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Ecological Specialisation of Reef Fishes Peaks in Global Biodiversity Hotspots

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ABSTRACT

Aim: The role of ecological specialisation in shaping biogeographic and evolutionary patterns remains unresolved. To date, few studies have quantitatively examined consumer niche breadth at a global scale. We describe global biogeographic and diversification patterns of specialisation, measured using trophic and thermal niches, for a highly diverse assemblage of consumers: reef fishes. First, we investigated the confluence of specialisation with global biogeographic patterns in species richness and reef area. Then, we tested whether these patterns could be explained by differences in diversification rates and geographic ranges.

Location: Tropical reefs across the globe.

Time Period: Present.

Major Taxa Studied: Reef fishes.

Methods: To estimate trophic specialisation, we compiled a comprehensive dataset on reef fish trophic interactions from published gut content analyses, including dietary information for ~5000 individuals across 387 fish species. We used the geographic range of species and global temperature data to estimate thermal specialisation of reef fishes. We used distributional data and Bayesian Structural Equation Modelling to test for the correlation between biogeographic variables, species richness, and the prevalence of trophic or thermal specialisation in reef fish assemblages. Moreover, we used linear models to test for a correlation between reef fish diversification rates, geographic range, and their degree of trophic and thermal specialisation.

Results: Our analysis suggests that species richness is positively associated with trophic specialisation in reef fishes, with isolated and species-depauperate communities supporting assemblages dominated by trophic and thermal generalists. We found no effect of trophic and thermal specialisation on diversification rates and geographic range at the species level.

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Main Conclusions: Our findings indicate that specialisation is favoured in large, biodiversity-rich regions, but specialists might show lower capacity for colonisation, with lower representation on smaller, isolated reefs. These results contribute to our understanding of the dynamics shaping fish biogeography on coral reefs.

1 | Introduction

Identifying the ecological and evolutionary drivers of species distributions is crucial to understand biogeographic patterns across environmental gradients (Chase et al. 2020). The concept of ecological niche is central to this endeavour, as it provides a theoretical framework to understand species distributions across space and time (Carscadden et al. 2020). The distribution of species is determined by both their environmental and resource requirements (Colwell et al. 2012). However, the environmental and trophic dimensions have been largely explored independently from one another (Futuyma and Moreno 1988; Colwell and Rangel 2009; but see Wisz et al. 2013; Pellissier et al. 2013). While resource requirements have been mostly considered in the context of community ecology (Devictor et al. 2010), environmental requirements are often the main factor behind the analysis of species distributions (Thuiller et al. 2005; Gravel et al. 2011, 2019). Consequently, we still know little about the direct impact of resource use on distribution patterns and the biological mechanisms causing them.

A crucial component of the ecological niche is the breadth of environments and resource types used by species to persist across their distribution (Carscadden et al. 2020; Colwell and Rangel 2009). Niche breadth has been extensively studied in ecology and evolution and has been identified as an important correlate of species abundance (Brown 1984), distribution (Gravel et al. 2011), colonisation capacity (Piechnik et al. 2008), and extinction risk (Colles et al. 2009; Colwell et al. 2012). Global change may also influence niche breadth (Carscadden et al. 2020). Indeed, the relationship between species geographic ranges and their environmental or trophic niche breadth may determine species vulnerability to extinction under rapid environmental change (Slatyer et al. 2013). A potential positive relationship between niche breadth and geographic range would imply that species with small geographic ranges also show a restricted niche, which exposes them to a higher risk of extinction (Colwell et al. 2012; Day et al. 2016). This is consistent with paleo-ecological studies that document a relationship between niche breadth and extinction rates across evolutionary time (Colles et al. 2009). Moreover, ecological specialisation can be an evolutionary dead end for some taxa (Burin et al. 2016; Gajdzik et al. 2019; Price et al. 2012; Siqueira et al. 2020), implying that species with narrow niche breadths have little plasticity and, therefore, a reduced capacity to persist or diversify (Day et al. 2016). While restricted niche breadth is generally associated with higher extinction risk at the global scale, ecological specialisation may favour species coexistence, thereby underpinning high richness in global biodiversity hotspots (Granot and Belmaker 2020; Jocque et al. 2010; Vázquez and Stevens 2004).

Coral reefs are the most diverse marine ecosystems on Earth and hold a strong gradient in species richness across several taxa (Tittensor et al. 2010). The mechanisms that determine global species distributions on coral reefs are relatively well known, especially for reef fishes (Barneche et al. 2019; Bellwood et al. 2005; Siqueira et al. 2021). Coral reef fishes are characterised by a steep gradient in species richness that peaks around the Indo-Australian Archipelago (IAA) and decreases across the Indian and the Pacific Oceans, following increased reef isolation (Bellwood and Hughes 2001; Pellissier et al. 2014). As such, evidence places the IAA as a center of species origination in the Miocene, and accumulation and survival later in the Pliocene (Cowman and Bellwood 2013). However, the distribution of species traits is not homogeneous along these gradients (Parravicini et al. 2021). For instance, while large carnivores dominate assemblages in isolated regions, small planktivores and herbivores are dominant in global biodiversity hotspots (Jacquet et al. 2017; Siqueira et al. 2021; Parravicini et al. 2021). Dispersal, for its part, is often invoked as the main mechanism explaining these patterns (e.g., Stier et al. 2014; Donati et al. 2019), as large carnivores tend to have longer pelagic larval duration (Luiz et al. 2013).

The breadth of the ecological niche could play a role in species distributions as it may influence the response of species to past perturbations and their colonisation capacity (Slatyer et al. 2013; Carscadden et al. 2020). In this regard, some studies have suggested that niche breadth, more than species trait averages, is a major determinant of species dispersal abilities because it correlates with species geographic ranges across a wide range of taxa (Comte and Olden 2018; Lester et al. 2007; Slatyer et al. 2013). Moreover, specialists tend to evolve in more stable environments at the expense of ecological flexibility but benefit from a competitive advantage in large, productive and species-diverse habitats (Piechnik et al. 2008; Colles et al. 2009; Carscadden et al. 2020). At the same time, generalists may be favoured in the colonisation of new, isolated and potentially depauperate environments (Sultan and Spencer 2002). Despite the strong mechanistic link between niche breadth and processes related to colonisation, global patterns of niche breadth have remained largely unexplored for tropical reef fishes, partially due to the lack of precise and detailed data on their dietary preferences (Parravicini et al. 2021).

Here, we examine the role of two major dimensions of the niche, namely, thermal and trophic niche breadth, in determining species distributions and assemblage structure across global tropical reef fishes. We collected information on the diets of more than 5000 individuals belonging to 387 fish species, alongside their global distributions and recent diversification rates. We first aimed to examine how reef isolation, reef area, and species richness interact with trophic and thermal specialisation in determining assemblage composition along these environmental gradients at a global scale. We further tested if the patterns of species distribution could be explained by species-level differences in geographical ranges and diversification rates (i.e., speciation rate minus extinction rate). Our comprehensive approach seeks to bridge the gap between theory and empirical data, paving the way for a more complete understanding of the influence of specific traits on coral reef species distribution.

2 | Material and Methods

2.1 | Data Collection

Dietary information for reef fish species was collected through an extensive literature review, building upon a published dataset of gut content analyses (Parravicini et al. 2020; Pozas-Schacre et al. 2021). This published dataset consists of gut content data for 615 species from Hawai'i, New Caledonia, Madagascar, Okinawa, the Marshall Islands, Puerto Rico and the US Virgin Islands. Despite the large size of this dataset, its geographic and taxonomic coverage was not sufficient to quantify trophic niche breadth at a global scale. Therefore, we improved these data by adding published gut content datasets from five sites in the Atlantic and retrieving dietary information for 78 additional fish species. Moreover, we obtained an unpublished high-resolution gut content dataset from Hawai'i for 143 additional fish species (see Table T1, Delecambre et al. 2025). Among these additional references, a small proportion of species were found in estuaries, sandy or muddy bottoms and were not strictly reef-dependent (e.g., Genyatremus luteus) and were therefore excluded from the database.

For each location in our dataset, these prior dietary information included fish individuals identified to the species level, and prey items identified to the lowest possible taxonomic level. The global database was filtered to only retain ray-finned fishes (Actinopterygii), excluding, for instance, Chondrichthyes (i.e., sharks and rays). Overall, we identified 752 distinct consumer species, of which 744 were Actinopterygii fish species. Prey items were identified via visual gut content analysis. This requires the identification of partially digested prey, which makes taxonomic assignment often difficult and imprecise (Buckland et al. 2017). As a consequence, several prey items could only be assigned broad taxonomic classes (e.g., filamentous algae, worms, plankton), with 'family' as the most commonly assigned taxonomic level. Therefore, we decided to use family as the taxonomic descriptor of prey items for all subsequent analyses, excluding all prey items only identified at the phylum, class or order level. Among the 744 consumer species, we removed 334 from the analyses because of the low resolution of prey item identification. This resulted in a gut content database of 410 species belonging to 54 families from 17 locations, including 146 species in the Atlantic, 278 species in the Indo-Pacific and 48 in the Tropical Eastern Pacific (TEP).

Since the trophic preferences of species may change according to the geographical location, we first examined whether the sample location of the data influenced global species-level estimates of trophic niche breadth. To do that, for the pool of species for which we had data in multiple locations, we conducted an analysis of variance testing whether trophic niche breadth differed among species, locations, and the species \times location interaction. We found that the species \times location interaction was not significant (Table T2), suggesting that the variation in trophic niche breadth for the same species in different locations can be ignored in the case of our dataset. Therefore, we proceeded to compute global estimates of trophic niche breadth regardless of the location.

We obtained the global distribution for each fish species in our dataset on a $5^{\circ} x 5^{\circ}$ grid using an existing species distribution database (Parravicini et al. 2014). These distributions allowed us to extract maximum, mean, and minimum sea surface temperature (SST) data for each grid cell from Bio-Oracle rasters (Assis et al. 2018). We estimated the thermal breadth for each species by coupling the distribution and SST data (detailed below; Kühsel and Blüthgen 2015).

To assess the relationship between trophic and thermal specialisation of reef fish assemblages and other known biogeographic gradients in each grid cell, we obtained data on present-day reef fish species richness, present-day reef isolation, present-day reef area, reef isolation, and reef area during the quaternary (hereafter called past isolation and past area, respectively) from Pellissier et al. (2014). Current and past areas were estimated in square kilometres (km²) and SST was expressed in degrees Celsius (°C). Current and past isolation were based on connectivity between coral reef habitat patches in the present and during the Quaternary. The estimates were based on the current global map of coral reef distribution and past reconstructions performed by Pellissier et al. (2014). Following Pellissier et al. (2014), isolation was measured using the nearest neighbour approach. We then used the information on global distribution from our fish species list to merge, for each species, the thermal and trophic niche breadth with the grid cell biogeographic variables and reef fish species richness. Hence, we ultimately obtained, for each grid cell, an assemblage of species along with their thermal and trophic niche information.

Finally, to evaluate the relationship between species niche breadth and recent diversification rates, we retrieved tip diversification rates for reef fishes from a published dataset (Siqueira et al. 2020) obtained with the program BAMM 2.5.0 (Rabosky 2015). This program estimates the number of distinct evolutionary events across a phylogeny through a Bayesian framework. The details of this analysis can be found in Siqueira et al. (2020), but briefly, BAMM was run independently in 100 phylogenetic trees that had tips imputed based on taxonomy. Although speciation and extinction can also be estimated in BAMM, it is worth noting that tip rate metrics of diversification are more accurate estimators of speciation rates than net diversification rates (Tile and Rabosky 2019). Therefore, we focused on tip diversification rates for the rest of our analyses, keeping in mind that they poorly represent extinction history. Merging our consumer dataset with tip diversification rates information resulted in a final dataset comprising 387 consumer species.

2.2 | Trophic and Thermal Niche Breadth

We measured trophic niche breadth as the taxonomic distinctness (TD) of prey families for each consumer species. In particular, we first aggregated gut content data for each individual fish at the species level, and computed TD from the 'taxondive' function of the VEGAN package in R (Oksanen et al. 2022). Taxondive is a function that calculates the average distance between all species pairs across a taxonomic tree (Clarke and Warwick 1998, 1999). Therefore, this index allowed us to obtain a measure of the diversity of prey for each consumer species accounting for the taxonomic relatedness between consumed prey. High values of TD are associated with trophic generalists, while low values correspond to trophic specialists. This metric is potentially affected by the number of fish individuals sampled, as a high sampling effort on a given species could yield a more complete known pool of consumed prey. However, this was not the case in our dataset, as the size of the trophic niche of a given species was weakly related to the number of individuals sampled within this species, as a Spearman's correlation test showed (r=0.20, Figure S1).

To assess thermal niche breadth for each species, we gathered the minimum and maximum SST values of each grid cell where the species was present. We thus described the thermal niche of a species by summarising the SST conditions that the species could experience according to its distribution. In particular, the thermal niche breadth was defined as the coefficient of variation of all SST values experienced by a species across its geographic distribution (Kühsel and Blüthgen 2015). Therefore, high coefficients of variation were attributed to thermal generalists, while low coefficients of variation represented thermal specialists.

2.3 | Assemblage-Level Analyses

To evaluate the biogeographic gradients in niche breadth, we computed assemblage-level metrics of niche breadth for each grid cell. The trophic niche distribution was skewed toward small values, so we used the geometric mean of the niche breadths of the species present in each grid cell for the trophic niche and the arithmetic mean for the thermal niche, in which the distribution was not skewed.

We then tested whether biogeographic variables potentially associated with the dispersal capacity of species (i.e., present and past coral reef area and isolation) influenced the mean assemblage-level breadth of the thermal and trophic niche. Beyond biogeographic variables, species richness of consumers may influence the breadth of prey items that are consumed by a species. Indeed, a decrease in trophic breadth is expected to reduce competition and favour species coexistence and, therefore, high species richness (MacArthur 1970).

To model trophic and thermal niche breadth, reef area and past reef area were log-transformed, and all quantitative variables were centered and scaled, as they originally displayed heterogeneous scales, dispersions, and units. In addition, grid cells with empty information for one or more of our predictors were removed from the database, resulting in 270 grid cells across the globe.

To incorporate the potential effect of reef fish species richness on trophic niche breadth, we used structural equation models (SEM), which allowed us to incorporate both direct and indirect effects of biogeographic variables mediated by reef fish species richness (Ullman 2006). We ran a SEM using a Bayesian framework with the R package BRMS (Bürkner 2021). In this case, we modelled the direct effect of biogeographic variables, including present isolation, present reef area, past isolation and past reef area, as well as their indirect effect mediated by reef fish species richness.

The model also included biogeographic region as a random effect on the intercept (see Parravicini et al. 2013). Moreover, the variance of the mean trophic niche breadth was strongly correlated to reef fish species richness, resulting in high heteroskedasticity. To account for this potential lack of independence, we specified a correlation term between trophic niche breadth variance and reef fish species richness, which allowed the model to meet residual independence assumptions. This was done manually through the *sigma* argument of our model function brm.

In the absence of clear hypotheses linking reef fish species richness to thermal niche breadth, we used a linear mixed model to examine the effect of biogeographic variables on the mean thermal niche breadth, also implemented in the package BRMS. In this model, we included a random intercept for each region.

In both models, priors were defined with the BRMS function get_prior, which suggested setting a weak effect of the explanatory variables, and a *student* distribution prior on the intercept. Both models were implemented by running four MCMC chains with 2000 iterations per chain, and disregarding the first 1000 iterations of each chain as burn-in. For each model, we examined all posterior predictive distributions, trace plots, and Gelman-Rubin diagnostics to assess convergence. All indicators were deemed satisfactory.

The assemblage-level patterns might be influenced by divergent responses of specialist versus generalist species. For example, an increase in assemblage-level niche breadth in certain locations may result from either an increase in generalist species or a reduction of specialists. To explore this potentially divergent response, we conducted a fourth-corner analysis, which models the presence–absence of each species as a function of both biogeographic variables and species traits (in our case, trophic and thermal niche breadth; Brown et al. 2014) and summarises these traits as community traits. We performed the fourth-corner analysis according to the approach implemented in the package MVABUND (Wang et al. 2022).

2.4 | Species-Level Analyses

To test whether niche breadth is correlated with geographic range, we examined the association between thermal and trophic niche breadth and the geographic range of each species, expressed as the area of occupancy (i.e., the number of grid cells in which a species is present), using Spearman's correlations. Moreover, we tested for a correlation between the two dimensions of the niche (thermal and trophic), designed to test whether thermally tolerant species are also trophic generalists.

Evolutionary metrics such as speciation and extinction rates are also associated with the breadth of the ecological niche. We thus used a Bayesian phylogenetic model to examine the relationship between thermal and trophic niche breadth and tip diversification rate. The Bayesian phylogenetic model was performed using the package BRMS (Bürkner 2021) with weakly informative priors, 2000 MCMC iterations across 4 chains including 1000 burn-in iterations. The phylogenetic tree comprising our species was obtained using the fishtree_phylogeny function of the FISHTREE package (Chang et al. 2019). In addition, we used a Quantitative Speciation and Extinction (QuaSSE) model, a traditional trait-dependent method, to confirm our results. This was run using the DIVERSITREE R package (FitzJohn 2012). QuaSSE allows for diversification rates to vary as functions of other trait values, here trophic and thermal niches. The extent to which the trait data is accounted for by models incorporating trait-dependent diversification is then assessed through a likelihood-based comparison, here using Akaike Information Criterion (AIC). However, several studies have shown that QuaSSE and other Speciation and Extinction (SSE) models can be subject to Type I errors (i.e., false positives) when used for model selection, mostly due to comparison of state-dependent models with too simplistic null models with no diversification rate variation (Rabosky and Goldberg 2015). Therefore, we backed this analysis with an Equal Split simulation-based method (ES-sim), that is known to be a good trait-dependent alternative to SSE models (Harvey and Rabosky 2018). Every time, the models were run for the trophic and the thermal niche independently at the species level.

2.5 | Sensitivity Analyses

Since our analyses may be sensitive to the taxonomic resolution employed to identify prey items (i.e., family level) or the metric used to describe niche breadth (i.e., TD), we conducted all of the analyses described above with a subset of our data allowing for prey identification at the genus level. Moreover, we conducted all the analyses using the richness of prey items (instead of TD) as a metric of trophic niche breadth (Carscadden et al. 2020; Colles et al. 2009). Finally, we tested whether any gut content sampled location in our database was driving the patterns due to a disproportionate importance in the estimation of trophic specialisation, that is, a jackknife approach. Therefore, we performed the analysis multiple times, each time excluding one sampled location. Results from these sensitivity analyses were largely consistent and are reported as Supporting Information S1.

All statistical analyses presented above were performed in R (version 4.4.3, R Core Team 2022).

3 | Results

Specialisation showed strong biogeographic patterns and was associated with hotspots of biodiversity and larger reef areas. Conversely, generalists were found in isolated and less diverse areas. The trophic niche breadth ranged from 1 for the most specialist species (131 species, 31.9% of the database; e.g., Holocentridae: *Sargocentron tiere* feeding exclusively on crabs) to 100 for the most generalist species, indicating maximum TD within the prey pool (71 species, 17.3% of the database; e.g., Bothidae: *Bothus ocellatus* consuming from gobies to mantis shrimps). The thermal niche breadth varied from 6.2 for the most specialist species (Gobiidae: *Elacatinus phthirophagus* living above 26.3°C and below 28.7°C) to 21.1 for the most generalist species (Bleniidae: *Meiacanthus kamoharai* living above 18.0°C and below 29.3°C).

3.1 | Assemblage-Level Analyses

The global distribution of the mean assemblage-level trophic and thermal niche breadth revealed a highly generalist assemblage in the South-West and North-East of the Atlantic (Figure 1), as well as across coastal and oceanic reefs in the Northern Indian and Eastern Pacific. In the Caribbean, most reefs host assemblages of trophic specialists and thermal generalists, while most reefs of the central Pacific host assemblages dominated by trophic generalists and thermal specialists. Reefs that are adjacent to temperate areas host assemblages dominated by thermal generalists or by both thermal and trophic generalists. Finally, in the centre of the IAA, the communities were largely composed of trophic and thermal specialists.

The SEM exploring the relationship between biogeographical variables, reef fish species richness, and assemblage mean trophic niche breadth showed relatively strong explanatory power $(R^2_{trophic niche}=0.59 \text{ and } R^2_{species richness}=0.66)$. Among the effects tested on mean trophic niche breadth, we identified four variables with an estimated effect different from zero at 0.95 probability (Figure 2, Table T3). Consistent with previous research, present and past isolation negatively impacted reef fish species richness. Present reef area had a strong, positive effect on reef fish species richness, while evidence for an effect of past area was weaker (<0.95 probability). Past and present isolation had a positive effect on mean trophic niche breadth, while reef fish species richness had a negative effect on assemblage mean trophic niche breadth. Finally, there was neither evidence of an effect of present nor of past reef area on the assemblage mean trophic niche breadth (<0.75 probability).

The linear mixed model investigating the effect of biogeographic variables on assemblage-level thermal niche breadth also showed



from 10.56 to 13.79). Lighter colours represent specialist assemblages while darker colours represent generalists.



FIGURE 2 | Summary of the structural equation and linear models showing the correlates of trophic and thermal niche breadth. We only display effects that were different from zero with a probability of 95% or higher in the models. The width of the arrows corresponds with the standardised effect size of the predictor (left and center variables) on the response (center and right variables). Purple and orange arrows show positive and negative relationships, respectively. Black icons represent present-day variables and grey icons represent past (Quaternary) variables.

strong explanatory power ($R^2_{\text{thermal niche}} = 0.70$). The assemblage mean thermal niche breadth was mainly driven by the effect of present-day variables. Isolation was positively correlated with assemblage mean thermal niche breadth, while area was negatively correlated. In this model, past isolation and past area had no distinguishable effects (<0.95 probability).

The results of the fourth-corner analysis were mostly consistent with our previous results. Reef fish species richness was negatively correlated with trophic niche breadth. Moreover, past isolation was positively correlated with trophic niche breadth. Isolation was also positively correlated with trophic niche breadth (Figure 3).

3.2 | Species-Level Analyses

Species geographic range, thermal niche breadth, and trophic niche breadth were weakly correlated (Spearman's correlation test, $r_{\text{range-thermal}} = -0.06$, $r_{\text{range-trophic}} = 0.03$, $r_{\text{trophic-thermal}} = -0.01$).

Using a Bayesian phylogenetic model, we then explored the relationship between each dimension of species niche (trophic and thermal niche breadth) and the tip diversification rates. In both cases, we found little support for a relationship. Our model identified a weak negative trend with a probability of 0.57 for the trophic niche and 0.79 for the thermal niche (Figure 4, Table T3). The model had little explanatory power with a Bayesian $R^2_{\text{diversification rate}} = 0.075$.

The comparisons of QuaSSE models suggested a significantly better AIC for the models including a linear relationship between speciation rates and the niche breadth, both for thermal and trophic niches (*p*-value <0.01). However, the ES-sim test did not support these correlations ($r_{\text{thermal}} = -0.12$; *p*-value_{thermal} =0.315 and $r_{\text{trophic}} = 0.15$; *p*-value_{trophic} =0.199), conflicting with the output from the QuaSSE framework, which is often subject to Type 1 errors.

3.3 | Sensitivity Analyses

Running our analyses with a different taxonomic resolution for prey items (i.e., genus), we obtained similar results for both assemblage and species-level analyses (Figures S2 and S3). Similarly, we showed that our results were not affected by the choice of the metric employed to describe trophic niche breadth (i.e., TD vs. prey items richness) (Figures S4 and S5). Finally, we found that our results remained largely consistent if data from specific locations were removed from the original trophic dataset (see Figures S6 and S7).

4 | Discussion

We demonstrate that past and present biogeographic factors, isolation and reef area, have constrained reef fish specialisation along the trophic and thermal niche dimensions. Ultimately, specialists dominate the global biodiversity hotspots (IAA), while generalists are favoured in isolated, diversity-depauperate



Environment

FIGURE 3 | Fourth-corner modelling results. Coefficients for all environment-trait interactions are displayed with orange and purple squares, which represent negative and positive relationships, respectively. The size of the squares represents the magnitude of the effect size of the coefficients (ranging from -0.13 to 0.14).



FIGURE 4 | Posterior distributions of the effect size of trophic and thermal niche breadth on tip diversification rates. The posterior distributions are calculated from a Bayesian phylogenetic model.

regions. We reveal that these patterns are neither caused by variations in geographic ranges nor by evolutionary rates. Our findings shed light on the origins and maintenance of biogeographic patterns in coral reef fish assemblages.

Although specialists are hypothesized to occupy smaller geographic ranges, leading to higher extinction and lower speciation rates (Day et al. 2016; Slatyer et al. 2013), compared to generalists, we found no association between niche breadth and geographic range at the species level. Consistently, there was no influence of trophic or thermal niche breadth on recent diversification rates. The hypothesis that specialisation is associated with small geographic ranges and higher extinction risk stems from the idea that specialisation represents an evolutionary dead end, where specialists are incapable of expanding their niche breadth, which reduces their capacity to colonise new environments (Day et al. 2016). While this may be true in terrestrial settings, where the trophic interactions are mostly identity-based, the trophic niche of aquatic organisms tends to follow size constraints, which allows for niche expansion. Moreover, species often specialise under abundant resources or stable conditions, which should reduce their vulnerability to extinction (Elmhagen et al. 2000). Further, the oscillation hypothesis posits that lineages tend to fluctuate between specialisation and generalisation over time (Janz and Nylin 2008), and specialist lineages are capable of switching to a generalist strategy whenever their favoured resource becomes scarce (Colwell et al. 2012). This phenomenon of changing preferred resources or enlarging the trophic niche has been observed, for example, in corallivore butterflyfishes (Lawton et al. 2012). Thus, there is little consensus on the role of niche breadth in determining variations in evolutionary rates. While several studies show a higher diversification rate in specialist lineages (Rolland and Salamin 2016), others document a higher diversification rate in generalist lineages (Forister et al. 2015; Gajdzik et al. 2019). Our results suggest that trophic and thermal niche breadth are not associated with geographic range in highly diversified reef fishes and specialisation does not lead to higher diversification at the global scale.

Our results also revealed that, as reef isolation (either present or from Quaternary) increases, the mean trophic and thermal niche breadth of the assemblage increases. Trophic generalists are often the first species to colonise remote areas, most likely because they feed on a large diversity of resources, which enhances their chances of survival outside their original range (Holt et al. 1999; Piechnik et al. 2008; Verberk et al. 2010; Stier et al. 2014). At the same time, thermal generalists can flourish under a wide range of temperatures, allowing them to flexibly move across different environments (Vázquez and Stevens 2004). In our study, reef isolation during the Quaternary also influenced assemblage niche breadth and was the main driver of global trophic niche

breadth distribution. Reef fish richness declines away from the central IAA hotspot of biodiversity and is dominated by planktivorous species, a trophic guild largely associated with trophic specialisation (Siqueira et al. 2021; Cowman et al. 2017). The IAA area may have offered abundant and predictable resources for Quaternary planktivorous fishes facing resource limitation and extinction elsewhere (Siqueira et al. 2021). Thus, past environmental changes have left a strong imprint on the present-day distribution of tropical reef fishes and their ecological characteristics (Parravicini et al. 2021; Pozas-Schacre et al. 2021). These hypotheses are dependent on the principle of adult-stage colonisation of remote areas. The possibility of coral reef species being geographically distributed according to larval traits, such as pelagic larval duration, has also been explored (Luiz et al. 2012). While larval stage trophic niche breadth is less marked, pelagic larval duration is often associated with other species traits potentially affecting diet and foraging activities (Luiz et al. 2013; Stier et al. 2014).

The relationship between species richness and trophic specialisation has been observed across a wide range of ecosystems and taxa, with species richness often linked to niche breadth because highly diverse and specialised faunas tend to occur in the tropics where climatic conditions are relatively stable (Granot and Belmaker 2020). However, in the case of trophic specialisation, this is often questioned in favour of the 'niche packing' theory, where species richness is enhanced by the ability of specialist species to co-exist without competing for resources (Chesson 2000; MacArthur 1970). Furthermore, it is possible that trophic specialists outcompete generalists, due to their potentially higher foraging efficiency when their preferred prey are abundant (Macarthur and Levins 1967). This hypothesis would explain why high diversity assemblages are predominantly composed of specialist species, as well as why there is a lack of correlation between niche breadth and geographic range. Generalist species may not necessarily have a large range; rather, they may simply persist in depauperate and remote areas because, once they colonise these areas, they are not exposed to as strong competition as in species-rich assemblages. This aligns with the competition-colonisation trade-off, whereby colonisation thresholds are common in species that are mostly outcompeted (Calcagno et al. 2006; Levins and Culver 1971).

Our work is subject to certain limitations. First, both trophic and thermal niche breadth retrieved for this work are in fact trophic and thermal preferences of fishes. However, in the absence of an experimental approach, preference is the closest proxy of tolerance that can be acquired. The definition of trophic niche breadth is subjective, and the analyses were not performed with high prey taxonomic resolution. This is due to the challenges associated with the collection of a global dataset on trophic interaction from several sources with different taxonomic expertise. Moreover, the visual assessment of fish gut contents is not the most precise method for the categorization of resources given the required high-level taxonomic expertise and inherent limitations of identifying partially digested items. In contrast, molecular tools such as DNA gut content metabarcoding offer the opportunity to identify prey items with enhanced taxonomic resolution and do not rely on morphological features that are blurred by digestion (Casey et al. 2019). Nevertheless, at present, there are simply not enough DNA gut content metabarcoding data to employ for

large-scale biogeographic analyses. Moreover, while previous biogeographical studies are conducted on a larger number of species (Parravicini et al. 2013), matching gut content and distributional data reduced the global pool of species for which ecological information was available. Finally, niche breadth did not account for potential intraspecific variability within consumer species due to ontogeny or geography. Ideally, we would have been able to obtain region specific estimates of trophic specialisation. However, our analysis on the subset of species that were sampled in different locations revealed that niche breadth specialisation varied mostly among location pools and not among locations for the same species. This may be due to the fact that niche breadth is an aggregate metric, which may be robust to small variation of diet preferences among species. Despite the above limitations, we use the most comprehensive dataset of reef fish diet available to date. As such, complementary analyses using expanded datasets, potentially leveraging metabarcoding techniques and accounting for intraspecific variability will be critical to generalise our findings.

5 | Conclusions

Ecological niche breadth plays a major role in species distributions and is important for assessing species vulnerability to extinction in the face of global change. Overall, we provide new insights about the role of ecological specialisation in determining species distribution and coexistence. We reveal that specialist and generalist fishes have similar, recent rates of diversification. However, being a specialist may offer a competitive advantage in highly diverse settings, while being a generalist may offer an advantage for colonisation in remote locations. Thus, in the context of climate change, conservation measures should focus on vulnerable species based on biogeographic location and evolutionary history, regardless of whether they are specialists or generalists.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

We confirm that the data and code supporting the results have been archived in Dryad. Shared link: http://datadryad.org/stash/share/J5nzV P3wgnesADOpcbV6mz6Frn0UKs65mOkek-Hca38.

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Supporting Information

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