



REPORT

# Spatial structuring of coral traits along a subtropical-temperate transition zone persists despite localised signs of tropicalisation

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**Abstract** Climate-driven species range expansions are underway with more tropically affiliated species, including Scleractinian corals, becoming increasingly abundant at higher latitudes. However, uncertainty remains on how these range shifts will affect reef-scale ecosystem processes, which will ultimately depend on the traits of the taxa that dominate these assemblages. Here, we quantified spatiotemporal patterns in the taxonomic and trait structure of coral assemblages along the subtropical-temperate coast of Western Australia (27°–34°S). Coral abundance was generally low and coral cover < 5% across our study sites. Coral assemblages shared similarities in morphological trait structures across the latitudinal gradient, mostly characterised by taxa with simple morphologies; yet subtle differences were also observed across latitudes, with high-latitude corals characterised by slower growth rates and reduced

maximum colony sizes. We found a 3.4-fold increase (from 1 to 3.4 individuals m<sup>-2</sup>) in coral abundance at one heavily disturbed location, where canopy-forming seaweeds were replaced by turfing algae, a pattern that was partly driven by an increase in the relative contribution of warm affinity taxa, such as *Acropora* spp. We predicted these changes would be reflected in different components of functional diversity; yet, despite a localised signal of tropicalisation, we only observed subtle changes in the functional identity, richness, evenness, and divergence. The spatially invariant trait structure of coral assemblages suggests that the nature of ecosystem functions will likely remain unchanged during early stages of tropicalisation, and hence their contribution to temperate reef-scale ecological processes will depend on dominance over other benthic foundational species.

**Keywords** Tropicalisation · Marginal reefs · Temperate reefs · High-latitude corals

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## Introduction

The composition of contemporary ecological communities is shaped by the complex interplay between ecological, evolutionary, and biogeographical factors (Vellend 2010). Disentangling the mechanistic link between changes in the abiotic and biotic environment and species range shifts has become a fundamental aspect of ecological research, as species from many taxonomic groups are rapidly shifting their geographic distributions (Chen et al. 2011; Pinsky et al. 2020; Poloczanska et al. 2013; Wernberg et al. 2011). Trait-based approaches (i.e. classifications based on morphological, behavioural and/or physiological characters) offers a promising framework to forecast the response of species to environmental changes under future climatic scenarios

(Mouillot et al. 2013; Harvey et al. 2021), as well as providing a link between changes in the taxonomic composition of assemblages and ecological processes that underpin the movement and/or storage of energy and materials (i.e. ecosystem functions, Tilman 2001; Gagic et al. 2015; Bellwood et al. 2018). Over biogeographical scales, regions with similar environmental history often pose similar trait compositions (Lamanna et al. 2014; McLean et al. 2021), a pattern associated with environmental filtering of traits that are adapted to maximise fitness in those environments (Violle et al. 2007; Bosch et al. 2021). As climate change rapidly shifts environmental conditions, fundamental reshuffles in the trait composition and structure of local assemblages are being extensively reported across many taxonomic groups (McLean et al. 2018; McWilliam et al. 2020), with often unknown consequences for ecosystem functioning (Pecl et al. 2017). Despite this increasing knowledge, we still lack a thorough understanding across many regions of the world, particularly for marginalised high-latitude regions.

The composition of high-latitude (i.e. marginal) coral assemblages is governed by a combination of physical (i.e. optimum temperature, light availability, aragonite saturation) and biological (i.e. competition, larval dispersal, settlement cues) factors (Abrego et al. 2021; Kleypas et al. 1999; Sommer et al. 2014). Corals that thrive in high-latitude regions are typically characterised by traits related to environmental tolerance (i.e. light, turbidity, wave exposure) (Mizerek et al. 2016). However, some of these biophysical limitations may be alleviated as a consequence of climate change, thus enabling increased abundance, diversity and reef-building capacity of corals at higher latitudes (Wernberg et al. 2016; Ribeiro et al. 2022; Yamano et al. 2011; Kumagai et al. 2018). Indeed, further range expansions of corals into higher latitudes are predicted to occur under climate change projections (García Molinos et al. 2016), as these reefs may provide suitable habitat areas for the recruitment and persistence of corals (Adam et al. 2021; Cacciapaglia and van Woesik 2015; Landry Yuan et al. 2023). Understanding how changes in the abundance and composition of coral assemblages affect their underlying trait structure is thus a key research gap with fundamental implications for reef-scale ecological processes (Denis et al. 2017; Gómez-Gras et al. 2021; McWilliam et al. 2020; Sommer et al. 2021; Zawada et al. 2019).

In tropical-temperate biogeographical transition zones, poleward range expansions and an increasing abundance of reef-building (Scleractinian) corals (hereafter, corals) at higher latitudes have been reported in multiple regions; including the Caribbean (Precht and Aronson 2004), the Mediterranean (Serrano et al. 2013; Serrano and Coma 2012), Korea (Denis et al. 2013, 2015), Japan (Kumagai et al. 2018; Yamano et al. 2011), the East Coast of Australia (Baird et al. 2012; Booth and Sear 2018; Schmidt-Roach

et al. 2013 but see Mizerek et al. 2021) and the West Coast of Australia (Ribeiro et al. 2022; Thomson 2010; Tuckett et al. 2017). The increasing abundance of more tropically affiliated habitat-forming foundation species as temperate species recede can result in novel ecosystem configurations (i.e. species compositions and relative abundances that have not occurred previously, *sensu* Hobbs et al. 2006) with significant ecological consequences (Vergés et al. 2019; Zarzychny et al. 2023)—a phenomenon known as “tropicalisation” (Vergés et al. 2014). Regime shifts to novel benthic foundational habitats can have large-scale ecological impacts (Filbee-Dexter et al. 2016; Maliao et al. 2008; Norström et al. 2009), as habitat-forming foundation species support numerous key ecosystem processes and services (Barbier et al. 2011; Filbee-Dexter and Wernberg 2018).

The Leeuwin Current (LC) is a major driver of patterns of biodiversity in Western Australia (WA) and changes in its intensity and/or timing have large implications for marine communities (Cresswell and Golding 1980; Pearce et al. 2011). The LC intensifies during the Austral autumn; however, during the 2010–2011 Pacific *La Niña* this intensification was abnormally strong and led to an influx of unusually warm water to higher latitude reefs (Benthuyssen et al. 2014; Pearce and Feng 2013). This resulted in an extreme marine heatwave (MHW), where sea surface temperatures (SSTs) reached up to  $> 3$  °C above the average summer maxima (Pearce et al. 2011; Pearce and Feng 2013). The MHW caused a regime shift in the benthic community at the northernmost distribution of kelps, with severe loss of golden kelp (*Ecklonia radiata*) across ~100 km of coastline, and a substantial increase in turf algae (Pessarrodona et al. 2021; Wernberg et al. 2016). At the same time there was a four-fold increase in the abundance of the subtropical-temperate specialist, *Plesiastrea versipora* (Juszkiewicz et al. 2022), possibly due to a combination of increased physiological performance due to higher temperatures and competitive release from the loss of kelp (Ribeiro et al. 2022; Tuckett et al. 2017). This biogeographical setting, and the subsequent regime shift in the dominant benthic foundational species, offers a unique opportunity to assess how environmental and biotic factors shape spatial signatures in the trait structure of coral assemblages at higher latitude reefs.

Here, we surveyed coral assemblages across subtropical and temperate reefs in WA (27.7°S–34.2°S) in two time points, 6 years apart. This time period coincides with a year (2015) immediately after an extreme marine heatwave event (2011) and subsequent warm summers (2012, 2013) that caused a fundamental re-structuring of shallow-water coastal assemblages in the region (Wernberg et al. 2016), as well as a year (2021) following a cooling phase (2016–2020) and a severe winter cold-spell (2016) that has been linked to declining persistence and activity levels of mobile ectothermic animals of tropical affinity (Bosch et al. 2022;

Stuart-Smith et al. 2022). We hypothesised that the taxonomic structure of coral assemblages would change over the 6-year period, and these changes would be more pronounced in the northernmost sampling locations where the kelp had disappeared. We additionally used a trait-based approach to assess spatial and temporal changes in the functional identity and diversity of the coral assemblages and hypothesised that different components of functional diversity would reflect the changes in taxonomic structure of the assemblage, with coral functional traits in tropicalised areas becoming more similar to tropical corals (i.e. faster growth rates, capacity to build three-dimensional structures).

## Materials and methods

### Study sites

Benthic communities on reefs in subtropical and temperate WA are typically characterised by diverse assemblages of macroalgae, including the dominant habitat-forming golden kelp (*E. radiata*) (Wernberg et al. 2003), whilst coral cover is low (<5%) (Ross et al. 2021). We surveyed 17 wave exposed, shallow (6–10 m depth), nearshore (0.5–1.5 km from the coast) sites across *ca.* 7° of latitude within five locations in 2015 and 2021: Kalbarri (27.7°S, *n*=2 sites), Port Gregory (28.1°S, *n*=4 sites), Jurien Bay (30.3°S, *n*=3 sites), Perth (Marmion Marine Park, hereafter Marmion) (31.8°S, *n*=5 sites), and Hamelin Bay (34.2°S, *n*=3 sites) (Fig. 1). There are clear transitions in geomorphological and ecological patterns across this subtropical-temperate transition zone, with northern locations characterised by limestone reefs dominated by turf algae and *Sargassum* (Fig. 1b, c), whilst southern locations are characterised by a mixed of limestone and granite reefs with dominance (>80% in

the southernmost locations) of *Ecklonia radiata* (Fig. 1d–f) (Wernberg et al. 2003; Wernberg et al. 2012).

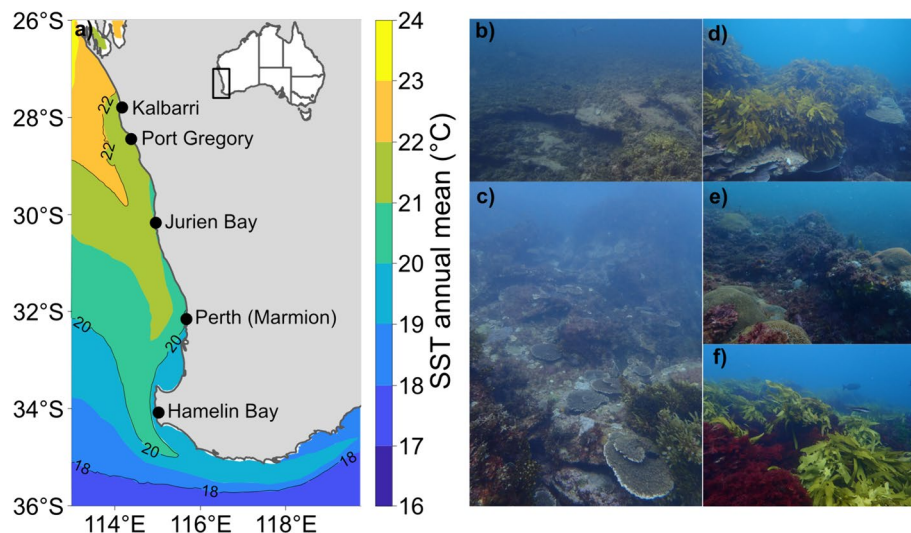
### Coral community data

At each sampling site, we photographed all corals greater than 1 cm in diameter within five 15 m<sup>2</sup> (1 m width × 15 m length) transects, and later identified them to genus level using taxonomic guides for the region (Richards 2018). Additionally, we visually estimated the dominant benthic group (i.e. *E. radiata*, *Sargassum* spp., turf algae) within each transect. Principal component analysis (PCA) was used to visually assess the differences in coral assemblage structure among sampling locations and years (2015 vs. 2021). The PCA was based on a Bray–Curtis dissimilarity matrix, with species abundances log<sub>10</sub> (*x* + 1) transformed to downweight the contribution of very abundant species. Due to small sample sizes in many coral genera, we pooled transect-level abundances at the family-level and tested for both differences in total coral abundance and differences in the abundance of each coral family. We used generalised linear mixed effect models (GLMMs) to test for differences in observed abundance between 2015 and 2021. All models were built using the ‘glmmTMB’ package in R (Brooks et al. 2017), using a negative binomial distribution. Sites, nested within each location, were used as a random error term to account for the hierarchical spatial structure of the sampling design. All models were inspected for violations of statistical assumptions using the ‘DHARMA’ package in R (Hartig 2021).

### Coral trait space

Spatiotemporal patterns in the functional structure of subtropical and temperate coral assemblages were examined

**Fig. 1** a Map of the southwest coast of Australia showing the five study locations. Coloured contours reflect mean annual sea surface temperature isotherms along the Western Australian coastline. Representative photographs of benthic community structures at b Kalbarri (27.7°S), c Port Gregory (28.1°S), d Jurien Bay (30.3°S), e Marmion (31.8°S), and f Hamelin Bay (34.2°S). Photographs: Albert Pessarrodona (b), Chenae Tuckett (e), Defne Sahin (c, d, f)



using a trait-based approach. Seven traits were selected based on their ability to capture coral-related ecosystem processes, as per McWilliam et al. 2018, 2020 (Table S1). Specifically, we used: growth rate (GR), skeletal density (SD), corallite width (CW), interstitial branch spacing (IB), colony height (CH), surface area to volume ratio (SV), and maximum colony size (CS) (Table S1). For each genus, trait scores were calculated from the mean trait values of species recorded within each region (Marsh and Veron 1998). Species level trait values were obtained from the Coral Trait Database (Madin et al. 2016) (Table S2). *Acropora* corals were further classified into growth forms (branching, plating, digitate, and corymbose) to allow for morphological trait score variability. We then generated a multidimensional coral trait space based on the seven traits selected to represent the functional structure and diversity of the coral communities. To visualise differences in trait space across sites, locations and sampling times, we computed a Principal Coordinate analysis (PCoA) on a Gower dissimilarity matrix, as it allows for a mixed type of traits (Gower 1971), using the 'mFD' R package (Magneville et al. 2022). We retained the first four PCoA axes to provide the most parsimonious choice that minimised the differences between original trait-based distances and Euclidean distances in the PCoA (MAD=0.319, Fig. S1 and Fig. S2) (Maire et al. 2015). These axes explained 80% of the variation in the original trait dissimilarities. A Kruskal–Wallis test was performed to calculate the correlation between individual traits and PCoA axes (Table S3).

### Shifts in the functional trait structure

Temporal changes in the trait structure of coral assemblages were visualised by computing their abundance-weighted position in the multi-dimensional functional space (Functional identity, Fide). We then tested for temporal changes in the functional diversity of coral assemblages by computing three complementary indices: functional richness (Frich), functional evenness (Feve), and functional divergence (Fdiv) (Mouillot et al. 2013; Villéger et al. 2008). Functional richness describes the volume occupied by all assemblages in the multidimensional space and was calculated as the 4D convex hull that connects all the points comprising that assemblage. Functional evenness describes the uniformity in the distribution of species in the trait space, weighted by their relative abundances, and was calculated as the minimum spanning tree linking all the genera in the assemblage. Functional divergence describes the portion of abundance that is related to the most extreme trait values (i.e. taxonomic groups that are placed on the edge of the convex hull). We omitted our southernmost location, Hamelin Bay, from this part of the analysis as the number of coral genera present was lower than the number of trait dimensions (i.e. PCoA

axes) included. All analyses were performed in R<sub>4.0.3</sub> (R Core Team 2020).

## Results

### Temporal changes in the coral assemblages

Over the two sampling periods we recorded corals from a total of 18 genera from 8 families (Table S2). Port Gregory had the most diverse assemblage with 18 genera from 8 families, whilst Hamelin Bay had the least diverse assemblage with 4 genera from 2 families. Multivariate analysis showed little change in coral assemblage structure among sampling locations between 2015 and 2021, with the exception of Port Gregory (Fig. 2d).

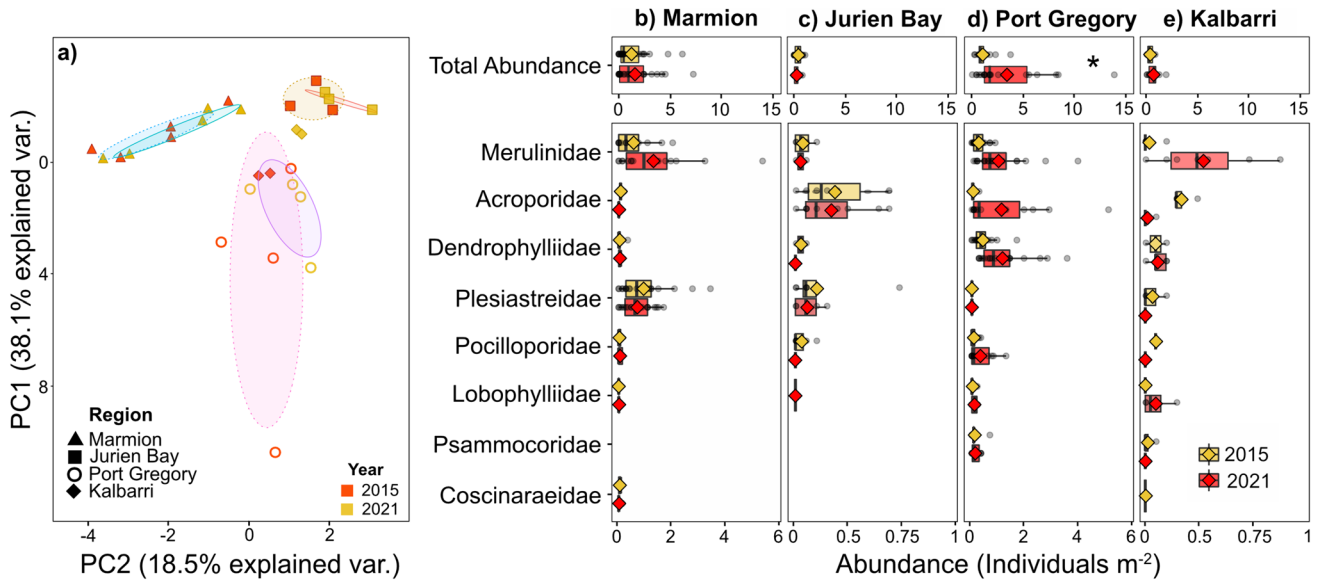
Total coral abundance increased between 2015 and 2021 across subtropical and temperate reefs in Western Australia, doubling from 3 individuals m<sup>-2</sup> to 6 individuals m<sup>-2</sup>. However, this increase was solely driven by one mid-latitude location, Port Gregory, where a significant 3.4-fold increase in the abundance of corals was observed (Fig. 2c, Tables S4 and S5).

Dendrophylliidae and Merulinidae were the most abundant coral families in Port Gregory in 2015, accounting for 39% and 27% of the coral assemblage, respectively (Fig. 2d, Table S4). In 2021, Dendrophylliidae (*Turbinaria* spp.) and Merulinidae were still the most abundant families (34% and 30%, respectively); however, the relative abundance of Acroporidae (largely plating *Acropora* spp. and *Montipora* spp.) increased from 7% in 2015 to 24% in 2021 (Fig. 2d, Table S4). In other locations, such as Marmion and Kalbarri, the relative abundance of Merulinidae (mostly *Coelastrea* spp. and *Paragoniastrea* spp.) increased from 2015 to 2021 (Fig. 2b and e, Table S4). This was primarily due to the increases in the genera *Coelastrea* in Kalbarri, and *Coelastrea* and *Paragoniastrea* in Marmion (Table S4). The coral assemblage structure in Jurien Bay remained largely unchanged (Fig. 2c, Table S4). In Hamelin Bay, coral assemblage mainly consisted of the genera *Plesiastrea*, and their contribution to the overall benthic structure was negligible (0.1 individuals m<sup>-2</sup>, Table S4).

### Changes in functional diversity

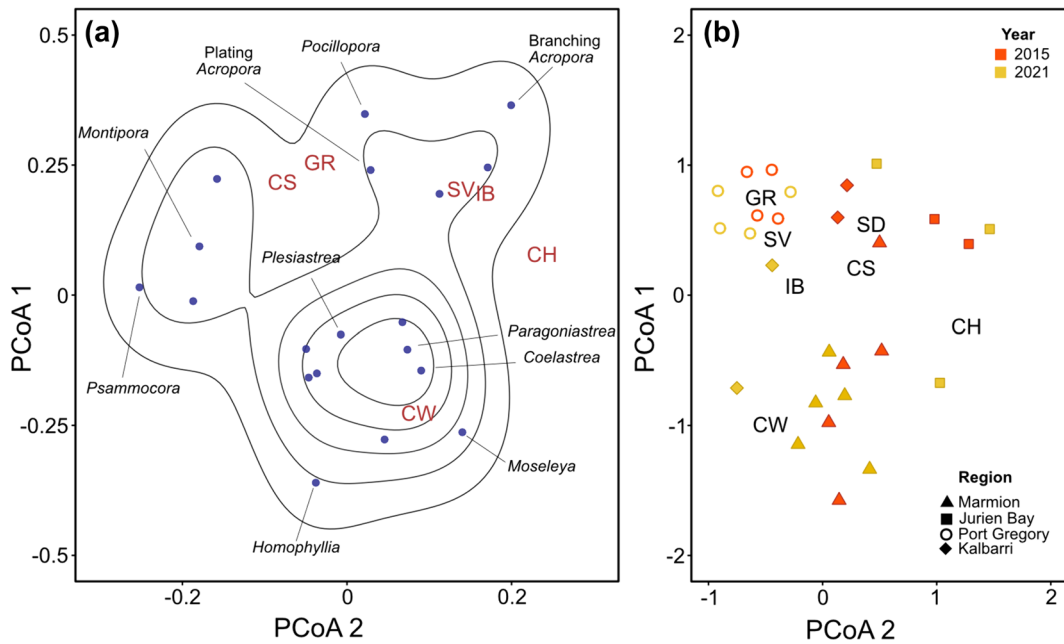
Most taxa were characterised by slow-growth rates, larger corallites, small surface areas, and simpler-dome shaped morphologies (Fig. 3a). A few taxa characterised by unique trait combinations (i.e. *Pocillopora*, *Psammocora*, and different growth forms of *Acropora*) clustered in the extremes of the trait space (Fig. 3a).

We observed some similarities in combination of coral functional traits along the subtropical-temperate



**Fig. 2** **a** PCA of coral assemblage structure at sampling locations in 2015 and 2021. The coloured ellipses (2015 represented with dotted outlines, 2021 represented with solid outlines) represent the 95% confidence intervals around the weighted average within each sampling site and time point. Confidence ellipses couldn't be drawn for Kalbarri due to the low ( $n=2$ ) number of sites. Abundance of dif-

ferent coral families within **b** Marmion, **c** Jurien Bay, **d** Port Gregory, and **e** Kalbarri in 2015 (yellow) and 2021 (red). Locations are arranged from high to low latitude, left to right. Diamonds indicate the mean abundance for each family. Please note different x-axis scales for the family level abundances



**Fig. 3** **a** Coral trait space showing the positions of 22 different taxonomic groups/growth forms (blue points) pooled across all sampling locations. Contour lines indicate the presence of distinct clusters of taxa. Acronyms identify the trait space: GR = Growth rate, SD = Skeletal density, CW = Corallite width, IB = Interstitial branching space,

CH = Colony height, SV = Surface area to volume ratio, CS = Maximum colony size. **b** Multidimensional trait space of survey location between the two sampling years. Each sampling location is positioned depending on the mean values of the seven functional traits weighted by the relative abundance of different coral groups

transition zone: assemblages were characterised by flat taxa with larger corallites, low surface areas and simple

dome-shaped morphologies across our sampling locations. Geographical variation in the functional structure was

associated with slower growth rates and smaller colony sizes with increasing latitude. We also observed a clear separation between the coral assemblages in Port Gregory and Marmion (Fig. 3b). Coral assemblages in Port Gregory were characterised by large, fast-growing taxa with high skeletal densities, whereas coral assemblages in Marmion were characterised by small, slow-growing colonies with low skeletal densities.

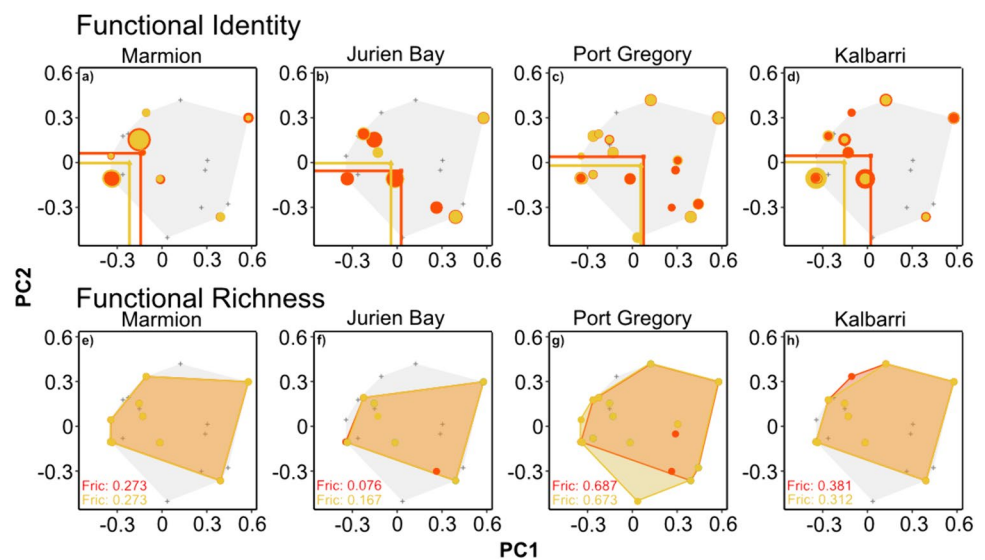
We observed subtle temporal changes in the functional identity (Fide) of coral assemblages in some locations. For instance, in Port Gregory (Fig. 4c), Fide shifted along the PCoA2 towards coral assemblages with smaller corallite widths, faster growth rates, and taller colonies. In contrast, coral assemblages in Jurien Bay (Fig. 4a) and Kalbarri (Fig. 4d) shifted along the PCoA1 toward larger corallite widths, slower growth rates, and smaller surface volume to area ratios.

Functional richness (Fric) differed across locations, with the highest Fric observed in Port Gregory and the lowest in Jurien Bay (Fig. 4e–h). Fric remained stable through time across all locations; apart from an expansion observed in the trait space occupied by the coral assemblages at Port Gregory (Fig. 4g). The variance and regularity of assemblage structure were not responsive to change, indicated by stable values of functional evenness (FEve) (Fig. 5a–d) and functional divergence (Fdiv) (Fig. 5e–h) between the sampling years.

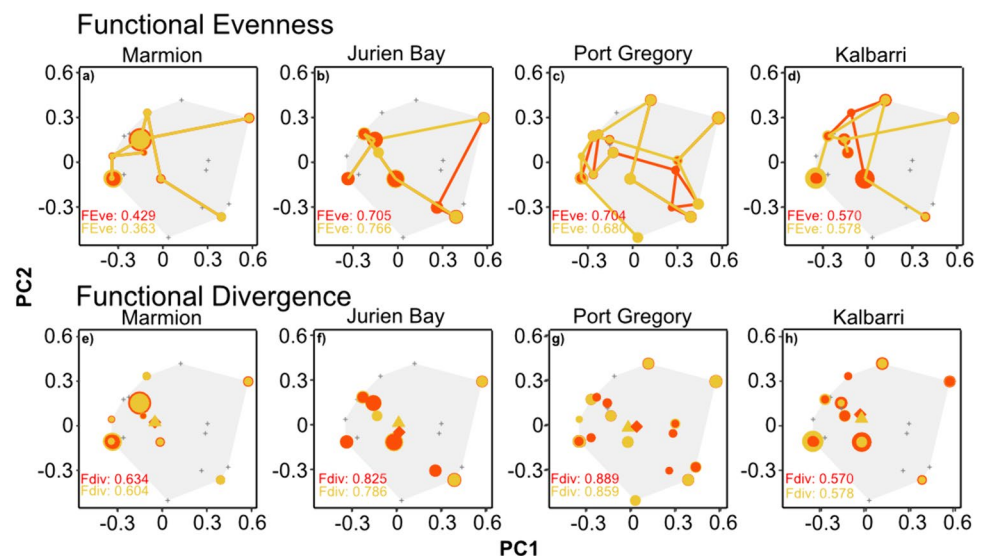
## Discussion

Our study captured spatiotemporal patterns in the taxonomic and functional trait structure of coral assemblages across a subtropical-temperate transition zone. Overall, we found a

**Fig. 4** a–d Functional identity of Marmion, Jurien Bay, Port Gregory and Kalbarri showing relative weights shown by red (2015) and yellow (2021) circles. e–h) Functional richness in Marmion, Jurien Bay, Port Gregory and Kalbarri, represented by the red convex hull from 2015 survey and yellow convex hull from the 2021 survey. Locations are arranged from high to low latitude, left to right



**Fig. 5** a–d Functional evenness of Marmion, Jurien Bay, Port Gregory, and Kalbarri showing relative weight of the groups in red and yellow for 2015 and 2021 surveys, respectively. e–g) Functional divergence of Marmion, Jurien Bay, Port Gregory, and Kalbarri showing relative weights shown by red (2015) and yellow (2021) circles and gravity centres shown by diamond and triangle for 2015 and 2021 surveys, respectively. Locations are arranged from high to low latitude, left to right



spatial signal in the functional characteristics of the surveyed coral assemblages which was connected to their latitudinal position. Across time, this fundamental spatial structuring of coral traits across this subtropical-temperate transition zone was maintained, with only subtle transitions in the trait structure observed at a mid-latitude location where drastic shifts from kelp to turf had occurred after the 2011 MHW (Wernberg et al. 2016; Pessarrodona et al. 2021). Changes in this mid-latitude region were associated with a significant increase in the abundance of corals and a signal of tropicalisation, with a nuanced shift from traits characteristic of temperate assemblages to traits characteristic of tropical counterparts. In particular, we found a shift from corals with large corallite widths, slow growth rates and simple morphologies towards corals with smaller corallite widths, faster growth rates and complex morphologies. This functional reshuffling at the warm range edge of temperate macroalgal forests could entail important shifts in the ecosystem processes supported by benthic foundational species if a shift from macroalgal dominance to coral dominance occurs in the region in response to global change scenarios (Verges et al. 2019). However, uncertainty remains on the direction to which these assemblages will continue changing given potential competition with other foundational species (Ribeiro et al. 2022), and resilience under future disturbances and environmental conditions.

Coral assemblages in Western Australia exhibited similarities in their trait structure across the latitudinal gradient, mainly dominated by dome shaped or flat taxa with large corallites and small surface areas. These traits are likely maximising energy acquisition as seen in other high-latitude coral assemblages (Sommer et al. 2014). For instance, flat or dome shaped morphologies optimise photosynthetic energy acquisition under light limited conditions (Hoogenboom et al. 2008). Lower three dimensionality also promotes physical stability in environments with high wave energy (Cresswell et al. 2020; Gove et al. 2015) and low reef rugosity (Alvarez-Filip et al. 2011; Gouezo et al. 2019). While these common traits highlight adaptations to marginal environments, subtle differences in the trait composition of coral assemblages were also observed across regions according to their latitudinal position. For instance, we found corals with higher growth rates and more complex morphologies at lower latitudes, which may be due to increased influence of tropically affiliated corals, which typically have higher growth rates (Andersen et al. 2017). Together, these patterns along the latitudinal gradients may be mediated by environmental filtering, which is known to be strong in regions characterised by high environmental stress (Sommer et al. 2014). A drawback of our study is that we used mean trait scores from an online database which is mainly dominated by studies from tropical coral reef ecosystems (Madin et al. 2016), and therefore did not account for intra-specific variation in

traits in response to environmental variation (Shipley 2013). This is particularly pertinent for those traits that are strongly shaped by environmental gradients such as temperature, for instance individual colony size variation across latitudinal gradients in coral assemblages (Chong et al. 2023). Understanding the contribution of intra-specific trait variance to species responses to environmental variation and their effects on ecosystem functioning is a hot topic of research in ecology and evolutionary biology (Albert 2015), and future studies in the region should account for this to test the robustness of the results presented here.

Despite the spatial structuring of coral traits along the latitudinal gradient being mostly maintained across time, we observed considerable changes in their taxonomic structure at some locations (Marmion, Kalbarri and Port Gregory), with the most significant change observed at Port Gregory (28.1°S). Port Gregory was also the only location where we found a significant increase in overall coral abundance and relative contribution of more tropically affiliated corals (i.e. plating and corymbose *Acropora*) to the overall assemblage. The alleviation of competitive interactions between corals and receding canopy-forming seaweeds is likely to be one of the main drivers of the increase in coral abundance at Port Gregory (Ribeiro et al. 2022), which has also been observed in other parts of the world (Japan; Kumagai et al. 2018). Port Gregory was heavily impacted by an extreme marine heatwave in 2011, which resulted in the loss of over 90% of canopy-forming seaweeds (i.e. *Ecklonia radiata* and *Sargassum* spp.). While the *Sargassum* cover has returned to pre-heatwave conditions, kelp cover has not and the system has since been dominated by low-lying foliose and turfing algae (Wernberg et al. 2016; Bosch et al. 2022). Low-lying foliose and turfing algae are known to be associated with larger and more abundant hard corals on subtropical reefs of Western Australia (Thomson et al. 2012) and could have mediated the observed changes in Port Gregory.

In addition to competitive release from canopy-forming seaweeds, multiple other factors may have led to the observed spatial and temporal changes in coral assemblages, which may also influence the future distributions of suitable coral habitats in tropical–temperate transition zones (Abrego et al. 2021; Beger et al. 2014; Sommer et al. 2017). For instance, gradual increases in SSTs may have played a role as observed in other parts of the world (Japan; Kumagai et al. 2018); however, in Port Gregory this is likely to be minor since SSTs have returned to pre-heatwave conditions (Bosch et al. 2022). The differences observed between Port Gregory and Kalbarri may have been influenced by the topographic features of these two locations. Port Gregory has higher rugosity (reef complexity), which is known to enhance coral settlement and survivorship (Alvarez-Filip et al. 2011; Carlson et al. 2024; Gouezo et al. 2019). Complex reefs also tend to have greater variation in a range of

physical parameters such as light, sediment cover and water motion (Toohey 2007), which can all influence rates of coral settlement and survival (Mundy and Babcock 1998; Birrell et al. 2005; Koehl and Hadfield 2010). Similarly, the survivorship of fragile species (i.e. taxa with fine branching growth forms) could be negatively affected by physical disturbance in exposed reefs (Edmunds et al. 2010; Gouezo et al. 2019; Madin and Connolly 2006; Williams et al. 2013). Other important factors such as larval supply and settlement could be contributing to the observed differences; however, these were not investigated as a part of this study.

We predicted that the temporal changes in the taxonomic structure of corals would be reflected in several indices of functional diversity. However, our results do not support this hypothesis because most dimensions (i.e. functional richness, functional evenness, and functional divergence) were not responsive to changes in the relative contributions of different taxonomic groups. It is possible that the time between our two sampling periods (i.e. six years) may not have been long enough for significant changes in functional diversity to manifest, especially considering the life history strategies of taxa that were highly abundant at the mid (i.e. Jurien Bay) and southern (i.e. Marmion) locations (i.e. stress tolerant taxa with slow growth rates) (Darling et al. 2012). The lack of strong temporal patterns in the trait structure of coral assemblages is also likely linked to their generally low abundance and cover (< 5%) across the study region, with changes at the functional level often requiring abrupt changes in the abundance of dominant taxonomic groups with distinct traits (McLean et al. 2018). Nevertheless, the functional identity of coral assemblages in Port Gregory shifted slightly from slower-growing massive corals, which typically define subtropical coral assemblages, towards more tropically affiliated species, characterised by faster-growing colonies and structurally more complex morphologies such as corymbose and tabular growth forms of *Acropora* spp. These groups of corals, particularly tabular *Acropora* play a key role in reef recovery and reassembly (Johns et al. 2014; Ortiz et al. 2021). Given their ‘competitive’ life-history strategies (i.e. capable of dominating assemblages through efficient use of resources) (Darling et al. 2012; Gold and Palumbi 2018; Madin et al. 2016; Pratchett et al. 2015), it is possible that the relative abundance of corymbose, plating and tabular *Acropora* may further increase over the coming years and promote higher structural complexity (e.g. habitat provisioning) (Angelini et al. 2011; Denis et al. 2017; Graham and Nash 2013; Kerry and Belwood 2015; Khan et al. 2017) and carbonate accretion (Perry et al. 2013; Vecsei 2001).

The abundance and diversity of coral assemblages at higher latitudes are governed by multiple abiotic and biotic factors (Abrego et al. 2021; Mizerek et al. 2016; Sommer et al. 2014). While some of these factors (e.g. competitive

release from other foundational species, Ribeiro et al. 2022; and, optimal thermal conditions, Landry Yuan et al. 2023) may favour the establishment of novel coral assemblages, other factors (e.g. light restrictions, declining aragonite saturation, genetic isolation) may limit their potential establishment at higher latitudes. Additionally, some of the factors that are expected to favour more tropically affiliated corals (i.e. optimal thermal conditions) could result in the loss of cooler-affinity taxa in high-latitude reefs as these corals can be more susceptible to bleaching (Bridge et al. 2014; Kim et al. 2019; Moriarty et al. 2023; Sommer et al. 2024; Thomson et al. 2011). The persistence of the subtropical assemblages supported by more tropically affiliated corals will also depend on the capacity of these species to persist under future disturbances and environmental conditions, including predicted habitat simplification under ocean acidification and warming (Agostini et al. 2021). Corals with ‘competitive’ life-history strategies are known for their vulnerability to bleaching events (Darling et al. 2013; Marshall and Baird 2000; Mcclanahan 2004; Wooldridge 2014), particularly compared to corals with ‘stress-tolerant’ life-history strategies (i.e. taxa with massive growth forms) (Loya et al. 2001; Van Woesik et al. 2011). Despite their higher susceptibility to bleaching events, however, *Acropora* corals have also been shown to recover in short periods (Morais et al. 2021) and may be the dominant species when the periods between disturbances are longer than two years (Pratchett et al. 2020). Further, expanding coral assemblages are predicted to be prone to seasonal temperature variations and cold-spells in higher latitude reefs, with likely species-specific susceptibility (Abrego et al. 2021; Tuckett and Wernberg 2018; Bringloe et al. 2022; Mcilroy et al. 2019). In fact, a tropicalised coral assemblage mainly dominated by multiple *Acropora* spp. in subtropical Japan experienced mass mortality following an extreme cold-spell event (Lerriorato and Nakamura 2019), while coral assemblages that are more temperate affiliated, dominated by *Plesiastrea versipora*, are shown to tolerate extreme cold spells (Tuckett and Wernberg 2018).

The overall abundance, composition, and persistence of coral assemblages play a crucial role in their ability to function as habitats. In our study, our surveyed reefs had < 5% coral cover, while a 5–10% coral cover was reported overall for the subtropical and temperate coast of Western Australia (Ross et al. 2021). Although these coral communities do not provide the full range of ecosystem functions seen in tropical coral reefs, the anticipated increase in habitat suitability and species richness (Adam et al. 2021) suggests that these assemblages hold the potential to contribute more significantly to reef-scale ecological processes. To date, much of the work on novel reef function has largely focused on transitions from coral to seaweed dominance in tropical zones (Bellwood et al. 2004; Hughes et al. 2017; Tebbett et al. 2023; Woodhead et al.



2019) here, we show the potential of tropicalised coral assemblages in temperate-tropical transition zones to provide important ecological functions beyond the historical distribution of coral reefs and emphasise the need to focus on these less marginal reefs.

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#### Declarations

**Conflict of interest** The authors declare no competing interests.

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