Received: 7 February 2023 | Revised: 14 November 2023 | Accepted: 20 November 2023

DOI: 10.1111/jbi.14768

Journal of Biogeography WILEY

RESEARCH ARTICLE

Variation in functional composition of reef fishes along a tropical-to-temperate gradient

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Funding information
Australian Research Council; HORIZON EUROPE Marie Sklodowska-Curie Actions; Japan Society for the Promotion of Science

Abstract

Aims: Transformation of species and functional composition on subtropical reefs are ongoing due to poleward range shifts of some tropical species, with largely unknown consequences to ecosystem functioning. Trait-based approaches are powerful tools to quantify such changes. Here, we evaluated changes in the trait composition of coral-associated fish assemblages along a tropical-to-temperate environmental gradient of ca. 1400 km in southern Japan with abundance-weighted trait expression to assess how trait composition changes with increasing latitude.

Location: Ryukyu Islands and southern Pacific coast of Japan.

Taxon: Reef fish.

Methods: We tested for shifts in trait space and functional redundancy, based on five morphological, life history and behavioural traits: maximum length, pelagic larval duration, trophic level, substrate preference and reproductive mode. Our trait database was coded with two approaches, first, by attributing a single value to each trait per species, and second, by fuzzy coding that allows more than one value per trait and hence considers some intraspecific trait variation.

Results: We found a reduction in specialist habitat traits (coral substrate preference, nesters and herbivores) and an increase in generalist traits (predators) with increasing latitude, along with a contraction in trait space from tropical-to-temperate reefs. Functional redundancy declined with increasing latitude. These trends were closely linked with latitudinal gradients in temperature, along with changes in other environmental factors such as turbidity and photosynthetically active radiation.

Main Conclusion: Functional turnover and contractions are thus likely due to the marginal conditions for coral-associated fishes at higher latitudes, favouring generalist species, whereas increased resources at lower latitudes favour high redundancy and niche partitioning. Accounting for intraspecific trait variation indicated the same trends but highlighted increased functional vulnerability across all sites. We show that trait complexity in coral-associated fish communities decreases from tropical-to-temperate reefs, highlighting the reduced functional scope that comes with marginal environmental conditions.

KEYWORDS
functional shift, intraspecific trait variability, Japan, latitudinal gradient, reef communities

1 | INTRODUCTION

Climate influences the distribution of species and ecological communities, especially along latitudinal gradients in reef ecosystems, where temperatures range from tropical to temperate (Feary et al., 2014). The relationship between environmental conditions and variation in community structure is intensified by climate change, altering the structure of reef fish communities (Stuart-Smith et al., 2021). Rising sea surface temperatures lead to the reorganisation of marine ecosystems (Hughes et al., 2017), often resulting from poleward shifts in the geographic ranges of tropical species into marginal high-latitude environments (Vergés et al., 2014, 2019). These changes in species' ranges are likely accompanied by shifts in trait distributions at the community scale, and it has been proposed that they ultimately lead to changes in ecosystem functioning (Hughes et al., 2017; Vergés et al., 2014, 2019). For example, tropical herbivorous fish have been expanding their ranges into temperate areas, leading to overgrazing on temperate reefs (Vergés et al., 2014). Such changes in community structure could alter carbon and nutrient cycles and result in food web restructuring (Gilson et al., 2021; Vergés et al., 2019).

The diversity of species and their traits influence ecosystem functioning, stability and resilience to disturbances (Hooper et al., 2005; Hughes et al., 2017). Relationships between the diversity of species, their environments and subsequent effects on ecosystem functioning are linked to the abilities of species to occupy different niches and exploit limited resources (Brandl et al., 2019). Trait-based approaches are therefore often used to measure niche partitioning and ecosystem functioning (Brandl et al., 2016; Cook et al., 2022; Frainer et al., 2017; Miller et al., 2023). These approaches tend to focus on interspecific variation and often do not consider intraspecific variation limiting opportunities to interpret the relationships between trait diversity and ecosystem function (Raffard et al., 2019). For instance, in coral reef functional studies, intraspecific variation of traits is rarely accounted for, as most fish traits are difficult to measure individually. Therefore, most trait-based coral reef studies apply one value per trait per species (Brandl et al., 2016; Floyd et al., 2020; Mouillot et al., 2014; Stuart-Smith et al., 2015, 2021), assuming that variation in traits among species is more extensive than intraspecific variation in traits. However, even within species, traits can vary greatly in different environmental settings, as has been demonstrated for terrestrial plants (Albert et al., 2010; Jung et al., 2010; Messier et al., 2010; Pérez-Ramos et al., 2012). It is likely that intraspecific trait variation is important for marine ecosystem functioning. On coral reefs, not only can closely related species vary greatly in their traits, but traits can also vary within a species depending on where they live (Brandl et al., 2019; Chevene et al., 1994). For example, certain fish traits, such as growth rates, body sizes and reproductive timing, can vary within species along temperature gradients (Binning & Roche, 2015; Heibo et al., 2005; Robertson et al., 2005; Ruttenberg et al., 2005; Trip et al., 2008), indicating intraspecific trait variation may be an important factor in structuring fish communities, and by extension, trait communities (Visconti et al., 2020).

The ability of species to move poleward in response to climate change is mediated by their traits (Brandl et al., 2019; Feary et al., 2014). In fishes, traits such as large size, high mobility and pelagic spawning likely increase a species' ability to increase its range (Feary et al., 2014). Habitat generalists are also more likely to shift their ranges compared with tropical habitat specialists, who may be unable to find suitable habitats in temperate regions (Stuart-Smith et al., 2021). The trait composition of reef fish communities is known to change with latitude, where a larger variety of trait combinations are seen in areas of high species diversity such as the tropics (Stuart-Smith et al., 2013). It is important to assess how these different combinations of traits between communities at different latitudes are being affected by potential range shifts and the knock-on effect this may have on ecosystem functioning.

Functional diversity is defined as the variety of functions performed by species within a community (Petchey & Gatson, 2006). Highly diverse ecosystems such as coral reefs are characterised by high functional redundancy, where several species perform similar functional roles (Mouillot et al., 2013). This redundancy buffers important ecosystem functions against the loss of species that are unable to adapt to increasing temperatures (Fonseca & Ganade, 2001; Yachi & Loreau, 1999). Functional redundancy and its inverse, functional vulnerability, can therefore be important indicators of ecosystem functioning and resilience, especially when also considering the intraspecific variability of traits. Most studies that incorporate functional redundancy have found positive correlations between functional redundancy and community stability and resilience to disturbance (Biggs et al., 2020); however, how valid this still is when incorporating intraspecific variability is unknown.

The Pacific coast of Japan provides a rare almost continuous expanse of steppingstone reefs along its latitudinal gradient, where some corals are at their poleward range limit (Yamano et al., 2011). We explored the variation in the functional composition of coral-associated fish assemblages along the tropical-to-warm temperate gradient in Japan, comparing approaches that apply intra- and interspecific trait variation. We ask the following questions: (i) Do traits associated with generalist species increase in abundance at higher latitudes as expected? (ii) Does trait space reduce with increasing latitude and reflect a simplification in community trait assembly, as expected due to decreasing temperature supporting less functional diversity? and (iii) Do functional entities, functional vulnerability and functional redundancy patterns confirm the expected functional contraction of fish communities given the increasingly harsh environments for tropical species with increasing latitude? By considering intraspecific variation in traits along environmental gradients, we posit that we will gain a fine-tuned understanding of how ecosystems function and how they might respond to climate change, which will ultimately facilitate their management and conservation under climate change.

2 | MATERIALS AND METHODS

2.1 | Study sites & data collection

Visual census fish surveys were carried out at 31 sites along the Pacific coast of Japan, located between 24° and 35° northern latitude, with climates ranging from tropical to temperate (Figure 1a). This thermal gradient creates several areas with different environmental properties which were clustered into regions: tropical, warm subtropical, cold subtropical and warm temperate (Floyd et al., 2020) (Figure 1a). Sites were unevenly distributed along the Pacific coast of Japan (Tropical = 4, Warm Subtropical = 11, Cold Subtropical = 12 and Temperate = 4), due to a lack of data availability at either end of the gradient, as there is only one island group (=Yaeyama group [sites 1–4]) classed as tropical and access to some temperate sites on mainland Japan is restricted. Surveys were carried out along belt-transects (25 m × 5 m) in coral habitat, at a standardised depth of 8–12 m during the northern summers in 2015 for all sites except sites 20–31, which were surveyed in 2016. At our most northern site (Tateyama [Site 5]), surveys were conducted at 3 m depth as the coral habitat did not extend to deeper depths. We recorded all target species along the transects, while swimming along five replicate transects per site (see Table S1 in the Supplementary material for target fish families). The abundance of each species was counted visually and standardised using log(1 + x) to meet normality assumptions.

2.2 | Fuzzy set theory

Unlike traditional trait-based approaches, the fuzzy coding method allows species to be placed in more than one category per trait to account for uncertainty in ecological characteristics (Cheung et al., 2005; Chevene et al., 1994; Jones & Cheung, 2018) and some degree of intraspecific trait variation. For example, it is difficult to know whether a fish species is of medium or large size, as size may vary with environment or habitat. Cheung et al. (2005) therefore used fuzzy set theory when describing the maximum length of fish, allowing fish species to be placed in more than one category, whereby in some communities a species is classed as a medium fish and as a large fish in others, with the degree of membership to each category (i.e. small, medium or large) defined by relative abundance. For example, a fish species with a maximum size of 68 cm can be classified as large or medium, with a degree of membership of 0.7 (large) and 0.3 (medium; Cheung et al., 2005). Here, we used this fuzzy approach such that fishes whose traits vary within a species (Table 1) could be placed into several categories for the same trait, the fuzzy trait database can be accessed from: https://doi.org/10.5061/dryad.ns1rn8q03.

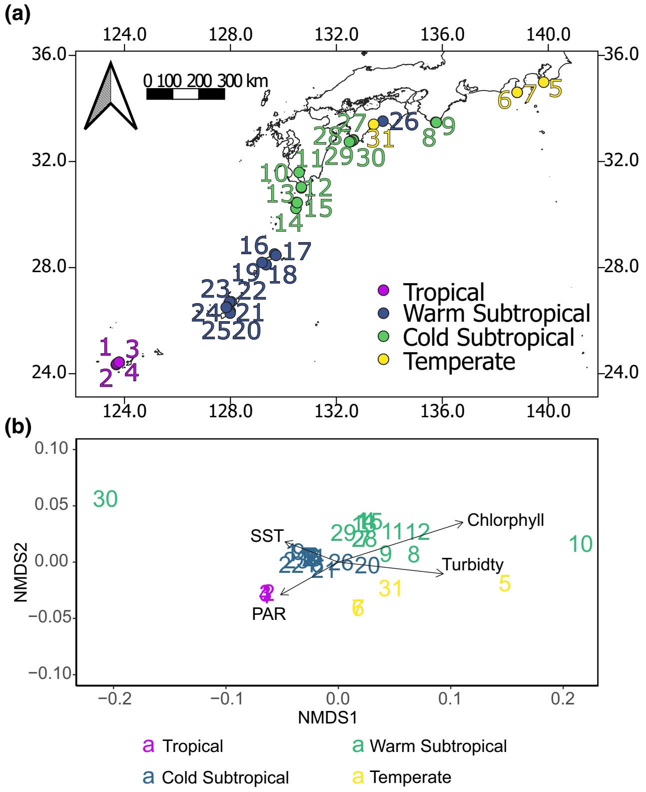

FIGURE 1 (a) Map of the 31 sites surveyed along the Pacific coast of Japan, between 24° and 35° N. Climates ranged from tropical (purple), warm subtropical (blue) and cold subtropical (green) through to warm temperate (yellow). (b) Environmental clustering of the 31 sites along the Pacific coast of Japan. The mean sea surface temperature (SST) (°C), turbidity (K490), photosynthetically active radiation (PAR) and chlorophyll were used to cluster the sites and are shown as vectors on the NMDS. Ward clustering split the sites into four clusters or 'regions' which are indicated by the four different colours.

2.3 | Gradients in trait communities along the tropical-to-temperate transition

Community-weighted trait means (CWM) were utilised to test the hypothesis that the prevalence of traits within communities would vary along the latitudinal gradient and between environmental clusters and that these patterns would be affected by intraspecific variation. Site-by-species abundance and species-by-trait matrices were combined through the 'functcomp' function from the 'FD' package in

TABLE 1 Five traits used to investigate community assembly and functional change along the Pacific coast of Japan and their ecological and functional relevance in this study. The format used for each of the trait approaches is also shown.

Trait	Data format	Ecological relevance of traits	Effect on ecosystem functioning	Effect on range expansion
Maximum length	4 categories: Very small (0–10 cm), small (11–50 cm), medium (51–100 cm), large (<101 cm)	Size relates to energy requirements of a species and its predator–prey relationships (Mouillot et al., 2014).	Linked to regulation of food webs and nutrient cycling (Holmlund & Hammer, 1999).	Size is related to thermal tolerance and dispersal ability (Nakamura et al., 2013).
Pelagic larval duration (PLD)	4 categories: short (0–40 days), medium (41–80 days), long (81–120 days), very long (<121 days)	PLD is an important early life history trait. It relates to larval growth rates and ultimately individual survival (McLeod et al., 2015).	Relates to individual fitness, therefore to overall fish biomass and community composition. This will in turn affect ecosystem functioning (Violle et al., 2007).	PLD shows variation along latitudinal gradients and variation in response to temperature (Cook et al., 2022, Takahashi et al., 2012, Vergés et al., 2019).
Trophic level	6 categories: Detritivore, herbivore, planktivore, piscivore, predator, corralivore.	Different trophic levels impact ecosystem functioning at different levels (Mouillot et al., 2014).	Varying trophic impacts on fish biomass, regulation of food webs and nutrient cycling.	Flexibility in trophic level affects the ability to expand range into less productive areas (Vergés et al., 2019)
Substrate preference	4 categories: Coral, rocky, sand, seagrass	Affects availability of prey and ecological niche (Mouillot et al., 2014).	Differing substrates affect productivity and nutrient cycling in different ways (Vergés et al., 2019)	Directly links to the degree of dependence of species on specialist habitat.
Reproductive method	5 categories: Brooders, demersal, nesters, scatterers, live bearers	Important life history trait (McLeod et al., 2015).	Relates to individual survival and so ecosystem functioning (Violle et al., 2007).	Relates to habitat requirements (Jung et al., 2010).

R (Laliberté et al., 2014). For categorical data, the CWM represents the abundance of each trait at each site (Lavorel et al., 2008). CWM for each trait at each site were then plotted against latitude for all three trait approaches. Linear models were used to assess the relationship between latitude and each of the traits.

The 31 sites were then clustered into four groups based on four environmental factors obtained through Bio-Oracle (Tyberghein et al., 2012) for June and July of 2015 and 2016: mean sea surface temperature (SST) (°C), turbidity (K490), photosynthetically active radiation (PAR) and levels of chlorophyll *a* (mSPU). A Euclidean distance matrix was computed for the environmental variables using the function 'vegdist' from the 'vegan' package (Oksanen et al., 2020). Ward clustering was then utilised to split the distance matrix into four environmental clusters (tropical, warm subtropical, cold subtropical and warm temperate), hereafter referred to as regions, that we visualised using nonmetric multidimensional scaling (nMDS; Figure 1b).

2.4 | Species traits

Species traits were compiled from the primary literature and FishBase (Froese & Pauly, 2021). Five traits were selected to describe the morphological, behavioural and biological functional niches of the reef fish species surveyed (Brandl et al., 2019, Miller et al., 2023; Table 1). Two different trait databases were created from the trait information: a categorical single-trait value database and a fuzzy-coded trait database. The categorical single-trait database followed traditional trait-based techniques and allowed for one value per trait per species. These values were obtained from FishBase, where the mean (numerical traits) or the dominant reported value (categorical traits) was assigned (Anderson, Houk, et al., 2022, Anderson, Mclean, et al., 2022, Cook et al., 2022, Miller et al., 2023, Clay et al., 2023). Traits for the categorical trait database included two numerical (maximum length and pelagic larval duration [PLD]) and three categorical (trophic level, substrate preference and reproductive method) data formats. The maximum length and PLD were assigned to four categories to make them comparable to the fuzzy database (Table 1). The fuzzy trait database applied the same categories as the categorical database but allowed species traits to be placed in more than one category (Cheung et al., 2005; Chevene et al., 1994; Jones & Cheung, 2018). Values for the fuzzy database were obtained from FishBase (Froese & Pauly, 2021) and other literature (Craig, 1996; Shibukawa & Suzuki, 2002; Wilson et al., 2008), capturing a range of trait values per species. Each trait value was assigned a weighting between 0 and 3, relating to the affinity of the species for the trait value, where 0 indicated no affinity and 3, complete affinity. These were then standardised so that the sum of each trait was equal to 1. These weightings were assigned depending on the abundance of the trait value within the literature and thus were not site-specific, for example, where a secondary trait value was available, the most dominant reported value was assigned a 2, and the secondary value 1. This strategy allowed for some intraspecific variability along the temperature gradient in response to different environmental pressures to be estimated based on abundance-weighted trait expression.

2.5 | Variation in functional composition and trait space

We utilised ordination techniques to test the hypothesis that community structure varies among environmental regions and that trait space contracts towards the northern poleward latitudes. Convex hulls visualised changes in trait space among regions (Cornwell et al., 2006; McWilliam et al., 2018). The 'mFD' package was used to calculate convex hulls and associated metrics (Magneville et al., 2022). For both trait approaches, we used the function 'funct.dist', as it calculates a Gower dissimilarity matrix using the gaudis function, which allows for trait grouping and fuzzy coding, but still produces a Gower dissimilarity matrix (de Bello et al., 2021). Based on either the categorical or the fuzzy traits approach, multidimensional functional spaces were built using the 'quality.fspaces()' function of the mFD package through a PCoA analysis using all the species present across all regions. Their quality was assessed using the mean absolute deviation between trait-based distances and distances in the functional space (see Supp. Table 2), a four-dimensional space was kept for the categorical trait approach, and a five-dimensional space was kept for the fuzzy traits approach. The functional richness of each region was computed as the proportion of the functional space occupied by species belonging to the given region. The 'mFD' package also allowed for the calculation of correlation metrics between each trait and each principal component axis using the 'traits.faxes.cor' function (Magneville et al., 2022). Envfit from the vegan package was used to plot trait vectors onto the regional hulls (Oksanen et al., 2020) (Figure S1). Functional beta diversity was also calculated using the 'beta.fd.multidim' function of the 'mFD' package, which calculates functional turnover, nestedness and dissimilarity. Beta diversity metrics were calculated pairwise between regions, where high levels of turnover indicated very few trait combinations were shared between regions, and highest nestedness where one region contained a subset of the trait combinations within another (Magneville et al., 2022).

2.6 | Functional entities, redundancy and vulnerability

To test the hypothesis that the functional contraction of fish communities would be seen along the latitudinal gradient, functional entities (FE) were calculated for each site for each of the trait approaches. The number of FE indicates the number of unique trait combinations at each site and was calculated using the 'species_to_FE' function created by Villeger (2017) and based on mathematical theory by Mouillot et al. (2014). Functional redundancy (FR), which relates to the average number of species per FE, and functional vulnerability (FV), which relates to the proportion of FEs that have only one species in them, were calculated using the 'FE_metrics' function (Villeger, 2017). These metrics were calculated to test the hypothesis that functional redundancy would decline and that functional vulnerability would increase with increasing latitude and that accounting for intraspecific variation would affect the observed patterns. FR and FV were separately regressed against latitude to test the effect of latitude on functioning. ANOVAs were performed to test for differences between the metrics across categorical and fuzzy coding trait approaches to assess the importance of intraspecific variation on functioning.

All analyses were performed in R (R Core Team, 2020), and all plots were created with the package 'ggplot2' (Wickham et al., 2016).

3 | RESULTS

Environmental clustering identified four regions, corresponding to the tropical, warm subtropical, cold subtropical and temperate areas along the latitudinal gradient (Figure 1b). Sites at lower latitudes were

TABLE 2 Correlation between the first two axes calculated using Gower distance-based principle coordinate analysis' (PCoA) and traits for reef fish recorded along the Pacific coast of Japan in this study.

Trait approach	Axis	Trait	Test	Statistic value	*p*-Value
Categorical	PCoA 1	PLD	Kruskal–Wallis (η^2)	0.474	<0.0001
		Substrate preference		0.413	<0.0001
		Reproductive method		0.346	<0.0001
	PCoA 2	Reproductive method		0.513	<0.0001
		Trophic level		0.293	<0.0001
Fuzzy	PCoA 1	Short PLD	Linear Model (r^2)	0.458	<0.0001
		Reproductive method—Nesters		0.373	<0.0001
		Trophic level—Predator		0.316	<0.001
		Very small maximum size		0.278	<0.0001
	PCoA 2	Short PLD		0.423	<0.0001
		Trophic level—Predator		0.256	<0.0002

characterised by higher SSTs and higher levels of PAR (Figure 1b). Site 26 clustered with warm subtropical sites due to higher PAR values compared with other sites in this region characterised by highly variable environmental conditions (Leriorato & Nakamura, 2019).

3.1 | Gradients in trait communities along the tropical-to-temperate transition

There was very little difference between trait approaches when using CWM to assess variation in functional composition; therefore, we only present results from the fuzzy-coded trait approach. We found no significant relationship between the maximum lengths of reef fishes and latitude. The prevalence of the trait 'short PLD' in fish communities decreased significantly with an increase in latitude ($F=91.22$, df = 1, 29, $p<0.001$, $r^2=0.75$) (Figure 2a). Predators became more abundant across the fish communities as latitude increased ($F=17.3$, df = 1, 29, $p<0.001$, $r^2=0.80$) (Figure 2b), whereas the abundance of herbivores ($F=18.32$, df = 1, 29, $p<0.001$, $r^2=0.37$) and planktivores ($F=14.34$, df = 1, 29, $p<0.001$, $r^2=0.31$) significantly decreased with increasing latitude (Figure 2b). Coral preference ($F=49.01$, df = 1, 29, $p<0.001$, $r^2=0.62$) (Figure 1c) and nesting reproduction decreased significantly as latitude increased ($F=75.82$, df = 1, 29, $p<0.001$, $r^2=0.71$) (Figure 2d).

3.2 | Variation in functional composition and trait space

The first two axes of the PCoA produced from the categorical trait approach explained 44.98% of the variation (PCoA1 = 25.40%, PCoA2 = 19.58%) (Figure 3a), with the first PCoA axis mostly driven by PLD, substrate preference and reproductive method (Table 2). The second PCoA axis was mostly driven by the reproductive method and trophic level (Table 2). For the fuzzy trait approach, the first two PCoA axes explained 41.83% of the variation (PCoA1 = 26.62%, PCoA2 = 15.21%) (Figure 3b). The first PCoA axis was mostly driven by PLD, size, trophic level, and reproductive method, and the second PCoA axis was mostly driven by PLD and trophic level (Table 2). The trait vectors indicate correlations between traits and PCoA axis for both trait approaches (Figure 3).

For the categorical trait approach, 85% of the functional richness was occupied by the tropical region, 86% by the warm subtropical region, 90% by the cold subtropical region and 89% by the warm

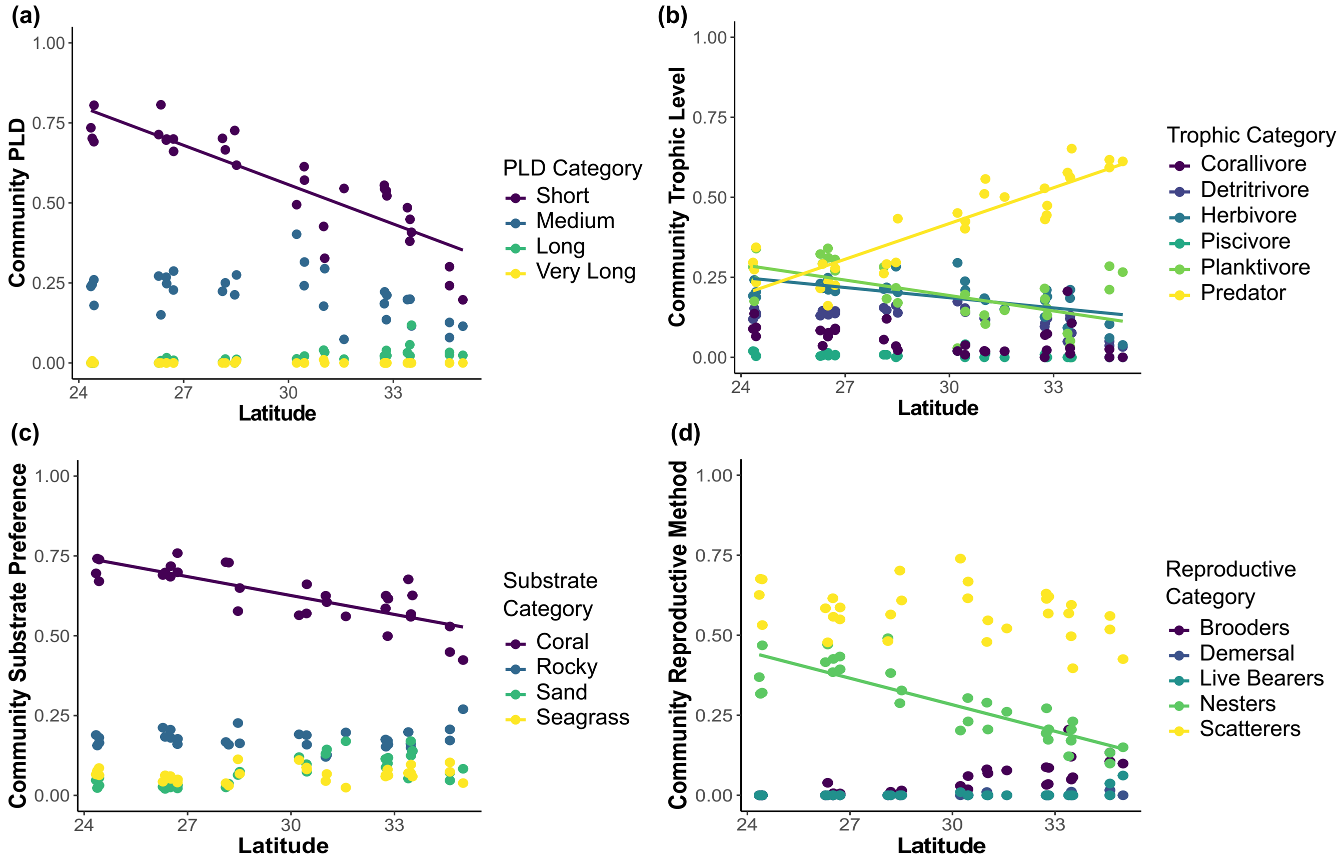

FIGURE 2 Relationships between the community-weighted means (CWM) of four reef fish traits and the latitude of each of the 31 sites surveyed along the Pacific coast of Japan. Lines represent significant relationships using linear models. (a) CWM of the pelagic larval duration (PLD) of fish. Colours indicate different durations of PLD. (b) CWM of the trophic level of fish. Colours relate to different trophic categories. (c) CWM of fish substrate preference. Colours indicate substrate categories. (d) CWM of fish reproductive category. Colours indicate reproductive categories.

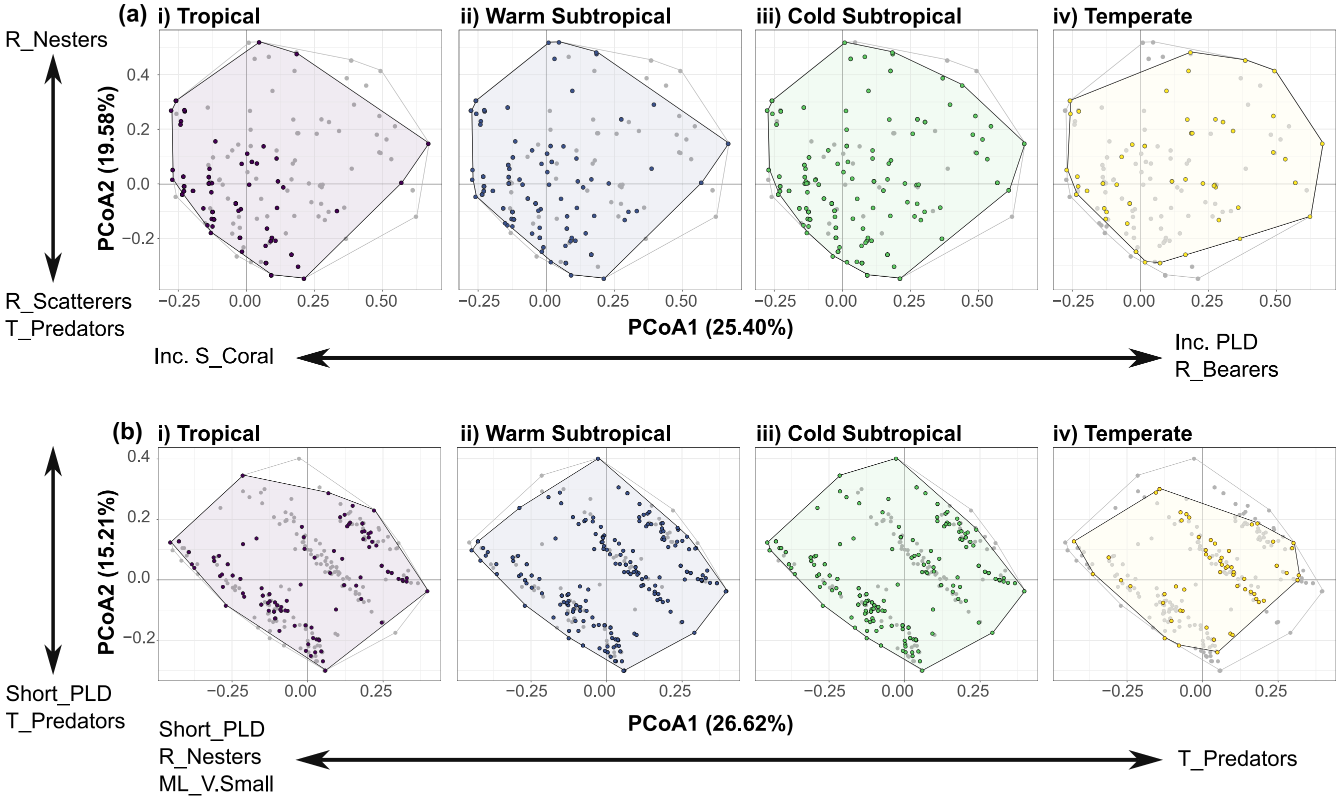

FIGURE 3 Representation of the functional richness of each region across the first two functional axes in the two functional spaces built for the two trait-based approaches: (a) regional functional richness based on the functional space built with the categorical trait approach and (b) regional functional richness based on the functional space built with the fuzzy trait approach. For each trait approach, (i) purple, (ii) blue, (iii) green and (iv) yellow convex hulls and points represent the functional richness and species for tropical, warm subtropical, cold subtropical and temperate regions, respectively. Grey convex hulls represent the overall functional space for each trait approach and grey points indicate the distribution of all reef fish species across the four regions. Arrows indicate correlations of trait vectors with the PCoA axes (ML, max length; PLD, pelagic larval development; R, reproductive mode; S, substrate preference; T, trophic level).

temperate region (Figure 3a). For the fuzzy trait approach, the tropical, warm subtropical, cold subtropical and temperate regions occupied 90%, 93%, 97% and 70% of the overall trait space, respectively (Figure 3b). The tropical and the temperate regions were the most functionally dissimilar when applying the categorical and fuzzy trait approaches (Table 3). There were also high levels of dissimilarity between the cold subtropical and the temperate regions when applying the fuzzy trait approach (Table 3). The highest levels of turnover were seen between the tropical and temperate regions for both trait approaches (Table 3). When applying the categorical trait approach the tropical and cold subtropical ecoregions had the highest level of nestedness, whereas for the fuzzy trait approach the cold subtropical and temperate regions were the most nested (Table 3).

3.3 | Functional entities, redundancy and vulnerability

The number of functional entities declined significantly as latitude increased for both the categorical ($F=4.645$, df = 2, 28, $p<0.05$, $R^2=0.20$) and the fuzzy ($F=13.39$, df = 2, 28, $p<0.0001$, $R^2=0.45$) trait approaches (Figure 4a), although the categorical approach generally featured fewer functional entities than the fuzzy trait approach ($t=-4.10$, df = 47.60, $p<0.001$) (Figure 4a). Functional redundancy decreased significantly as latitude increased for both the categorical ($F=112.6$, df = 1, 29, $p<0.0001$, $R^2=0.79$) and the fuzzy ($F=52.27$, df = 1, 29, $p<0.0001$, $R^2=0.63$) trait approaches (Figure 4b) and was significantly lower for the fuzzy approach than the categorical approach ($t=5.40$, df = 35.82, $p<0.0001$; Figure 4b). Functional vulnerability increased significantly at higher latitudes for both the categorical ($F=97.14$, df = 1, 29, $p<0.0001$, $R^2=0.76$) and fuzzy ($F=59.44$, df = 1, 29, $p<0.0001$, $R^2=0.66$) approaches (Figure 4c) and was significantly lower for the categorical than the fuzzy approach ($t=-4.55$, df = 50.22, $p<0.0001$; Figure 4c).

4 | DISCUSSION

Our study examined the changes in the functional composition of coral-associated fish communities along the tropical-to-warm temperate environmental gradient in Japan, contrasting two approaches that applied either intra- or interspecific trait variations. Fish communities showed some poleward contraction in functional composition, in which fish trait abundances (PLDs, trophic levels, substrate

TABLE 3 Jaccard metrics calculated from Gower distance-based principle coordinate analysis' (PCoA) based on reef fish traits in this study. Table includes functional dissimilarity, turnover and nestedness between four regions along the Pacific coast of Japan for two trait approaches: categorical (one value per trait) and fuzzy (multiple values per trait).

Trait approach	Jaccard metric		Tropical	Warm sub	Cold sub
Categorical	Dissimilarity	Warm sub	0.31		
		Cold sub	0.408	0.209	
		Temperate	0.463	0.452	0.432
	Turnover	Warm sub	0.011		
		Cold sub	0.071	0.129	
		Temperate	0.461	0.245	0.12
	Nestedness	Warm sub	0.299		
		Cold sub	0.337	0.08	
		Temperate	0.002	0.207	0.312
Fuzzy	Dissimilarity	Warm sub	0.337		
		Cold sub	0.387	0.193	
		Temperate	0.509	0.538	0.541
	Turnover	Warm sub	0.044		
		Cold sub	0.063	0.146	
		Temperate	0.367	0.118	0.063
	Nestedness	Warm sub	0.294		
		Cold sub	0.324	0.047	
		Temperate	0.142	0.42	0.487

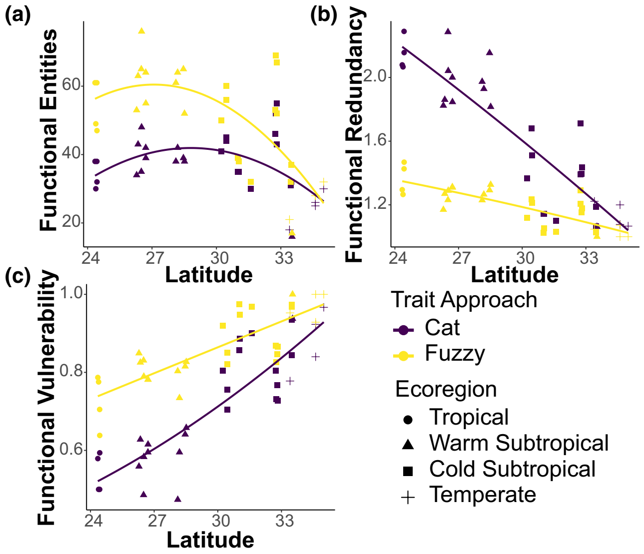

FIGURE 4 Reef Fish functional change across study sites along the Pacific coast of Japan as latitude increases, showing (a) The change in the number of functional entities, where functional entities were calculated based on reef fish trait combinations; (b) change in functional redundancy; and (c) change in functional vulnerability. Functional redundancy and vulnerability were calculated based on functional entities, following Mouillot et al. (2014). Colours indicate trait approach, and point shapes indicate which region each site belongs to.

preferences and reproductive methods) varied along the latitudinal gradient. More specialist traits (i.e. coral-specific substrate preference) were associated with the higher sea surface temperatures (SSTs) seen in tropical and subtropical regions, consistent with the hypothesis that higher temperatures allow for more niche partitioning (Cebrian, 2002; Floeter et al., 2004; Russ, 2003). Functional richness was lower in the temperate region, and high levels of functional dissimilarity were seen between the temperate and the other regions. Notably, we recorded a more pronounced contraction and higher levels of dissimilarity when the intraspecific variation was accounted for. Warmer temperatures in the tropical and subtropical regions were associated with higher numbers of functional entities, greater functional redundancy, and lower levels of functional vulnerability, indicating a greater safety net against disturbance in these regions (Mouillot et al., 2014). In our analyses, redundancy was lower when the intraspecific variation was accounted for, suggesting that tropical and cold subtropical fish communities may be more vulnerable to disturbances and climate change than currently considered by approaches which do not take intraspecific variability into account (Fonseca & Ganade, 2001; Yachi & Loreau, 1999).

4.1 | Changing trait communities on a tropical-to-temperate gradient

We found the prevalence of short PLD reef fish decreased with latitude and across regions, consistent with previous findings that shorter PLDs are associated with higher temperatures (Denit & Sponaugle, 2004; Green & Fisher, 2004; Robitzch et al., 2016). This result was also mirrored by the PCoA results, which indicate PLD increased along the latitudinal gradient (Figure 2.) Longer PLDs are likely more beneficial in marginal temperate conditions where reef cover is reduced as they facilitate increased dispersal (Shanks, 2009; Shanks et al., 2003).

The abundance of herbivores (tropical = 23%, temperate = 11%) decreased, and the abundance of predators (tropical = 37%, temperate = 51%) increased poleward from the tropical-to-temperate regions (Figure 2). Such patterns in abundances may be linked to the higher diversity of fish occurring in tropical areas which allowed the evolution of low-energy food resource use (Harmelin-Vivien, 2002). This hypothesis relates the higher temperatures in the tropics to more efficient energy transfer, allowing more fish species to use low-energy food resources such as algae, seagrass and detritus (Floeter et al., 2004; Harmelin-Vivien, 2002).

Another trend seen across the latitudinal gradient in this study was the loss of coral specialist species in more northern temperate regions. Specifically, coral-associated species and nesters decreased heading into higher latitudes, a relationship that is likely linked to the decrease in the diversity and abundance of corals at high latitudes (Veron & Minchin, 1992). Again, this relationship was mirrored by the PCoA results, which indicated that coral-associated nesters were more prevalent in the tropical and subtropical regions and less so with the temperate region (Figure 3). Nesting species rely on structurally complex topography in their nesting sites, which protects their young. These results suggest that habitat generalists are more speciose and abundant in temperate areas, consistent with the hypothesis that generalists are more adaptable to environmental change and less favourable temperate habitats, as they are less restricted by specific diets or habitats than specialists (Kingsbury et al., 2020; Stuart-Smith et al., 2021). Therefore it is likely that tropical generalists, which are more adaptable, are better able to expand their ranges poleward (Kingsbury et al., 2020), compared with tropical specialist species. Nevertheless, high-latitude reefs may accommodate more specialist fish species in the future if an increase in zooxanthellate corals transforms habitats in response to warming (Veron & Minchin, 1992).

4.2 | Variation in functional composition and trait space

Functional richness was largest in the cold subtropical region when accounting for interspecies variation and in the warm subtropical region when accounting for intraspecies variation (Figure 3). This higher level of functional richness in the subtropical regions, along with high levels of nestedness between the cold subtropical region and the tropical region (interspecies variation) and the temperate region (intraspecies variation) indicates these regions may serve as a refuge for both tropical and temperate species, while also containing their own endemic species (Beger et al., 2014). When only accounting for interspecies variation, the smallest trait space was seen in the tropical region, whereas when accounting for intraspecies variation the temperate region had the smallest trait space. It is likely that only accounting for interspecies variation did not reveal the full range of niches occupied within the tropical region, making functional richness appear smaller than it actually is (Zhao et al., 2014). Functional space contraction along the same latitudinal gradient has previously been confirmed in molluscs (Floyd et al., 2020).

Functional turnover was highest between the tropical and temperate regions, indicating they have the most differing traits, which is to be expected (Feary et al., 2014), as they are at opposing ends of the environmental gradient investigated here. When accounting for interspecies variation, functional dissimilarity was also highest between the tropical and temperate regions, further supporting that these are the most functionally different communities. Patterns in functional nestedness showed that the tropical and subtropical regions contained similar sets of functional strategies, potentially indicating the expansion of tropical species into subtropical regions, which has been seen in other regions (Vergés et al., 2019). However, accounting for intraspecific variation reveals a different pattern, with functional dissimilarities and nestedness highest between the cold subtropical and temperate regions, possibly representing poleward range expansion, even into temperate areas.

4.3 | Functional entities, redundancy and vulnerability

The number of functional entities was higher in warmer regions, which is consistent with niche partitioning at higher temperatures and in the more diverse communities of the tropics (Brandl et al., 2019). Functional redundancy also showed a negative relationship with increasing latitude, supporting the idea that more functionally diverse communities are more resistant to environmental change as their functions are protected by higher functional redundancy of species (Guillemot et al., 2011; Mouillot et al., 2014; Walker, 1992). Functional vulnerability thus had the opposite pattern, with higher functional vulnerability at higher latitudes, showing temperate regions to be more vulnerable to environmental changes (Mouillot et al., 2014). Thus, even if species are expanding their ranges poleward in response to environmental change, the ecosystem could still be vulnerable to environmental change in their new local environment due to lower functional redundancy (Guillemot et al., 2011, Mouillot et al., 2014).

However, some research questions the existence of functional redundancy when niche partitioning makes overlapping functions unlikely. For example, Loreau (2004) suggested that lower functional redundancy is more likely for coexistence, with niches overlapping less than previously thought. When accounting for intraspecific variation, our results indicate lower levels of functional redundancy and higher levels of functional vulnerability (Figure 4), which may support Loreau's theory (Loreau, 2004). Lower functional redundancy may also suggest local and range-expanding species will be able to coexist due to smaller niche partitioning (Miller et al., 2023). If the intraspecific variation is larger than previously assumed and allows for more niche partitioning, communities may be more vulnerable to environmental changes than previously assumed.

5 | CONCLUSIONS

Here, we found significant functional turnover and contraction of reef fish assemblages with increasing latitude along the Pacific coast of Japan, likely due to the marginal environmental conditions for coral-associated fish at higher latitudes. These patterns are closely linked with latitudinal gradients in temperature (along with changes in other environmental factors) along the Pacific coast of Japan and suggest that fish species may be extending their ranges poleward, although further studies along the latitudinal gradient are required to confirm this hypothesis. Our results demonstrate the importance of considering both inter- and intraspecific trait variation when investigating patterns in functional composition. In the current study, accounting for intraspecific variation indicated that fish communities may be more vulnerable to environmental change than previously thought based on analyses using only interspecific variation. Considering the intraspecific variation in traits may fine-tune estimates and allow for better understanding of the future of marine communities, compared with assigning single-trait values.

ACKNOWLEDGEMENTS

This research was funded by grants from the Japanese Society for the Promotion of Science (JSPS) 'Zuno-Junkan' grant entitled 'Studies on origin and maintenance of marine biodiversity and systematic conservation planning' to JDR, the Australian Research Council Centre of Excellence for Environmental Decisions (CE110001014) and an EU Marie Sklodowska Curie Fellowship (TRIM-DLV-747102) to MB and an Australian Research Council Discovery Early Career Research Award (DE230100141) to BS. Ecological surveys did not require permits for any of the field sites in this study. We specifically thank Dr. T Naruse, University of the Ryukyus for accommodation at Iriomote-Jima Island, Okinawa, as well as Mr. S Dewa, Diving Service Umiannai in Kagoshima, and Mr. K Nomura, Kushimoto Marine Park Center in Wakayama for arranging field surveys. We also thank Diving Service Toneriko at Iriomote-Jima Island, Okinoshima Diving Service Marine Snow at Tateyama, Nakagi Marine Center at Shimoda, Yakushima Diving Service Mori-to-Umi at Yakushima Island and Relax Diving Service and Aquadive Kohollоa at Amami-Oshima Island for logistical support.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Trait databases and CWM values for both the categorical and fuzzy approaches are available at: https://doi.org/10.5061/dryad.ns1rn8q03. Fish abundance and raw survey data are subject to controlled access to protect the novelty of collaborative papers still in preparation but are available from Maria Beger (m.beger@leeds.ac.uk) upon request.

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Author Contributions: Charlotte G. Clay and Maria Beger conceptualised the study; Charlotte G. Clay, Katie M. Cook and Maria Beger built fish trait databases; James D. Reimer, Maria Beger, Brigitte Sommer, Masami Obuchi, Masaru Mizuyama, Iori Kawamura and Hiroki Kise conducted fieldwork and collated ecological data; Masami Obuchi and James D. Reimer organised project logistics; James D. Reimer obtained the main funding for data collection; Charlotte G. Clay conducted data analysis and wrote the main draft; and all authors provided comments and edits on the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Clay, C. G., Reimer, J. D., Sommer, B., Cook, K. M., Mizuyama, M., Obuchi, M., Kawamura, I., Kise, H., & Beger, M. (2024). Variation in functional composition of reef fishes along a tropical-to-temperate gradient. *Journal of Biogeography*, *51*, 454–466. https://doi.org/10.1111/jbi.14768