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Biotic Mechanisms Strengthen Functional and Phylogenetic Convergence of Reef Fish Assemblages at Higher Latitudes

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Keywords: competitive exclusion | environmental filtering | functional diversity | latitudinal diversity gradient | limiting similarity | phylogenetic diversity

ABSTRACT

Aim: How communities of organisms come together has long fascinated scientists, with renewed interest in using functional and evolutionary patterns to infer mechanisms of community assembly. Ecological theory predicts that biotic interactions could lead to either divergence in the event of niche partitioning or convergence through the exclusion of competitively inferior species, but most macroecological studies attribute the latter to environmental influences. Here, we investigated the relative importance of these two opposing mechanisms across broad spatial gradients. We hypothesised stronger signals of: (*i*) convergence at high latitude owing to ecological generalism and (*ii*) divergence at low latitudes owing to specialisation.

Major Taxa Studied: Reef-associated bony fishes.

Location: Global.

Time Period: 2006–2019.

Methods: We used a global dataset on marine reef fish assemblages comprising 2476 species at 3325 sites to disentangle the biotic drivers of community assembly across > 100° of latitude. We then applied a framework to remove environmental influences before examining whether any signs of biotic interactions remained in the trait and phylogenetic diversity of local communities relative to the (environmentally constrained) regional species pool, drawing on six functional traits and a phylogeny of bony fishes.

Results: Local fish assemblages were more functionally and phylogenetically similar to each other than expected based on the regional species pool at higher latitude reefs (i.e., show greater convergence). This pattern was evident after accounting for major sources of local environmental variation, suggesting exclusion of weak competitors. Functional convergence was mainly driven by traits related to resource acquisition, with high-latitude assemblages converging towards more energetic carnivorous and planktivorous diets.

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Main Conclusions: Our results suggest that biotic interactions drive greater trait and phylogenetic convergence from tropical to temperate zones. Likely mechanisms include increasing generalism and overlap in ecological strategies towards the poles, leading to the exclusion of weak competitors.

1 | Introduction

Understanding the drivers of species composition at the local scale has long been a central focus in ecology (MacArthur and Levins 1967; Ricklefs 1987). Historically, species found in local assemblages have been viewed as subsets of the regional species pool that (i) can find environmental and habitat conditions suitable and (ii) can co-exist on the finite set of ecological resources available, filling sufficiently different niches to avoid competitive exclusion (Weiher et al. 2011). This balance between the processes of "environmental filtering" and "limiting similarity" has often been inferred using functional traits; aspects of an organism's biology, physiology, life history and behaviour that indicate how they interact with their environment and with other organisms (McGill et al. 2006; Díaz et al. 2013). Under strong environmental filtering, local assemblages are expected to exhibit trait convergence relative to the regional species pool, as species share traits that allow them to tolerate local environmental and habitat conditions (Vellend 2010). Alternatively, stronger competitive processes are expected to result in trait divergence, as the species present show more ecological distinctiveness as a result of interspecific competition reducing the number of close competitors (i.e., niche partitioning) (HilleRisLambers et al. 2012).

Along these lines, phylogenetic patterns have also been used to infer assembly mechanisms with similar expectations (Cadotte et al. 2019), under the assumption that traits contributing to physiological tolerances (i.e., abiotic factors) and/or relative competitive ability (i.e., biotic interactions) are phylogenetically conserved across multiple clades (Webb et al. 2002; Cavender-Bares et al. 2009). Phylogenetic niche conservatism is, in fact, ubiquitous among many disparate taxonomic groups in the tree of life, although its strength can vary greatly among trait types that capture different aspects of species' ecological strategies (Ackerly 2009; Cano-Barbacil et al. 2022; Tuya et al. 2024). Nevertheless, phylogenetic information typically reflects coarse multivariate and generally conserved aspects of ecological similarity, whereas functional traits often reflect recent evolutionary divergence that speaks to competition for limited resources (Cadotte et al. 2019). Integrative studies that combine functional and phylogenetic information over large geographic scales are thus key, not only to decouple the ecological and evolutionary processes shaping local community composition, but also for mapping ecosystem functionality and prioritising conservation efforts (Hähn et al. 2024).

To date, most applications of functional and phylogenetic information to understand assembly processes have been restricted to a particular region (Weiher et al. 2011). These same tools, however, can be adapted in a biogeographic context to understand how the mechanisms driving community assembly change from region to region and across broader spatial gradients (Violle et al. 2014; Hähn et al. 2024). For instance, ecological theory relates the intensity of local competition to the well-described latitudinal gradient in species diversity. Specifically, species-rich tropical communities are expected to exhibit greater trait divergence because of a stronger and longer history of ecological interactions (Vermeij 2005; Schemske et al. 2009), physiological specialisation driven by low environmental variation (Janzen 1967; Carscadden et al. 2020; Delecambre et al. 2025) and/or increased rates of coevolution (Stenseth 1984), all leading to niche partitioning and non-overlapping traits observed in contemporary communities.

Conversely, in temperate communities, increased environmental variation is predicted to drive adaptation towards 'fixed targets', or trait values associated with generalism (Pianka 1966; Schemske 2002). For instance, high latitude communities are typically dominated by large-bodied individuals in many taxa, i.e., 'Bergmann's rule' (Fisher et al. 2010; Coghlan et al. 2024), a trait that is correlated with increased mobility (Griffiths 2010), larger home ranges (Reiss 1988) and greater dispersal and colonisation potential in animals (Bradbury et al. 2008; Luiz et al. 2012). Coupled with the overall lower richness and increased connectivity at higher latitudes (Mittelbach et al. 2007; Edgar et al. 2017), a higher degree of habitat and dietary generalism is expected to homogenise the regional species pool (Barneche et al. 2019; Ford and Roberts 2020; Stuart-Smith et al. 2021). As a result, there is a higher probability that any two members of a temperate community are more functionally and phylogenetically similar (i.e., show greater convergence) than otherwise expected from the broader regional species pool (Dynesius and Jansson 2000).

Critically, biotic interactions can also lead to either trait divergence *or* convergence among co-occurring species, depending on the circumstances (Mayfield and Levine 2010). Divergence occurs in the event of competitive sorting along niche axes, such as partitioning of soil properties among coexisting terrestrial plants (HilleRisLambers et al. 2012; Suárez-Castro et al. 2022). Conversely, convergence occurs when coexisting species have strong differences in their competitive ability for a limiting factor, such as light in terrestrial plants, therefore excluding species with competitively inferior traits (Mayfield and Levine 2010). This dichotomy is problematic, as many studies have interpreted trait convergence as evidence for strong environmental filtering, when it may instead indicate a significant signal of biotic interactions above and beyond any environmental drivers (Lamanna et al. 2014).

One way to isolate the effect of biotic interactions on community assembly from those associated with environmental filtering is to first control for (or remove) the effects of the environment. Once environmental effects are removed, patterns in functional or phylogenetic diversity can then, in theory, be interpreted as driven by biotic interactions, as in the framework proposed by de Bello (2012) (Figure S1). This approach relies on the careful definition of the regional species pool to only include species that have similar general habitat requirements and environmental tolerances. Then, within a given pool of species with shared habitats and environmental tolerances, values of local functional or phylogenetic diversity can be compared to this environmentally filtered pool to determine if either of the two explicitly biotic mechanisms identified above are operating: competitive sorting along niche axes leading to divergence or weak competitor exclusion leading to convergence. In the absence of either, one would infer dominance of environmental control or of stochastic processes. By restricting species in the larger pool to those with shared habitat/environmental associations, this approach essentially asks if there is any remaining biological signal driving community assembly above and beyond what is attributed to larger-scale variations in the environment.

The framework proposed above does not require the construction of complicated null models, where trait or phylogenetic distances are randomised among communities (Gotelli 2000; de Bello et al. 2012). Moreover, the ability of null models to discriminate assembly rules can be sensitive to methodological aspects, such as the choice of metric and the magnitude of the observed values of diversity (Münkemüller et al. 2020). Under this framework, significant divergence or convergence is instead detected by measuring the difference between the local diversity and the diversity of the environmentally filtered species pool, which can be compared to the null expectation that the difference is zero using a simple and interpretable *t*-test. Additionally, these effect sizes can be used as responses in modelling frameworks to understand how their magnitude is shaped by global environmental gradients, in contrast to other methods used to identify assembly processes that yield insightful but largely qualitative inferences regarding community assembly (Dray et al. 2014).

Reef fishes represent an ideal taxon with which to test how mechanisms of community assembly vary across global gradients, as they are an extremely diverse group of vertebrates, occupy a wide range of ecological roles and are comparatively well-described and understood (Villéger et al. 2017). Richness of marine fishes follows the classic pattern with latitude, increasing towards the equator (Tittensor et al. 2010; Edgar et al. 2017), thus generating testable hypotheses with respect to the role of local biotic interactions. Further, functional trait diversity among marine fishes does not always adhere to the same global pattern as richness (Stuart-Smith et al. 2013), suggesting that functional traits may provide further insight into the biological processes limiting observed local diversity. To date, only a few basin-specific empirical studies have tested for the relative importance of neutral dynamics, environmental filtering and biotic interactions in community assembly across latitudinal gradients in marine fishes (Ford and Roberts 2020; Bosch et al. 2021). In these studies, greater convergence in functional traits and evolutionary relationships was identified in local fish assemblages at higher latitudes, an effect that was mainly attributed to a greater effect of environmental filtering and homogenising dispersal in temperate regions. However, the degree to which such patterns could reflect any biological processes remains to be tested.

Here, we present an analysis of biotic drivers of local assembly using data from a global survey of reef-associated bony fish communities by the Reef Life Survey program (RLS, www.reeflifesurvey.com) (Edgar et al. 2020). We calculated functional diversity using multiple functional traits representing differences in morphology, trophic ecology, behaviour and habitat use (Table S1) and phylogenetic diversity using a published phylogenetic tree for ray-finned fishes (class Actinopterygii) (Rabosky et al. 2018). We used the framework proposed by de Bello (2012) to restrict the regional pool to those species that share similar environmental and habitat preferences (Figure S1), then ask the following questions about the role of biotic interactions in community assembly across global gradients: (i) do temperate marine fish assemblages display greater trait and phylogenetic convergence, therefore indicating exclusion of competitively inferior species; (ii) is convergence in temperate regions driven by traits related to mobility and generalism, in terms of habitat and resource use; (iii) do tropical marine fish assemblages display trait and phylogenetic divergence as a result of competitive sorting and niche partitioning; (iv) is divergence in tropical regions driven by traits related to habitat and resource specialisation; and (v) does broad-scale variation in the abiotic environment influence the strength of local biotic interactions?

2 | Methods

2.1 | Reef Life Survey Data

Fish community data were collected through the Reef Life Survey program, a global hybrid volunteer-science initiative that combines visual censuses from scientific and skilled volunteer SCUBA divers. Briefly, divers ran a 50-m transect across shallow reef habitats (7.4 ± 3.8 m, mean ± SD depth) and visually recorded the identity, abundance and size of every observed ray-finned fish species within 5-m-wide lanes on each side and 5-m above the length of the transect (500 m^2 area). Further specifics about the survey methods, including diver training, quality control, biomass conversion, data consistency and management can be found in Edgar and Stuart-Smith (2014) and Edgar et al. (2020). In all, we used data from 7044 transects at 3325 sites in 81 'Marine Ecoregions of the World' (MEOWs, Spalding et al. 2007) and spanning 100° of latitude and every continent except Antarctica (Figure S2). To control for varying temporal effort across the globe, we retained a snapshot of the data, corresponding to surveys (i.e., transects) undertaken only from 1 year at each site (from 2015, or the closest year to this at which the site was surveyed). We chose this year as it was roughly in the middle of the RLS dataset, and most sites were surveyed within 3 years of 2015 (i.e., most data come from the period 2012–2018).

For this analysis, we averaged the abundance and biomass of each species across transects at the site level, as the number of individual surveys varied across geographic space. We note, however, that this approach can still bias comparison of biodiversity estimates if the sampling effort (i.e., number of transects) per site was insufficient to adequately characterise the community, which is directly related to the species-abundance distribution of the communities compared (Chao and Jost 2012). To assess this, we evaluated the degree of sampling completeness at each site, using coverage-based rarefaction techniques implemented via the *iNEXT* R package (Hsieh et al. 2016). Coverage-based rarefaction compares communities based on their degree of completeness, which is the proportion of the total number of individuals in a community that belong to the species represented in the sample (Chao and Jost 2012). This analysis showed that most communities had sampling completeness levels between 0.97 and 0.99 (10th and 90th percentile, respectively; Figure S3), but there were some outlying sites with low coverage. To standardise this, we decided to only analyse sites with sampling completeness levels > 0.90, an adaptive threshold that captures communities that were sufficiently sampled (Chao and Jost 2012).

2.2 | Fish Functional Traits and Phylogeny

In total, 2476 unique fish taxa were recorded from 143 families. Six functional traits representing differences in morphology, trophic ecology, behaviour and habitat use were scored for each: maximum length (cm), trophic guild, water column position, habitat, diel activity and gregariousness (Table S1). The traits selected represent relevant axes of ecological niche variation in reef fishes, expected to influence habitat and resource partitioning among locally co-occurring species and have been widely applied in previous biogeographical trait-based analysis (Stuart-Smith et al. 2013; Mouillot et al. 2014; Bosch et al. 2021). Body size is a universal trait directly linked to species' metabolic demands (Gillooly et al. 2001), constraining predator–prey interactions within size-structured marine food webs (Coghlan et al. 2024) and correlating with a broad suite of life-history parameters that influence species' performance along environmental gradients (Thorson et al. 2017). Trophic guild determines the role species play in the movement and/or storage of energy and materials and, therefore, contributes critically to ecosystem functions such as food web regulation and nutrient cycling (Parravicini et al. 2020). Water column position, habitat and diel activity can be important in modulating the nature and strength of biotic interactions across time and space dimensions, such as partitioning foraging areas among competing species (Streit et al. 2019) and escaping predation from diurnally or nocturnally active predators (Campanella et al. 2019). Gregariousness is an important facet of fish behaviour that is linked to foraging success and predator avoidance in some species (Stier et al. 2013).

Trait values were mostly based on data obtained from FishBase (www.fishbase.org), although some were allocated based on expert knowledge (see Supporting Materials S1 in Stuart-Smith et al. 2013). The species-by-trait matrix was converted into a Gower's distance measure, which combines both continuous and categorical information into a single distance measure, using Podani's correction for ordinal data (Gower 1971; Podani 1999). To balance the contribution of different types of traits to the dissimilarity matrix (e.g., categorical vs. ordinal vs. numeric), we computed Gower distances using the argument *"weight"* of the *gawdis* R package (de Bello et al. 2021). Importantly, this set of traits characterises relatively independent and non-redundant facets of species' ecological niches, which could otherwise influence the dissimilarity matrix used to assess the degree of trait convergence versus divergence in local assemblages (Lepš et al. 2006; Coulon et al. 2023).

We additionally sourced an all-taxon assembled phylogenetic tree from time-calibrated phylogenies in the ray-finned fish tree of life (Rabosky et al. 2018) and computed cophenetic distances as a proxy for ecological similarities (Losos 2008). The phylogenetic tree, downloaded as nexus format via the *fishtree* package in R (Chang et al. 2019), contained information for roughly 90% of the species recorded (2224 out of the 2476). The missing species, which were generally identified at a higher taxonomic level (genus or above), contributed only 1.8% of the total biomass observed across the entire dataset, and there were no systematic biases in their geographic location. Hence, we excluded these observations from the phylogenetic analyses.

2.3 | Defining the Sub-Ecoregional Species Pools

To test for the effect of biotic interactions on community assembly, we implemented the framework described in de Bello (2012). This required the construction of a restricted species pools consisting of species with similar environmental and/or habitat requirements. We note that, by definition, the dataset is already constrained to only coral and rocky reefs, but to generate the restricted species pools, we first tallied all species observed within a given MEOW (Spalding et al. 2007) and then restricted the species pools based on site-level abiotic characteristics within each MEOW, including depth, sea surface temperature (mean and range), salinity (mean and range), nitrates (mean and range), net primary productivity (mean and SD) and wave energy (mean and SD), as well as geomorphological variables and an index of human population density (see Table S2 for details). The restriction of species pools based on similar site-level abiotic properties was done using *k*-means clustering. We determined the optimal number of 'sub-ecoregions' per MEOW by iteratively fitting to an increasing number of clusters and comparing using the Duda–Hart test (Duda and Hart 1973). *K*-means clustering was conducted using the *fpc* package in R (Hennig 2014). Species pools that were based on fewer than 5 species were discarded from any subsequent analyses. This exercise produced 920 species pools (i.e., 'sub-ecoregions') within 81 MEOWs for the final analysis, with an average of 11.3 species pools within each MEOW.

Because the coarse spatial grain (~5 km) of wave exposure values extracted from the WAVEWATCH hindcast may not accurately capture the scale at which wave energy influences fish community composition in coastal environments, we ran a supplementary analysis using a scoring index of exposure from Stuart-Smith et al. (2018). This index included four categories: (1) sheltered, with only wind waves < 1 m from non-prevailing direction, (2) wind-generated waves 1–3 m from the prevailing direction, (3) exposed to ocean swells < 3 m, either indirectly with exposure to prevailing winds, or directly but sheltered from prevailing winds, and (4) exposed to open ocean swell from prevailing direction. We also included fine-scale habitat information, extracted from photoquadrats taken by RLS divers along each transect (20 images per 50 m transect, spaced at 2.5 m intervals). The percent cover of major benthic functional groups was calculated using the Squidle + (https://squidle.org/) annotation software (see details in Edgar et al. 2020). We considered five benthic functional groups: coral, macroalgal canopies, dead coral, turf and other sessile benthos, as these have been shown to represent extremes in the availability of nutritional resources to fish consumers (Fraser et al. 2020) that can influence local assembly mechanisms (Bosch, Pessarrodona, et al. 2022). The supplementary analysis included 45% (1511) of the original sites for which we had this information, which covered a similar latitudinal span (−51° to +55°, range 107°), and included 309 species pools (i.e., 'sub-ecoregions') within 48 MEOWs, with an average number of 6.44 species pools within each MEOW.

2.4 | Community Assembly Indices

For each site, which we considered to be a separate community, we calculated functional and phylogenetic diversity using an attribute diversity framework based on generalisations of Hill numbers (Chao et al. 2014). This framework quantifies the effective number of functional and phylogenetic entities in an assemblage, which are defined by a threshold parameter (τ) that defines whether species are considered functionally or phylogenetically equally distinct (Chao et al. 2010, 2019). Species with distance below τ belong to the same virtual functional or phylogenetic group and, therefore, are assumed to compete more strongly. Here we define τ as the average trait or phylogenetic dissimilarity in the Gower or cophenetic distance matrices, respectively, of those species co-occurring in each sub-regional species pool. This framework produces a parametric family of diversity indexes that vary as a function of 'q', a parameter that controls the importance of species' relative abundances. Importantly, these metrics obey the replication principle and, therefore, do not suffer from the interpretational problems of other widely used metrics such as Rao's quadratic entropy (Rao's Q) (Ricotta and Acosta 2014). The FD and PD indices were calculated based on compositional data (presence/absence; i.e., $q = 0$) using functions in the *mFD* R package (Magneville et al. 2022), excluding sites with fewer than three species. To check inferences from the larger analysis, we further recalculated the functional and phylogenetic diversity using abundance- and biomass-weighted indices, with $q = 1$, so species' contribute proportionally to their relative abundances or biomasses (i.e., Shannon diversity, Chao et al. 2014, 2019).

We calculated diversity indices identically for each of the newly defined sub-ecoregional species' pools (Div_{pool}, i.e., one for which environmental filters have been accounted) and then subtracted this from that of each local assemblage (Div_{comm}) to generate an effect size: $ES = Div_{comm} – Div_{pool}$. If the local assemblage has higher functional or phylogenetic diversity than the sub-regional pool ($Div_{comm} > Div_{pool}$, or $ES > 0$), then that local assemblage exhibits greater variation in functional traits or phylogenetic distance than the sub-regional species pool (divergence), which, in this framework, we interpret as a stronger role of limiting similarity or niche partitioning. If the local assemblage has lower diversity than the regional pool ($Div_{comm} < Div_{pool}$, or $ES < 0$), then that local assemblage exhibits less variation in traits or phylogeny than the regional species pool (convergence), which we interpret as evidence of the exclusion of weak competitors. If the difference is close to zero ($Div_{comm} \approx Div_{pool}$, or $ES \approx 0$), then the assemblage is simply a random subset of the sub-regional pool, which we interpret as showing dominance of environmental control or stochastic processes rather than either of the aforementioned biological processes (de Bello et al. 2012). We tested for significant differences from zero using a Student's t-test, with $\alpha = 0.05$. Prior to this, we visually inspected the data for violation of normality assumptions (Figure S4). For comparisons of effect sizes between latitudinal zones, we used a Welch's t-test to account for unequal variances. We considered local assemblages $\leq 20°$ of latitude as tropical and those $> 20°$ of latitude as temperate.

2.5 | Analysis of Global Drivers

We used generalised linear mixed effects models (GLMMs) to predict the continuous variation in the above effect sizes with latitude while accounting for broader environmental covariates across regions. These included mean sea surface temperature (SST), mean nitrates and mean salinity derived from the BIO-ORACLE dataset at ~9.2 km resolution (Tyberghein et al. 2012), mean net primary productivity and mean wave energy derived from the Marine Socio-Environmental covariates dataset at ~5 km resolution (Yeager et al. 2017), human population density from LandScan at ~1 km resolution, depth and species richness from the Reef Life Survey data. For the latter, we calculated both local community richness and sub-regional pool richness. These metrics were highly collinear ($r = 0.77$), and therefore, we only retained local richness for the analysis. The remaining predictors had correlations $r < 0.7$ and variance inflation factors (VIF) < 5, indicating limited multicollinearity (Figure S5, Table S3). Prior to model implementation, some predictor variables were $\log_{10}$-transformed to improve their distribution, and all predictors scaled (mean 0 and SD 1) so their effects can be directly comparable.

Because we expected a hump-shaped relationship between latitude and ES values, we specified the latitude effect as a second-order polynomial. We allowed the intercept of the main effects to vary by the random effect of the corresponding sub-ecoregion identified during the k-means clustering. Mixed models were constructed using the *lme4* package in R (Bates et al. 2015), with partial effects and 95% confidence intervals, based on the variance of the fixed effects only, calculated using the *effects* package in R (Fox 2003). Standardised effect sizes and variance explained (R^2) were calculated using the *piecewiseSEM* package (Lefcheck 2016). We held a study-wide $\alpha = 0.05$ to assess statistical significance. Violation of model assumptions was visually investigated by checking residual patterns and spatial autocorrelation via semivariograms and Moran's I test. The latter revealed the presence of significant spatial autocorrelation in the model residuals (Moran's $I = -0.03$, $p = 0.001$ for the functional model; Moran's $I = -0.06$, $p < 0.001$ for the phylogenetic model). However, given this value was very close to zero and that the correlation mainly occurred at very small distances (< 30 km, Figure S6), this degree of spatial autocorrelation is unlikely to affect the robustness of our results.

3 | Results

3.1 | Latitudinal Variation

Based on our comparison of local to regional diversity, we found evidence that local assemblages exhibited less variation in functional traits than sub-regional species pools, indicating significant functional convergence in both tropical ($t_{1285} = -13.62$, $p < 0.001$) and temperate realms ($t_{2037} = -46.24$, $p < 0.001$) (Figure 1a). Functional convergence was, on average, 3.6× stronger in temperate communities than in tropical ones, based on comparison of effect sizes (mean $ES_{Trop} = -0.17$ vs. $ES_{Temp} = -0.64$, Welch's $t_{3237.3} = -24.50$, $p < 0.001$). Phylogenetic distances also exhibited less variation within local assemblages than within sub-regional species pools, indicating significant phylogenetic convergence in tropical ($t_{1285} = -50.30$, $p < 0.001$) and temperate realms ($t_{2037} = -62.11$, $p < 0.001$). In this case, the magnitude of differences between realms was smaller, with phylogenetic convergence being, on average, 1.4× stronger in temperate communities compared to tropical ones ($ES_{Trop} = -2.12$ vs. $ES_{Temp} = -3.11$, Welch's $t_{3311} = -15.11$, $p < 0.001$) (Figure 1b). Overall, the FD and PD metrics displayed similar patterns in community assembly, although the latter displayed stronger signals of absolute convergence in both tropical ($ES_{FD} = -0.17$ vs. $ES_{PD} = -2.12$) and temperate realms ($ES_{FD} = -0.64$ vs. $ES_{PD} = -3.11$).

The functional (trait) and phylogenetic effect sizes displayed an inverse parabolic relationship with latitude, decreasing towards the poles (Figure 2). We also calculated FD metrics for each trait individually to understand whether conflicting patterns among individual traits may have altered or weakened the overall trends. These results revealed that the larger global trends are driven primarily by trophic group (Figure 3, Table S4). Local fish assemblages showed greater convergence in resource (i.e., general diet) use with increasing latitude ($\text{Latitude}^2 = -7.05 \pm 2.71$, $p = 0.01$). At higher latitudes, a greater proportion of the

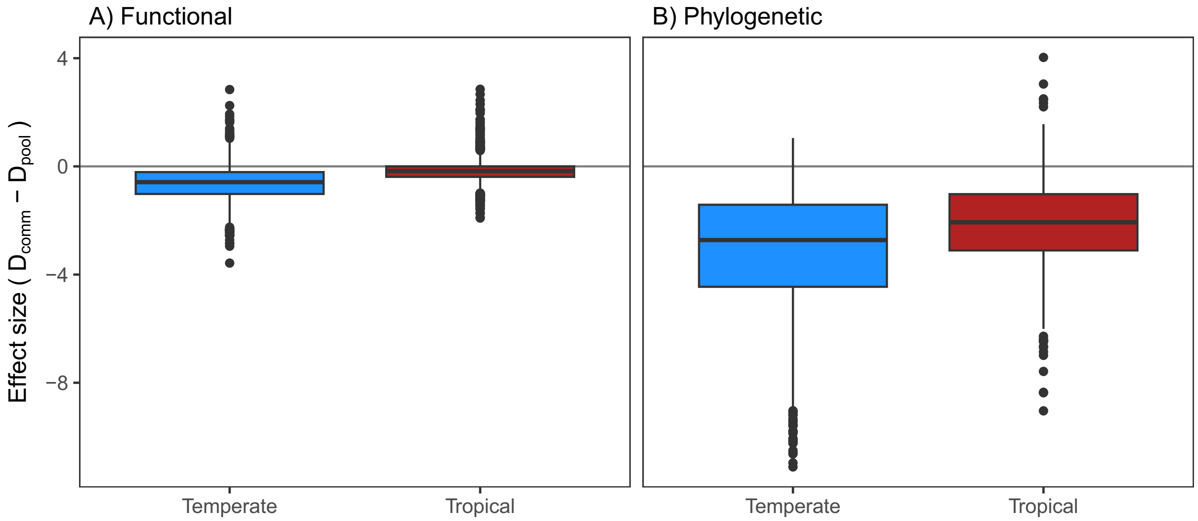

FIGURE 1 | (A) Functional and (B) phylogenetic patterns of community assembly reveal significant convergence in tropical and, to an even greater degree, in temperate ecoregions. Effect sizes were calculated as functional or phylogenetic diversity (based on presence/absence data) of the sub-regional species pool (D_{pool}) subtracted from the diversity of a local community (D_{comm}). More negative numbers thus reflect increased convergence among community members (i.e., greater similarity of traits or phylogenetic diversity). Tropical communities were defined as those between −20° and 20° latitude, and temperate ones anything outside of the tropical range.

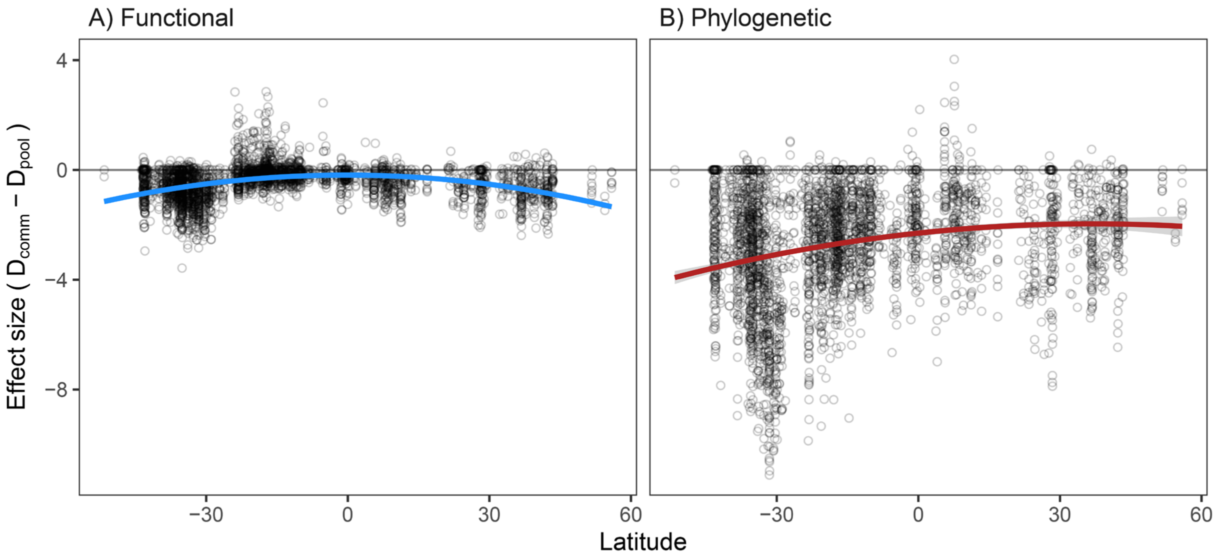

FIGURE 2 | (A) Functional and (B) phylogenetic convergence among reef fish community members increases with latitude. Points reflect the functional or phylogenetic diversity (based on presence/absence data) of a local community relative to the diversity of the species pool (i.e., effect size, ES). More negative numbers thus reflect increased convergence among community members (i.e., greater similarity of traits or phylogenetic diversity). Coloured lines indicate predicted fits from a second-order polynomial regressing each measure of effect size against latitude.

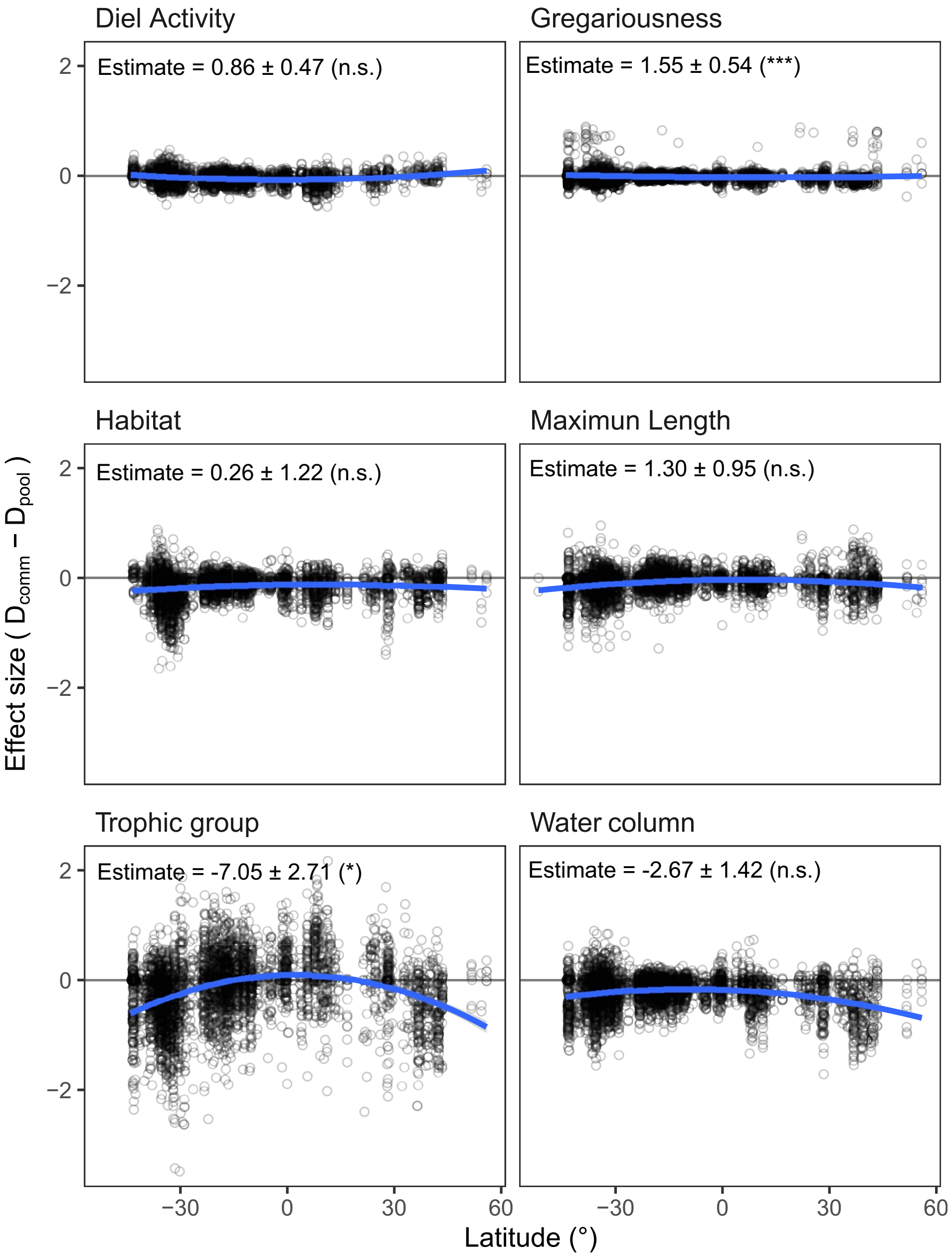

FIGURE 3 | Predicted fits ±95% confidence intervals from a second-order polynomial regressing effect sizes derived from each individual functional trait (calculated on presence/absence data) against latitude. The parameter estimate (±SE) and its significance are indicated in each panel. Interpretation of the y-axis is shown in Figure 2.

total community abundance was dominated by carnivores ($F_{13,450} = 1819{,}9$, $p < 0.001$) and planktivores ($F_{11,412} = 591.87$, $p < 0.001$), the largest increase for any modality of these traits near the poles (Figure S7). In contrast, low-latitude regions had a more even distribution of total community abundance among the modalities of these traits, indicating greater differentiation in resource use.

Contrary to expectations, the trait of maximum length displayed a flat relationship with latitude, indicating that interspecific variation in maximum body size was unrelated to the patterns of convergence found across latitude here. This contrasts with the patterns observed for average individual body size (total length) of fishes recorded on any given survey, which increased with increasing latitude ($F_{13,487} = 1259.3$, $p < 0.001$; Figure S8). Individual fishes in temperate assemblages were, on average, 42% longer than those in tropical ones ($t_{9,014.9} = 44.27$, $p < 0.001$). The remaining traits displayed either a flat relationship or a weak inverse pattern (e.g., gregariousness) (Figure 3).

3.2 | Global Drivers

The relative effect of broad-scale environmental, geophysical and anthropogenic drivers in explaining global variation in effect sizes differed between functional and phylogenetic diversity metrics (Tables 1 and 2). The FD effect size was solely explained by nitrates and species richness, both of which had a significant positive effect (Table 1), revealing a trend from convergence to divergence with increasing species and resources (Figure S9). In all, this model

TABLE 1 | Output from a generalised linear mixed effects model regressing effect sizes based on functional traits (calculated on presence/absence data) against key predictors. The level of statistical significance is denoted as n.s. (non-significant), *** ($p \leq 0.001$), ** ($p \leq 0.01$), * ($p \leq 0.05$).

Predictor	Estimate	SE	df	Crit. value	*p*	Significance
Depth	0.0194	0.0101	2860.4887	1.923	0.0546	n.s.
SST (mean)	−0.0865	0.0538	981.3444	−1.606	0.1087	n.s.
Salinity (mean)	0.0180	0.0175	893.7625	1.027	0.3047	n.s.
Nitrates (mean)	0.0973	0.0157	966.0201	6.174	< 0.001	***
NPP (mean)	−0.0311	0.0169	1043.5469	−1.834	0.0669	n.s.
Log$_{10}$-human population	−0.0293	0.0169	1019.0550	−1.733	0.0834	n.s.
Wave exposure (mean)	−0.0044	0.0128	1784.1364	−0.348	0.7282	n.s.
Latitude^2	1.4639	2.7683	916.4678	0.529	0.5971	n.s.
Log$_{10}$-species richness	0.3800	0.0172	2915.7271	22.034	< 0.001	***

Note: Latitude was calculated as a second-order polynomial, and orthogonal axes were extracted and included as covariates in the model.

TABLE 2 | Output from a generalised linear mixed effects model regressing effect sizes based on phylogenetic distance (calculated on presence/absence data) against key predictors. The level of statistical significance is denoted as n.s. (non-significant), *** ($p \leq 0.001$), ** ($p \leq 0.01$), * ($p \leq 0.05$).

Predictor	Estimate	SE	df	Crit. value	*p*	Significance
Depth	0.1438	0.0274	3085.5879	5.233	< 0.001	***
SST (mean)	−1.8211	0.2435	887.3443	−7.478	< 0.001	***
Salinity (mean)	−0.1065	0.0820	802.2137	−1.299	0.1943	n.s.
Nitrates (mean)	0.4414	0.0725	815.0951	6.081	< 0.001	***
NPP (mean)	0.0335	0.0721	1253.0683	0.465	0.6423	***
Log$_{10}$-human population	0.3194	0.0729	1169.2215	4.380	< 0.001	***
Wave exposure (mean)	0.1163	0.0405	3296.4370	2.870	0.0041	**
Latitude^2	2.2625	12.7950	846.6058	0.177	0.8596	n.s.
Log$_{10}$-species richness	2.6079	0.0465	2993.4012	56.043	< 0.001	***

Note: Latitude was calculated as a second-order polynomial, and orthogonal axes were extracted and included as covariates in the model.

explained 25% of the variance ($R^2 = 0.25$) in the functional effect size based on the fixed effects alone and 55% ($R^2 = 0.55$) with the addition of the random effect of sub-ecoregion. In comparison, the PD effect size was significantly explained by a larger suite of predictors, including local species richness, sea surface temperature, nitrates, human population, depth, wave exposure and net primary productivity (ranked based on decreasing standardised regression coefficients, Table 2). Accordingly, this model explained a greater proportion of variance, both based on fixed effects alone ($R^2 = 0.35$) and with the addition of the random sub-ecoregional term ($R^2 = 0.88$). Among these, all but SST displayed a significant positive relationship, revealing a trend from convergence to divergence with high resource availability, greater depths, wave energy and human pressures (Figure S10). On the other hand, increasing SST led to stronger phylogenetic convergence independent of changes in latitude (Figure S10), suggesting that the patterns in PD convergence observed across latitudinal scales are not necessarily a function of co-varying gradients in SST.

Importantly, after accounting for global variation in these predictors, particularly local species richness, the quadratic effect of latitude on ES values became non-significant (Tables 1 and 2). This result signals the major role that historical processes have played in shaping the patterns reported here through already limiting the pool of species, and in extension the extent of trait variation, at high-latitude regions. It also reinforces the covariance between latitude and environment. Nevertheless, our models retrieve a significant and independent effect of latitude on functional effect sizes when solely accounting for variation in trophic group identity (Table S4), which supports the importance of ecological mechanisms via competition for specific energetic resources.

3.3 | Sensitivity Analysis

We conducted several additional analyses to assess the robustness of these results. First, we calculated abundance- and biomass-weighted indices of functional and phylogenetic diversity, under the assumption that patterns of niche partitioning or exclusion of weak competitors would more strongly manifest when taking into account dominance patterns. Overall, we found nuanced differences between biomass- and abundance-weighted indices. The former generally supported the inferences from analysis using compositional (presence/

absence) data, with significant functional and phylogenetic convergence in both tropical ($ES_{Trop} = -0.17$, $t_{1,285} = -7.38$, $p < 0.001$ for FD; $ES_{Trop} = -0.78$, $t_{1,285} = -16.36$, $p < 0.001$ for PD) and temperate realms ($ES_{Temp} = -0.36$, $t_{2,037} = -19.07$, $p < 0.001$ for FD; $ES_{Temp} = -0.82$, $t_{2,037} = -23.38$, $p < 0.001$ for PD) (Figure S11), although there was a consistent flattening of the latitudinal effect (Figure S12). In contrast, although phylogenetic diversity displayed convergence in both tropical ($ES_{Trop} = -0.33$, $t_{1,285} = -9.93$, $p < 0.001$) and temperate realms ($ES_{Temp} = -0.58$, $t_{2,037} = -18.27$, $p < 0.001$), functional diversity displayed significant divergence in tropical ($ES_{Trop} = 0.04$, $t_{1,285} = 2.46$, $p = 0.01$) but convergence in temperate realms ($ES_{Temp} = -0.17$ $t_{2,037} = -9.60$, $p < 0.001$) (Figures S13 and S14). Second, incorporation of fine-scale wave exposure and benthic habitat data at a subset of sites yielded the same qualitative inferences as for the broader analysis. For these sites, functional convergence was 1.5× stronger in temperate communities compared to tropical ones (mean $ES_{Trop} = -0.030$ vs. $ES_{Temp} = -0.046$, Welch's $t_{1508.3} = -8.4452$, $p < 0.001$), whereas phylogenetic convergence was again 1.8× stronger in temperate regions (mean $ES_{Trop} = -0.019$ vs. $ES_{Temp} = -0.035$, Welch's $t_{1498.6} = -13.569$, $p < 0.001$) (Figure S14).

4 | Discussion

Overall, our study reveals significant functional and phylogenetic convergence in local marine reef fish assemblages relative to their broader species pools in both tropical and temperate realms, with convergence increasing towards higher latitudes. Because our approach attempts to first remove the signal of environmental filtering in structuring the observed fish assemblages, our results suggest that the effects of biotic interactions on community assembly (i.e., through exclusion of competitively inferior species) could play a more substantial role at higher latitudes.

There are several possible explanations for this finding. First, increasing latitude was associated with greater convergence in traits that capture variation in resources used by reef fishes, a pattern that was reflected in the greater dominance within local assemblages of species that exploit energetic nutritional sources, such as higher trophic level carnivores and planktivores. Although debated, fishes living in colder high latitude reefs have been hypothesised to be physiologically constrained when exploiting basal nutritional resources (Gaines and Lubchenco 1982), which has been proposed as a potential mechanism through which the diversity and abundance of herbivorous fish decline with latitude (Ferreira et al. 2004; Floeter et al. 2005). Irrespective of temperature-driven effects, carnivorous fishes have greater energy absorption efficiency owing to the higher energetic and nutritional value of their prey (Knight et al. 2021), which may explain their persistence at high-latitude regions. Along the same lines, planktonic subsidies incorporated by reef planktivores, which tend to be more abundant at higher latitude reefs (Holland et al. 2020), can boost the biomass of fish consumers (Morais et al. 2021). In contrast, the evolution of different functional groups of herbivorous fishes is constrained at high latitudes, as limited competition for a comparatively energetically inefficient or chemically defended resource would render transitions to herbivory less likely over evolutionary timescales (Siqueira et al. 2019, 2020). Further, the high rates of niche partitioning, and low extinction probabilities owing to stable tropical environments, may facilitate niche divergence (or at least, less convergence) observed in tropical planktivores relative to temperate planktivores (Siqueira et al. 2021).

Beyond evolutionary constraints, fundamental differences between tropical and temperate realms in the breadth of available resources may also contribute to higher trophic convergence at high latitudes. In other words, if niche partitioning is an important process in high-latitude reefs but occurs within a less diverse or more homogeneous resource seascape (Schluter 2016), the apparent convergence may result from our inability to detect fine-scale resource partitioning using the coarse trophic categories applied to carnivorous and planktivorous guilds. In this context, recent empirical studies have shown that these guilds exhibit a wide range of morphological and behavioural adaptations that likely facilitate resource partitioning across spatial and temporal scales (Mihalitsis and Bellwood 2021; Ng et al. 2025).

The prevalence of second-order consumers may further increase convergence at high latitudes through the depression of functionally- and phylogenetically distinct species (via direct consumption) to the point where they are less frequently observed in the surveys. These predatory species are often characterised by large body sizes, greater dispersal abilities and/or lower site fidelity, leading to greater exchange of species among sites (Reuman et al. 2014; Barneche et al. 2019). Although most community assembly frameworks have traditionally only considered direct competitors for resources (de Bello 2012), the exclusion of species through predation has been shown to be a dominant driver of assembly in, for example, freshwater fishes (Chase et al. 2009; Giam and Olden 2016). In marine systems, generalist predators with larger mobility living at high latitudes have recently been found to suppress local diversity through direct consumption, which in turn homogenises the regional species pool (Ellingsen et al. 2020).

Along these lines, we expected that larger average body sizes of temperate fishes (which are typically omnivores or carnivores) would be reflected in a strong role of the trait of "maximum length" in driving the global convergence patterns towards the poles. Theoretical and empirical work has linked body size to dispersal potential (Hillebrand 2004; Bradbury et al. 2008), and several previous studies have shown average body size increases consistently across latitude (Fisher et al. 2010; Coghlan et al. 2024). We found no evidence for this expectation in our analysis, however, with locally co-occurring species exhibiting consistently less variation in maximum body size than the subregional species pool, with no overall differences in the magnitude of convergence across latitude. A potential explanation for this is that our index of functional diversity does not capture overall body size differences in community composition across latitude, but rather whether local assemblages are more or less similar in their reported maximum length compared to the subregional species pool. Hence, it is plausible that these patterns of convergence are driven by contrasting size distributions across latitude, where tropical species tend to converge towards smaller sizes and temperate species towards larger sizes, but local communities still occupy similar size ranges to those found in the subregional species pools (Bosch et al. 2021; Coghlan et al. 2024).

This, in turn, may have masked the processes through which body size variation influences biotic community assembly, such as dispersal and predation leading to homogenisation of local assemblages (Chase et al. 2009; Giam and Olden 2016; Ellingsen et al. 2020) and competition for highly energetic resources leading to weak competitor exclusion (Mayfield and Levine 2010; Suárez-Castro et al. 2022).

Functional and phylogenetic information generally revealed congruent patterns of community assembly, although the magnitude of convergence was stronger in the latter. Further, there were differences in the suite of environmental, geophysical and anthropogenic predictors, as well as the variance explained by the models in functional and phylogenetic effect sizes. Functional effect sizes were solely predicted by nitrates and local species richness, with a transition from convergence (i.e., weak competitor exclusion) to divergence (i.e., niche partitioning) as species richness and nutrients increased. In such cases, high availability of nutritional resources in species-rich assemblages may alleviate exclusion of weak competitors—and facilitate niche partitioning—by providing additional resources and therefore less overlap with potential competitors (Pellissier et al. 2018). This trophic perspective is supported by recent studies showing that trophic innovations have fuelled reef fish lineage diversification over evolutionary history (Siqueira et al. 2020; Ng et al. 2024), which aligns with our finding that latitudinal patterns in functional effect sizes were majorly driven by variation in the trophic composition of local assemblages. Importantly, the rise of these trophic innovations has occurred relatively recently in evolutionary history, predominantly in the past 20 Myr (Bellwood et al. 2017), which supports the expectation that functional traits can be more reflective of recent evolutionary divergence (Cadotte et al. 2019).

Perhaps surprisingly, as SST increases, assembly switches from divergence (niche partitioning, i.e., positive values) to convergence (weak competitor exclusion, or negative values), which is the opposite to the pattern expected if SST and latitude effects covaried. That is, patterns in convergence with SST and latitude ran in opposite directions to each other. The SST result also runs counter to other recent studies that found temperature to correlate with phylogenetic divergence in reef fishes of the eastern Atlantic Ocean (Bosch et al. 2021). Importantly, our approach first attempted to remove the confounding effect of the environment by restricting the regional pool to those species found in environmentally similar sites within a given 'Marine Ecoregion of the World' (MEOW, Spalding et al. 2007). Thus, species coexisting locally within these defined subsets of regions can be considered to have broadly similar physiological tolerances and vary only in response to a restricted range of temperatures found within each region. We interpret the strong influence of sub-regional temperature in our analysis as possibly reflecting individual metabolic responses, which often reflects deep evolutionary patterns conserved across phylogenies (Clarke and Fraser 2004; Brandl et al. 2023). Within a given region and species pool with a similar temperature regime, higher temperatures will increase energy demands, leading to stronger competition for resources and eventual exclusion of weak competitors (reviewed in Saito et al. 2021). Partitioning the multiscale role that temperature has in driving organismal physiology is a key frontier in understanding how and why organisms are found together, particularly in a changing climate (Brandl et al. 2023).

Most other covariates, including nitrates, NPP, depth, wave exposure and human population density, reduced the degree of phylogenetic convergence towards random assembly—or even towards significant divergence (niche partitioning). In such cases, these drivers may alleviate exclusion of weak competitors—and facilitate niche partitioning—by expanding the resource base, reducing stress and removing competitors (e.g., through human exploitation) that would make local communities appear as more random subsets or more diverse than expected based on the regional species pools. The role of humans in shaping reef fish community structure and function is well described (Duffy et al. 2016; Lefcheck et al. 2021; Bosch, Monk, et al. 2022), and our potential to disrupt natural assembly processes is increasingly recognised (Villéger et al. 2010; Martins et al. 2012).

Our finding of greater importance of biotic mechanisms of community assembly towards higher latitudes seemingly runs counter to a large body of theory implicating a stronger role of interspecific competition in the tropics driving trait divergence over evolutionary timescales (Pianka 1966; Mittelbach et al. 2007). It is thus possible that our finding of greater convergence at higher latitudes is an artefact of lower fish species richness at high latitudes (Stuart-Smith et al. 2013; Edgar et al. 2017). We argue that differences in richness may be considered more of a consequence than an artefact. Historical processes, coupled with contemporary ecological constraints, have limited diversity at high-latitude reefs (Gaboriau et al. 2019). For instance, changes in the extent of tropical reef habitat during the Quaternary glacial periods, owing to fluctuations in climate and sea level, have strongly shaped the regional taxonomic and phylogenetic structure of reef fishes (Pellissier et al. 2014; Leprieur et al. 2016). Evolutionary constraints, through the tendency to retain ancestral characters (e.g., physiological tolerances to thermal regimes), may have further limited expansion of fishes into suitable habitats during favourable environmental periods (Wiens and Donoghue 2004). Under these circumstances, only species with viable trait combinations would be able to disperse into suitable habitats, a pattern that explains the prevalence of large body sizes and piscivorous diets in regions that were isolated from the Quaternary climatic refugia (Parravicini et al. 2021). In other words, convergence could arise as a consequence of sampling fewer species from an already depauperate and functionally consistent pool (e.g., in terms of trophic group, see above), as would be found in high-latitude regions. In this context, we found a weak but significant signal of divergence in tropical regions when using abundance-weighted FD indexes, which could point towards higher resource specialisation in the tropics, as recently found across trophic and thermal niche axes (Delecambre et al. 2025).

It is also plausible that the coarse modalities of the traits used in our analysis do not fully capture nuanced differences in reef fish ecology that are functionally relevant, particularly when considering our metric of attribute diversity. If niche partitioning is stronger in the tropics but the trait variation representing this partitioning is constant across gradients (e.g., 6 traits for all species) or the threshold for similarity is reduced, we may under-estimate niche partitioning in tropical regions relative to temperate regions. Two clear examples are the cases of herbivorous and benthic invertivorous fishes, which are covered by only a few coarse modalities in our analysis (Table S1), but they are known to demonstrate a wide variety of specialised feeding modes and diet preferences (Choat et al. 2002; Clements et al. 2017; Parravicini et al. 2020). We tried to ameliorate this using phylogeny in lieu of functional traits, based on the assumption that phylogenetic distance may better reflect the entirety of functional variation among species than does a small suite of traits (Srivastava et al. 2012; Cadotte et al. 2019). Although phylogenetic convergence was, on average, stronger than functional indices, we still failed to recover very many examples of true divergence, even in speciose tropical assemblages where such divergence is most expected. Phylogeny is often a good predictor of reef fish geographical distribution (Pie et al. 2021) and ecological traits (Parravicini et al. 2020); however, the extent to which it adequately captures behavioural differences that determine fine-scale resource partitioning in reef fishes remains controversial (Brandl et al. 2015).

Our results also point to the scale-dependence of assembly processes vs. larger macroecological patterns (Suárez-Castro et al. 2022). An analysis of ant communities found that although environmental filtering was strongest at very large (continental) scales, local interactions were more important at smaller scales reflective of realistic dispersal scenarios (Lessard et al. 2012). This corroborating result emphasises that the resolution of our study—sites sharing similar abiotic characteristics within clear biogeographic boundaries (i.e., sub-ecoregions)—is a meaningful scale at which the effect of biotic interactions on community assembly is likely to be detected for reef fishes. Future studies that embrace a multiscale perspective, by sequentially increasing spatial grains to those where the effect of environmental filtering and neutral processes override local biotic processes, are key to identifying the scales at which biotic interactions are most meaningful for determining the structure of reef fish communities globally.

A potential caveat of our analysis is that we did not adequately account for the full suite of factors when defining the sub-ecoregional species pool, and thus, the latitudinal trend could still reflect residual environmental filtering. We have taken several steps to minimise this possibility. As a first pass, we grouped species based on "Marine Ecoregions of the World," which are "clearly distinct from adjacent systems, [determined] by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features," and are "strongly cohesive units, sufficiently large to encompass ecological or life history processes for most species" (p. 575, Spalding et al. 2007). These MEOWs are typically much smaller than the geographic ranges of the majority of species analysed here (Stuart-Smith et al. 2017) and benthic archetypes (Cresswell et al. 2017). Second, we used independent spatial datasets to cluster sites based on a suite of environmental, geomorphological and anthropogenic variables, including fine-scale information on wave exposure and benthic habitat data, and used the species observed across all sites within a cluster to construct a restricted regional pool. Nevertheless, here we attempt to remove the broad environmental constraints on regional composition, recognising that environment can (and does) exert an influence at even minute spatial and temporal scales. The collection of more resolved environmental and microhabitat data would allow for future tests of whether coarse indicators are sufficient to determine filtering or whether finer scale measurements are necessary.

Another important limitation is that we used only species recorded during visual surveys by divers, and therefore likely excluded many species that could potentially be at those sites but were absent or overlooked (despite relatively high sample completeness). For instance, many small-bodied species with cryptic behaviours that are under-estimated in visual surveys are known to finely partition available micro-niches (Brandl et al. 2018). Under-sampling these cryptobenthic fishes might under-estimate the degree of complementarity in functional strategies at the local level, which might explain the limited evidence of functional divergence across global gradients found here. Also, by restricting our analysis to only those species within the class Actinopterygii we have likely under-estimated the niche space occupied by coastal marine organisms, such as birds, mammals and sea urchins (Waechter et al. 2022). Some of these organisms typically play an increasingly important role in biotic interactions that influence community assembly at higher latitudes, such as herbivory by sea urchins (Poore et al. 2012), thus competing with fishes for available energy. Whether incorporating competitive interactions between distantly related taxonomic groups that perform similar functions could lessen or even reverse the patterns observed here represents a critical area for future research in functional ecology (Luza et al. 2023). Finally, we note that our analysis of trait divergence and convergence does not account for intraspecific trait variation, an important process that occurs during ontogeny and across geographic environmental gradients in fishes (Luiz et al. 2022). Compiling trait data across different populations and life stages of reef fishes remains unfeasible at the global scale investigated here, owing to the scarcity of intraspecific trait data for many regions and species. However, this represents a critical area for future research in the field of community assembly (Jung et al. 2010).

Many recent analyses of community assembly have found an overwhelming role of environmental filtering and a relatively minimal role of biotic interactions, an outcome which may lie with an insufficient ability to disentangle biological from environmental patterns driving functional and/or phylogenetic convergence (Lamanna et al. 2014; McLean et al. 2021; Bosch et al. 2021). Using both functional and phylogenetic approaches, we demonstrate that biotic interactions could play a more important role in structuring global reef fish communities than previously expected, above and beyond what is accounted for by several major axes of environmental variation. Future applications may seek to better understand the relative magnitude of environmental filtering vs. biotic interactions (something that is not possible under the framework used in this investigation) and to identify scales at which they are most meaningful (e.g., Giam and Olden 2016). A promising approach, recently proposed for observational community data, is through the integration of joint species distribution models with trait and phylogenetic data, which allows modelling the joint response of species to environmental gradients (i.e., environmental filtering) and species-to-species correlations (i.e., biotic assembly) at multiple spatial and temporal scales (i.e., Hierarchical Modelling of Species Communities, Ovaskainen et al. 2017). Nevertheless, our results support a significant signal of biotic interactions in structuring reef fish communities across a global scale, which is a key advance and highlights the dual role of environment and biology in shaping present-day ecological communities.

Author Contributions

N.E.B. and J.S.L. conceived the idea, designed the analytical approach, conducted the analysis, and wrote the original draft. All authors contributed to data gathering, commenting on analytical approaches and edited the original draft.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at DOI: https://doi.org/10.6084/m9.figshare.25750479.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.