged models, and AICc and R^2 values of the best models are also shown.

Response & Transformation			**PAR_Min**	**SST_Min**	**KD490**	**VAR_Long**	**VAR_Short**	**AICc**	**R^2**	**Weight**
Species Richness	4rt	RVI	**1**	0.09	0.19	0.11	0.09			
		Model average (5)	0.27798	-0.01114	-1.68365	0.3134	0.52416	4.1-7.6		
		Best model	0.2846					4.1	0.7646	0.447
Tropical Species Richness	4rt	RVI	**1**	0.08	0.4	0.07	0.08			
		Model average (5)	0.42901	0.11567	-0.386512	0.23019	2.47695	18.2-21.7		
		Best model	0.3908		-3.865			18.2	0.8265	0.319
Subtropical Species Richness	4rt	RVI	0.21	**0.9**	0	0.19	**0.9**			
		Model average (4)	0.02705	0.19989	-5.16858	-0.33127	-5.16858	-13.5 to -10		
		Best model		0.1894			-4.768	-13.5	0.6797	0.41
Tropical Abundance	4rt	RVI	**0.94**	0.24	0.36	0.43	0.14			
		Model average (10)	0.37023	-0.06627	-4.36248	1.58723	6.45346	20.3-24.2		
		Best model	0.4011					20.3	0.7137	0.174
Subtropical Abundance	4rt	RVI	0.23	**0.93**	0.26	0.15	0.44			
		Model average (9)	0.07248	-0.36342	-3.18955	-0.85293	-6.44388	8.1-11.8		
		Best model		-0.2676				8.1	0.3473	0.207
Shannon Diversity	-	RVI	0.08	**1**	0.32	0.08	**1**			
		Model average (4)	-0.06636	0.7212	-3.34325	0.32959	-22.43086	14.5-18.4		
		Best model		0.7621			-22.09	14.5	0.88	0.53
Functional Dispersion	-	Best model		**0.1197**		**-0.5319**	**-3.927**	-52.4	0.92	0.8

Table 2: Model fit of univariate regression models explaining the role of long-term mean values of sea surface temperature (SST_Mean), photosynthetically active radiation (PAR_Mean), pH and light attenuation with depth (KD490) in shaping patterns in high-latitude coral communities of eastern Australia.

Response & Transformation			**PAR_Mean**	**SST_Mean**	**pH**	**KD490**
Species Richness	4rt	Coefficients	0.3033	0.4477	27.98	-6.022
		R^2	0.67	0.67	0.57	0.35
		AICc	9.8	9.7	14.4	21.3
Tropical Species Richness	4rt	Coefficients	0.4811	0.7391	43.98	-10.51
		R^2	0.67	0.73	0.56	0.43
		AICc	25.7	22.5	30.6	35
Subtropical Species Richness	4rt	Coefficients	0.09319	0.1555	7.137	-1.769
		R^2	0.30	0.38	0.18	0.14
		AICc	-3.7	-5.9	-0.9	-0.3
Tropical Abundance	4rt	Coefficients	0.4638	0.6566	44.39	-9.588
		R^2	0.74	0.68	0.67	0.42
		AICc	18.7	22.1	22.5	32.3
Subtropical Abundance	4rt	Coefficients	-0.1056	-0.1884	-6.208	1.667
		R^2	0.18	0.26	0.06	0.06
		AICc	12	10.2	14.3	14.3
Shannon Diversity	-	Coefficients	0.4691	0.7389	42.55	-9.368
		R^2	0.54	0.62	0.44	0.29
		AICc	34	30.9	37.3	41.5
Functional Dispersion	-	Coefficients	0.03185	0.068	1.31	-0.5418
		R^2	0.11	0.24	0.02	0.04
		AICc	-19.9	-22.5	-18.2	-18.6

Table 3: Results of distance based Redundancy Analysis showing the environmental parameters that contribute significantly ($P \leq 0.05$) to explaining beta diversity patterns on high-latitude reefs of eastern Australia. F-values and significance codes are shown. * $P \leq 0.05$; ** $P < 0.01$

	beta_jtu	**beta_jne**	**beta_bray**
PAR_Min	6.6137**		2.6836**
SST_Min		7.1492**	2.8363**
KD490			
VAR_Long		5.5481**	
VAR_Short		4.0006*	2.9397**

Figure titles:

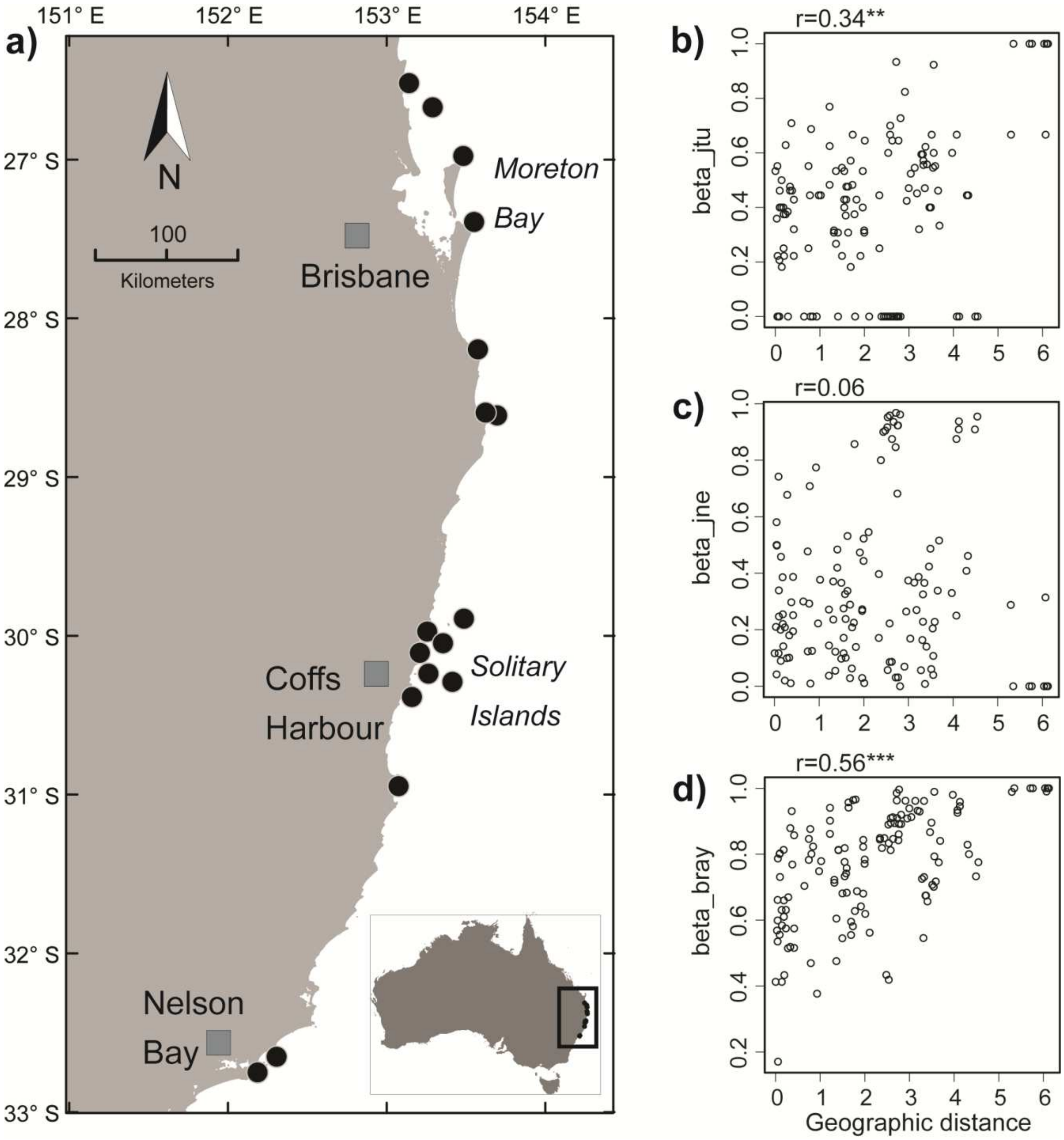

Figure 1. (a) Map of the study region and (b-d) beta diversity gradients of high-latitude coral assemblages of eastern Australia. Relationships between geographic distance (between all location pairs) and (b) species replacement (beta_jtu) (c) species nestedness (beta_jne), and (d) abundance-weighted beta diversity patterns (beta_bray). Mantel r statistic and significance codes are shown. * $P \leq 0.05$; ** $P < 0.01$; *** $P < 0.001$.

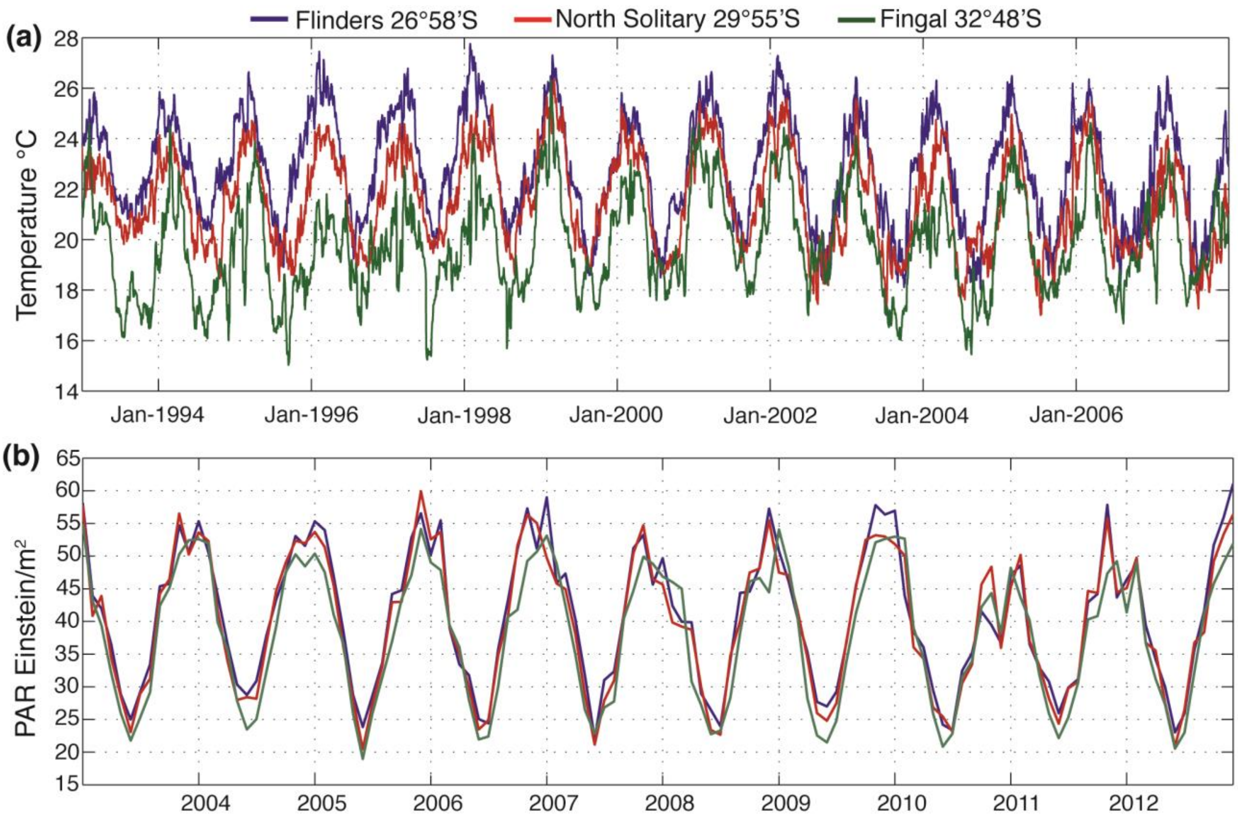

Figure 2. (a) Daily sea surface temperature records from the Bluelink Reanalysis data and (b) monthly mean PAR records from the Global MODIS Aqua Satellite for three locations along the east coast of Australia.

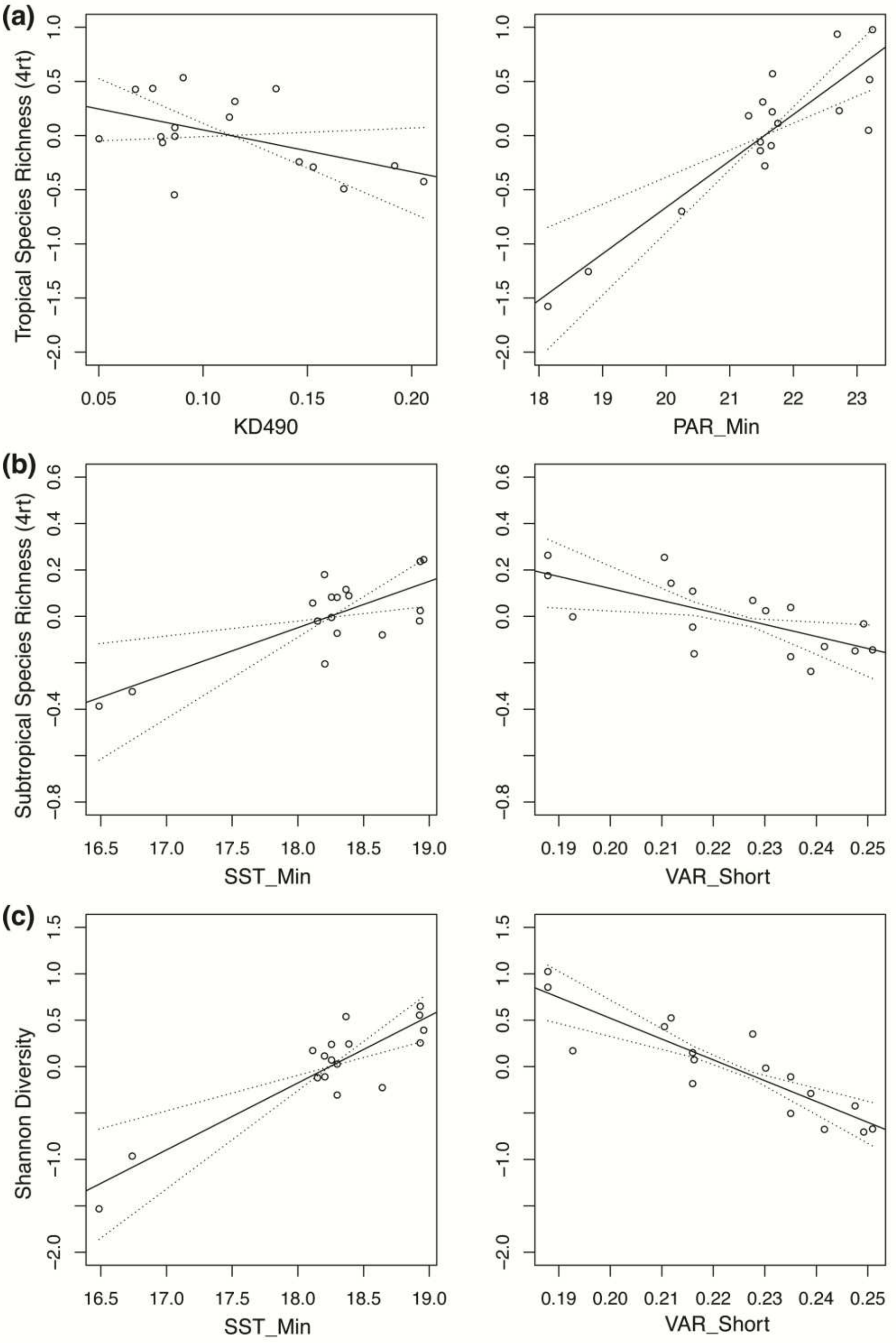

Figure 3. Model averaged partial coefficients from the generalised linear multiple regression models for the role of abiotic stress (SST_Min, VAR_Short, PAR_Min; solid lines) in driving patterns in (a) tropical species richness, (b) subtropical species richness, (c) Shannon diversity for high-latitude coral communities of eastern Australia. Only significant parameters are shown. Dashed lines indicate standard errors for the partial coefficients and circles are model residuals.

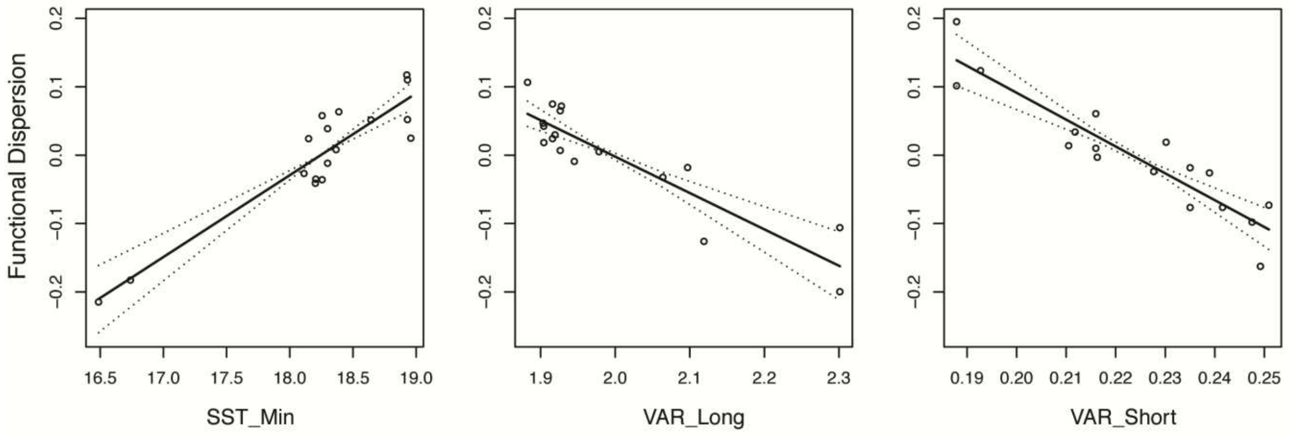

Figure 4. Partial regression plots from the generalised linear multiple regression models for the role of abiotic stress (SST_Min = annual minimum temperature; VAR_Long = long-term temperature variability; VAR_Short = short-term temperature fluctuations; solid lines) as a driver of distribution patterns in functional dispersion for high-latitude coral communities of eastern Australia. Dashed lines indicate standard errors for the partial coefficients and circles are model residuals.