

Neutral processes and taxonomic scale drive beta species-genetic diversity correlations in a submesophotic tropical reef fish

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Funding information

Agence Nationale de la Recherche, Grant/Award Number: ANR-18-CE02-0016

Handling Editor: Rosemary Gillespie

Abstract

If similar evolutionary forces maintain intra- and interspecific diversity, patterns of diversity at both levels of biological organization can be expected to covary across space. Although this prediction of a positive species-genetic diversity correlation (SGDC) has been tested for several taxa in natural landscapes, no study has yet evaluated the influence of the community delineation on these SGDCs. In this study, we focused on tropical fishes of the Indo-Pacific Ocean, using range-wide single nucleotide polymorphism data for a deep-sea fish (*Etelis coruscans*) and species presence data of 4878 Teleostei species. We investigated whether a diversity continuum occurred, for different community delineations (subfamily, family, order and class) and spatial extents, and which processes explained these diversity patterns. We found no association between genetic diversity and species richness (α -SGDC), regardless of the community and spatial extent. In contrast, we evidenced a positive relationship between genetic and species dissimilarities (β -SGDC) when the community was defined at the subfamily or family level of the species of interest, and when the Western Indian Ocean was excluded. This relationship was related to the imprint of dispersal processes across levels of biological organization in Lutjanidae. However, this positive β -SGDC was lost when considering higher taxonomic communities and at the scale of the entire Indo-Pacific, suggesting different responses of populations and communities to evolutionary processes at these scales. This study provides evidence that the taxonomic scale at which communities are defined and the spatial extent are pivotal to better understand the processes shaping diversity across levels of biological organization.

KEYWORDS

community structure, deep-sea fish, *Etelis coruscans*, Indo-Pacific Ocean, population genomics, species-genetic diversity correlations

Fabien Leprieur and Stéphanie Manel share senior authorship of this article.

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1 | INTRODUCTION

Spatial patterns of species diversity are traditionally described separately from spatial patterns of genetic diversity. However, the processes that underpin both levels of diversity have been proposed to be similar (Antonovics, 1976; Vellend, 2016; Vellend & Geber, 2005). These evolutionary processes included as follows: dispersal, which homogenizes alleles and species through the movement of individuals; drift, the random persistence of individuals and hence the random sampling of alleles and species; and selection, the non-random survival of individuals and hence the non-random sampling of alleles and species. If similar processes act across levels of organization, genetic and species diversity would be expected to covary across space, that is, a diversity continuum from micro- to macroevolutionary scales (e.g., Fournelle et al., 2016; Papadopoulou et al., 2011; Robuchon et al., 2019). Species-genetic diversity correlations (SGDCs) are a simple way to test whether species and genetic diversity covary across space (Vellend, 2005). In practice, genetic diversity is estimated in multiple sites for a focal species, and species diversity is estimated on the surrounding community (Laroche et al., 2015). If an association between both levels of diversity is found, it may be due either to (i) a 'parallel effect' of evolutionary processes (selection, drift and dispersal) on the two levels of diversity or (ii) to a direct 'causal effect' between species and genetic diversity (Vellend & Geber, 2005). Such causal effects might include the genetic divergence at the population level serving as the initial stage for the macroevolutionary divergence between species (Avise et al., 1987; Bowen et al., 2016).

SGDCs and their underlying processes have only rarely been evaluated in a marine environment (Manel et al., 2020; Messmer et al., 2012; Petersen et al., 2022; Vilcot et al., 2023), where species generally have greater dispersal capacity, bigger populations and much larger range sizes than in a terrestrial environment (Allen, 2008; Bowen et al., 2020). Two studies focusing on coral reef fishes have formally tested for covariation between genetic and species richness (i.e., α -diversity) in the Pacific Ocean (Messmer et al., 2012) and Hawai'i respectively (Selkoe et al., 2016), but mostly limited to mtDNA. Over a large spatial scale, Messmer et al. (2012) evidenced a decline in the combined genetic diversity of 11 coral reef fishes from West to East of the Pacific Ocean, paralleling the well-known Pacific gradient in species richness. This α -SGDC has been attributed to several non-exclusive factors such as the history of the region, the connectivity between habitat patches, and the available habitat area driving population and community sizes. It remains to be determined whether this parallel decline in diversity also applies to the genome-wide genetic diversity.

A few more studies have also reported concordant patterns of marine β -diversity (i.e., dissimilarity between sites) across levels of biological organization, without specifically testing for SGDC. A general concordance between population genetic partitions and biogeographic patterns has been noted by Bowen et al. (2016) and DeBoer et al. (2014), where both genetic and community structure were consistent with bioregions. However, Crandall et al. (2019) noted

that while finer geographic scales may exhibit great concordance, species distributions and population genetic structure across the entire Indo-Pacific Ocean are only loosely correlated. Dispersal is often found to be a major process shaping both intra- and interspecific spatial structure through the well-established patterns of isolation-by-distance in population genetics (Wright, 1943) and distance decay of similarity in community ecology (Nekola & White, 1999). These two patterns of increasing dissimilarity of populations and communities with increasing geographic distance separating them make the process of dispersal limitation and its influence relatively easy to detect, describe and understand (Kobayashi & Sota, 2016). If stochastic dispersal processes dominate at the level of alleles and species, as predicted by neutral theories (Antonovics, 1976; Hubbell, 2001), we can expect the two levels of β -diversity to covary spatially (see Baselga et al., 2022; Xie et al., 2021). Dispersal limitation associated with geographic isolation is already known to have left a strong imprint of both interspecific (e.g., Leprieur et al., 2016; Maxwell et al., 2022; Parravicini et al., 2013) and intraspecific (Crandall et al., 2019; Donati et al., 2021) diversities. Dispersal has also directly been linked to a continuum of β -diversity in several species of shallow tropical reef fishes in the Western Indian Ocean (Vilcot et al., 2023). However, whether a positive β -SGDC also holds for a deep-sea fish, and across a larger spatial scale remains to be tested.

In this study, we focus on reef-associated fishes, which are ideal biological models for investigating whether a diversity continuum exists across scales of biological organization. In island-like habitats such as tropical reefs, SGDCs are more likely to be positive and stronger than in continuous habitats, as equilibrium is more readily reached (Vellend et al., 2014). Specifically, we evaluate genetic diversity for a submesophotic tropical snapper that is a food resource for human populations in many regions. *Etelis coruscans* (Lutjanidae), commonly known as Onaga, Deepwater longtail red snapper, or Flametail snapper, is a coastal demersal snapper that relies on deep corals and rocky reefs. It is found at depths between 90 and 400m on continental shelves and islands throughout the Indo-Pacific. *Etelis coruscans* has a particularly large body size and long life span, even when compared to other members of the Lutjanidae (Uehara et al., 2020). With an estimated pelagic larval duration (PLD) of more than 45 days (Andrews et al., 2014), and a larval phase that occurs in shallow water (0–100m in a closely related species *Etelis oculatus*, D'Alessandro et al., 2010), dispersal is predicted to be relatively high for this species. In general, studies in deep-sea species (below 200m) are scarce, and to our knowledge, only few are exploring genome-wide and large-scale patterns of genetic diversity in a deep-sea fish (Gaither et al., 2018; but see Andrews et al., 2020 and Gaither et al., 2011 using mtDNA or microsatellite).

Additionally, no studies have thoroughly investigated how the strength of SGDCs may vary depending on the community delimitation (i.e., the set of species on which species diversity is evaluated), as suggested by Lamy et al. (2017). For instance, one might expect stronger SGDCs if (i) communities are composed of species with similar biological and ecological traits to those of the focal species (see He & Lamont, 2010), such as the PLD and body size,

which are major dispersal traits in tropical reef fishes (e.g., Riginos et al., 2014). If species of the community have similar dispersal abilities to the focal species, we can expect micro- and macroevolutionary processes related to dispersal to have shaped similarly diversity patterns at both intra- and interspecific levels (see Vilcot et al., 2023). One might also expect stronger SGDCs if (ii) fish communities are composed of species that are phylogenetically closer to the focal species, thus sharing a common evolutionary history. Closely related species are not only more likely to share similar traits (assuming gradual trait evolution), but would also have experienced similar past environmental changes and diversification histories. For large-scale patterns of tropical fish diversity, these include the formation of 'hard' and 'soft' barriers to dispersal and vicariance (Cowman & Bellwood, 2013), which can operate from micro- to macroevolutionary scales, and in turn lead to the spatial covariation of intra- and interspecific diversities (see Vilcot et al., 2023). However, there is often no clear rationale for why a particular community delineation was chosen, nor for the impact of that choice on the SGDC: for example, freshwater snails (Lamy et al., 2013), freshwater fish (Fourtune et al., 2016; Robuchon et al., 2019) and marine habitat-forming (MHF) species (Figuerola-Ferrando et al., 2023). Here, we postulate that the strength of the SGDCs may weaken as (i) the variability in life history traits and (ii) the taxonomic extent of the community increases, and that the use of different community delineations can provide insight into the processes acting on community formation across different levels of organization.

To understand the taxonomic and spatial extent of a potential covariation between intra- and interspecific diversities, this study aimed to simultaneously investigate the spatial variation of *E. coruscans* genetic diversity with tropical fish species diversity. By examining these species-genetic diversity correlations over the Indo-Pacific Ocean, we seek to elucidate the ecological and evolutionary processes shaping diversity across scales of organization in deep-sea tropical fishes. To achieve this objective, we analyse nuclear SNP data for *E. coruscans* collected across its Indo-Pacific range, from the Seychelles to Hawai'i, in conjunction with a comprehensive global database of marine fish occurrence (Albouy et al., 2019). Our approach first involved separate analyses of α - and β -genetic diversities for *E. coruscans* and α - and β -species diversities for tropical reef fish communities. We then tested for spatial covariations between genetic and species α - and β -diversities for different taxonomic scales (Etelinae, Lutjanidae, Eupercaria and Teleostei) and spatial scales (including or not the Western Indian Ocean). Lastly, using distance-based redundancy analysis, we assessed whether geographic distance or environment explained genetic and species β -diversity patterns. Specifically, we evaluated the following expectations based on previous studies. First, following Messmer et al. (2012), we expect a parallel decline in species and genetic α -diversity from the West to the East Pacific Ocean (E1). Second, we expect geographic distance to be the primary driver of both genetic and species β -diversities, resulting in positive β -SGDCs (E2), as already found by Vilcot et al. (2023) in shallow tropical fishes. Third, we expect a discordance between species and genetic

diversity patterns across the entire Indo-Pacific (E3), as suggested by Crandall et al. (2019). Last, according to Lamy et al. (2017), we expect positive SGDCs to disappear as the community gets taxonomically wider (i.e., from the genus to class levels) from the focal species, namely *E. coruscans* (E4).

2 | MATERIALS AND METHODS

2.1 | Genetic diversity in *Etelis coruscans*

2.1.1 | Sampling scheme

Tissue samples of *E. coruscans* (finclips or muscle tissue) stored in salt-saturated DMSO buffer were repurposed from a previous study by Andrews et al. (2020), collected throughout the Indo-Pacific between 2004 and 2010. Twenty-eight additional tissue samples from New Caledonia collected in the context of the ANR SEAMOUNTS project between 2019 and 2021 were included in this study. The sampling was designed to cover most of the range size of the focal species. In total, 369 tissues sampled from 34 stations covering 10 sites of the Indo-Pacific were used (Figure 1, Table S1).

2.1.2 | Genotyping and filtering

All of the 369 tissue samples were sent to Diversity Arrays Technology Pty Ltd (Canberra, Australia) for DNA extraction and DNA sequencing using the DArTseq method (Kilian et al., 2012; Sansaloni et al., 2011). SNP calling and basic filtering were performed by Diversity Arrays Technology Pty Ltd, resulting in 105,144 SNPs. SNP data were further filtered with the R package 'dartR' (Gruber et al., 2022). Individuals with more than 0.5 missing data (i.e., for which more than 50% of SNP has missing value) were removed. SNPs with a call rate lower than 0.7 (>0.3 missings), and a minimum allele frequency below 0.05 were excluded. The final data set consisted of 363 individuals and 21,948 SNPs (see Table S2 for the number of SNPs at each filtering step).

2.1.3 | Genetic diversity and structure estimation

The α -genetic diversity (α -GD) was estimated for each sampling site with the expected heterozygosity H_s (Nei, 1987) using the *basic.stats* function from the 'hierfstat' R package (Goudet & Jombart, 2015). Pairwise β -GD between sites were estimated with F_{ST} (Weir & Cockerham, 1984) using the *genet.dist* function of the 'hierfstat' R package (Goudet & Jombart, 2015).

Population genetic structure was first evaluated with a PCA on the 21,948 SNPs using the *glPca* function from the 'adegenet' R package. A discriminant analysis of principal components (DAPC) implemented in the *dapc* function of the R package 'adegenet' (Jombart, 2008; Jombart & Ahmed, 2011) was also conducted. Each individual's



FIGURE 1 Map of the 10 sampling sites across the Indo-Pacific Ocean. The number of *Etelis coruscans* individuals sequenced per site is indicated in brackets. Sites are colour-coded by longitude.

sampling site was used as prior information. The optimal number of PC axes to retain was optimized using the alpha-score ('adeget' R package). Respectively 53 and 54 number of PCA axes was retained when considering all sites, or all sites except Seychelles.

Genetic structure was further assessed using the Bayesian unsupervised clustering method in STRUCTURE 2.3.4 (Pritchard et al., 2000) called with the *gl.run.structure* function from the R package 'dartR' (Gruber et al., 2022). Analyses were conducted for $K=1$ to $K=9$ ancestral populations, with 5 repetitions each.

2.2 | Species diversity in the tropical fish metacommunity

2.2.1 | Presence data

Presence data for 15,595 fish species were provided by personal communication from an updated version of Albouy et al. (2019) data set. This data set combines the GASPARE database (Parravicini et al., 2013) with the Ocean Biogeographic Information System (OBIS, <http://www.obis.org>) on a 1° resolution grid covering all oceans. From this global database, we extracted the list of species present at each sampling station with a buffer of 50 km. Fish species presence lists at each station were further grouped together for each sampling site.

2.2.2 | Community delineation

Species diversity (SD) was calculated by testing various species assemblages defined according to different taxonomic levels

(hereafter referred to as communities). Specifically, we considered species presence lists per site for inclusion in either (i) the focal class (Teleostei), (ii) order (Eupercaria), (iii) family (Lutjanidae) or (iv) subfamily (Etelinae). Taxonomic information for each species was obtained from Fishbase (Froese et al., 2010) using the 'rfishbase' R package (Boettiger et al., 2012). This produces a total of four communities for which we also provided an estimation of the variation in the PLD. PLD is frequently used as a proxy for dispersal potential and connectivity in marine fishes (Selkoe & Toonen, 2011). The mean and standard deviation of PLD for each taxonomic level were calculated from the PLD of each species included in the database of Luiz et al. (2013).

2.2.3 | Community diversity and composition

For each community, the richness-based α -SD was estimated as the number of species present at each site. The β -SD between sites was quantified with the pairwise Jaccard's dissimilarity index (β_{jac} -SD) using the *beta.pair* function of the 'betapart' R package (Baselga, 2010; Baselga et al., 2018). We also computed the turnover (β_{jtu} -SD) component of Jaccard's dissimilarity index, which is independent of differences in species richness (α -SD) between sites due to nestedness (Baselga, 2012). This index is particularly recommended in large-scale β -diversity studies (see Maxwell et al., 2022 for tropical reef fishes) because it describes species turnover between sites, that is, the replacement of species from one site to another without the influence of richness gradients (Baselga, 2012).

To investigate spatial variation in species composition among sites, we applied a principal coordinate analysis (PCoA) based on the

β_{jac} -SD and β_{Jtu} -SD distance matrices with the function *dudi.pco* from the 'ade4' R package (Dray, Dufour et al., 2023).

2.3 | Species-genetic diversity correlations

For each defined community, α -SGDC was evaluated as the degree of association between α -GD and α -SD using Pearson's correlation coefficient (r). β -SGDC was also evaluated using Pearson's correlation coefficient between the β -GD and β -SD distance matrices and a Mantel test for the statistical significance (9999 permutations). We used the function *mantel* from the R package 'ecodist' (Goslee & Urban, 2007). Because the Type I error of the Mantel test can be inflated (Legendre et al., 2015; Raufaste & Rousset, 2001), we also conducted a Procrustes analysis using the *protest* function of the R package 'vegan' (Oksanen et al., 2022), which shows higher power than the Mantel test for evaluating the statistical significance of an association between two distance matrices (Peres-Neto & Jackson, 2001).

2.4 | Drivers of β -SGDCs

2.4.1 | Geographic and environmental distances

Two potential drivers of β -GD and β -SD were considered: geographic distance and environment. Geographic distance between sites was estimated as the shortest in-water distance between pair of sites with the *lc.dist* function of the 'marmap' R package (Pante & Simon-Bouhet, 2013), using GEBCO-gridded bathymetry data (<https://www.gebco.net>) and a minimum depth of 45 m. From this geographic distance matrix, we decomposed spatial relationships between sites using distance-based Moran's eigenvector maps (db-MEMs) with the 'adespatial' R package (Borcard & Legendre, 2002; Dray et al., 2006; Dray, Bauman, et al., 2023). Through this spectral decomposition, MEMs offers ($n - 1$) eigenfunctions, serving as independent variables that capture spatial structures at various scales within the study area. Environmental variables were extracted from Bio-ORACLE v2.0 (Assis et al., 2018) as global-scale layers in a grid system of 5 arcmin spatial resolution of (approx. 9.2 km at the equator), using the 'sdmpredictors' R package (Bosch & Fernandez, 2022). The seven following environmental variables were extracted at the mean bottom depth of each cell: salinity, mean temperature, minimum temperature, maximum temperature, chlorophyll concentration (mg/m^3), dissolved oxygen concentration ($\mu\text{mol}/\text{m}^3$) and nitrate concentration ($\mu\text{mol}/\text{m}^3$). The average value per station was calculated over a 50-km buffer zone around each station; then, the average value per site was calculated over sampling stations. From the seven environmental variables, we performed a principal component analysis (PCA) with the function *dudi.pca* from the 'ade4' R package (Dray, Dufour et al., 2023). Environmental distance between sites was computed as the Euclidian distance from the scaled and centred environmental variables, using the *vegdist* of the 'vegan' R package (Oksanen et al., 2022).

2.4.2 | Distance-based redundancy analysis

To determine the relative importance (R^2) of geographic distance and environment in explaining β -GD and β -SD, we used distance-based redundancy analysis (dbRDA), implemented in the *capscale* function of the 'vegan' R package (Oksanen et al., 2022). This constrained multivariate analysis is recommended in both landscape genetics and community ecology for evaluating the influence of spatial processes and environmental constraints in shaping β -diversity patterns (see Legendre et al., 2008; Meirmans, 2015). dbRDA builds linear models between the considered β -diversity matrix transformed by a PCoA and the two types of explanatory variables. We limited the number of response variables to avoid overfitting, due to the relatively low number of sites. The response variables retained were as follows: MEMs with Moran's I values >0.25 (i.e., the first MEM in our case) to account for positive and coarse spatial autocorrelations, and the first two axes (PC) of the PCA applied to the seven environmental variables, which account for more than 95% of the total inertia. To select the best model for each β -diversity response matrix, we applied a forward selection procedure between the null and the complete model (β -diversity \sim MEM1 + PC1 + PC2), automatized in the *ordstep* function of the 'vegan' R package (Oksanen et al., 2022). The significance of the models was tested using ANOVA-like permutation tests with 9999 permutations implemented in the *anova.cca* function (vegan R package).

2.4.3 | Covariance decomposition

For positive and significant β -SGDCs, the relative contribution of geographic and environmental distance to the covariation between β -GD and β -SD was assessed using a linear covariance decomposition, as implemented in Lamy et al. (2013). For each of the two linear models:

1. $\beta\text{GD} \sim \gamma_{\text{GD,geo}}(\text{geographic distance}) + \gamma_{\text{GD,env}}(\text{environmental distance})$,
2. $\beta\text{SD} \sim \gamma_{\text{SD,geo}}(\text{geographic distance}) + \gamma_{\text{SD,env}}(\text{environmental distance})$

We gathered the standardized regression coefficients (γ). First, the fraction of covariance between β -GD and β -SD (SGDC) that is due to parallel effects of each of the explanatory variable was given respectively by $\gamma_{\text{GD,geo}} \times \gamma_{\text{SD,geo}}$ and $\gamma_{\text{GD,env}} \times \gamma_{\text{SD,env}}$. If the explanatory variable has a similar effect on β -GD and β -SD, these covariance components are positive, otherwise it is negative. Second, the effect of covariance between geographic and environmental distance on SGDC is measured as $(\gamma_{\text{GD,geo}} \times \gamma_{\text{SD,env}} + \gamma_{\text{SD,geo}} \times \gamma_{\text{GD,env}})$, which may increase or decrease the direct effects of each explanatory variable. Third, the unexplained fraction of the SGDC was computed as the covariance between the residuals of (1) and (2).

All statistical analyses were performed using the program R version 4.2.1 (R Core Team, 2022).

3 | RESULTS

3.1 | Genetic diversity and structure

A total of 21,948 polymorphic SNP loci for 363 individuals of *E. coruscans* met the quality filtering criteria (Table S2). α -GD was lowest in Seychelles ($H_s=0.238$) and highest in Western Australia ($H_s=0.273$, Table 1). There was no evidence of a decline in genetic diversity from West to East Pacific Ocean (Figure S1).

All three analyses of PCA, DAPC with sampling sites as a prior and STRUCTURE without priors indicated that Seychelles was distinct from all other Indo-Pacific sites (Figure 2a,c, Figures S2 and S3a). β -GD also supported evidence for restricted gene flow between the Seychelles and the other sites, with all pairwise β -GD with the Seychelles being on average 40 times greater (mean $F_{ST}=0.2118$, range=0.1980–0.2185) than pairwise β -GD within the eastern Indo-Pacific sites (mean $F_{ST}=0.0054$, range=0.0008–0.0114, Table S3). The pairwise β -GD was the highest between the Seychelles and Fiji ($F_{ST}=0.218$, Figure S4c, Table S3).

When the Seychelles were removed from the data set, DAPC with sampling sites as prior showed evidence of three genetic groups: (i) Christmas Island, Western Australia, Guam, (ii) New Caledonia, Rotuma Island, Vanua Levu, Tonga, American Samoa, and (iii) Hawai'i (Figure 2b). When considering $K=2$ ancestral populations, STRUCTURE delineated two clusters coinciding with results from the DAPC: (i) Hawai'i grouping with Christmas Island, Western Australia and Guam, and (ii) New Caledonia, Rotuma Island, Vanua Levu, Tonga, American Samoa (Figure 2d, Figure S3b).

As noted in Andrews et al. (2020), there was no evidence of a temporal sampling effect on the genetic structure or diversity.

3.2 | Community diversity and structure

A total of 4878 Teleostei species presence were gathered across all sites, of which 616 were Eupercaria, 64 were Lutjanidae, and

15 were Etelinae (Table 1, Figure S5). α -SD was highest in Western Australia for Teleostei, Eupercaria and Lutjanidae (3303, 457 and 52 species, respectively), and in New Caledonia for Etelinae (14 species). While there was no difference in mean PLD across communities, Eupercaria and Teleostei had a greater variance in PLD (mean=36.3±15.6 and 33.9±16.3 days respectively) in comparison with the family Lutjanidae (34.4±9.59 days, Figure 3).

α -SD was lowest in Rotuma Island for Teleostei (813 species), in Hawai'i for Eupercaria and Lutjanidae (90 and 15 species respectively), and in New Caledonia for Etelinae (9 species, Table 1). The Teleostei and Eupercaria communities recovered the well-known pattern of α -SD decline from West to East of the Pacific, while the gradient was not as clear for the Lutjanidae and Etelinae communities (Figure S1). PCoA applied on total species dissimilarity (β_{jac} -SD) for Teleostei, Eupercaria and Lutjanidae communities indicated Hawai'i to be the most dissimilar (Figures S6 and S4g,i,k, Table S3). However, the β_{jtu} -SD that controls for species richness differences showed that Hawai'i was not as different from the other sites in terms of species turnover for the Lutjanidae family and the Etelinae subfamily. PCoA also evidenced an expected west-to-east gradient in species composition (Figure S6).

3.3 | SGDCs on different communities

When excluding the Seychelles, both Mantel test and Procrustes analysis showed a significant and positive correlation between β -GD (F_{ST}) and Etelinae β_{jtu} -SD (Mantel test: $r=.409$, $p=.009$) or Lutjanidae β_{jtu} -SD (Mantel test: $r=.578$, $p=.0007$, Table S4, Figure 4). However, the positive β -SGDCs relationship was lost when considering larger communities (i.e., Eupercaria and Teleostei). When all sites were included, the β -SGDC was only statistically significant when considering the β_{jtu} -SD of Etelinae, but only with a very weak Pearson's correlation coefficient (Mantel test: $r=.203$, $p=.003$). Moreover, no β -SGDCs were found when considering the total species dissimilarity (β_{jac} -SD, Table S4,

Site	Genetic diversity		Species diversity			
	N	Hs	Etelinae	Lutjanidae	Eupercaria	Teleostei
Seychelles	38	0.238	11	37	271	1696
Christmas Island	6	0.27	13	42	314	2029
Western Australia	26	0.273	13	52	457	3303
Guam	29	0.264	13	34	241	1435
New Caledonia	58	0.265	14	49	350	2604
Fiji Rotuma Island	20	0.265	13	33	169	813
Fiji Vanua Levu	20	0.265	14	48	283	1721
Tonga	29	0.264	14	38	207	1199
American Samoa	29	0.265	9	29	184	1061
Hawai'i	108	0.269	10	15	90	1123
Across all sites	363		15	64	616	4878

TABLE 1 α -diversity metrics for both genetic and species diversity at each sampling site. N indicates the sampling size of *Etelis coruscans* individuals per site.

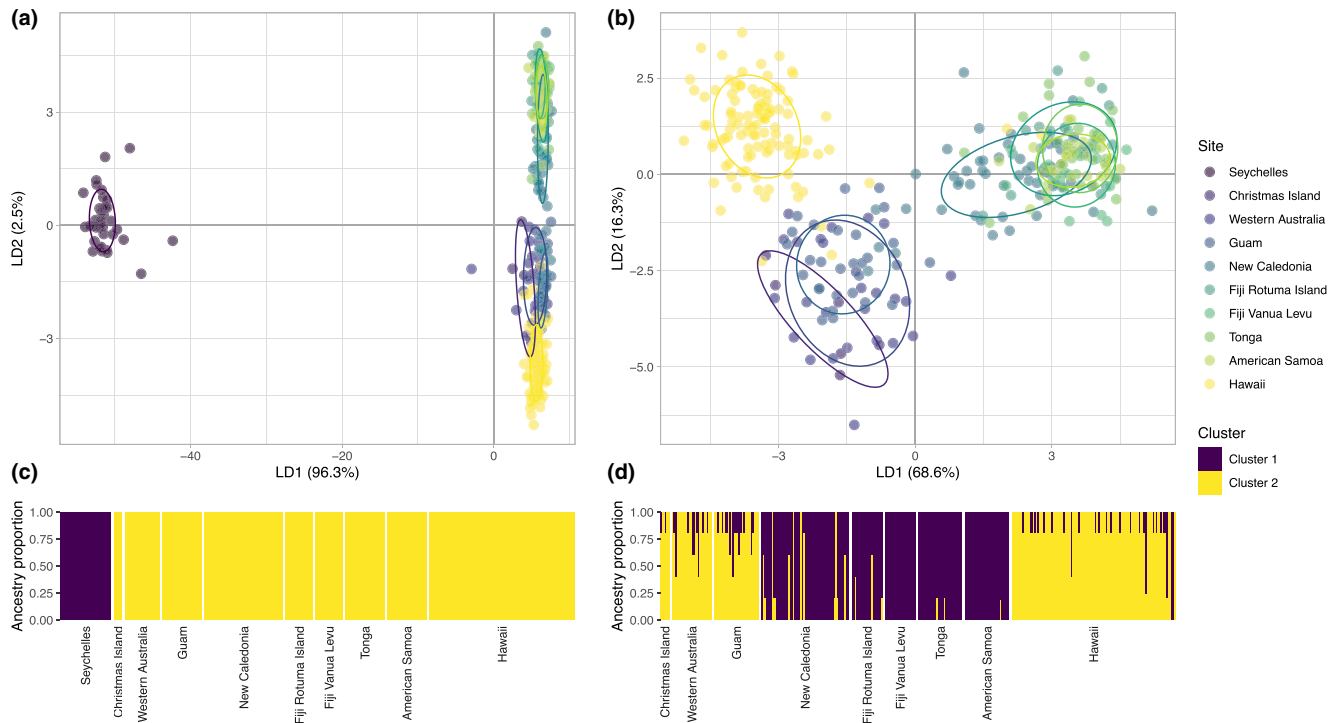


FIGURE 2 Population genetic structure on the set of 21,948 SNP data of *Etelis coruscans*. (a,b) Scatter plots from discriminant analyses of principal components (DAPC) performed using sampling sites as prior. Individuals are colour-coded by sampling site. (c, d) Ancestry proportions inferred from STRUCTURE with no prior assuming $K=2$ ancestral populations. Panels (a, c) display results considering all sites and panels (b, d) display results for all sites except Seychelles.

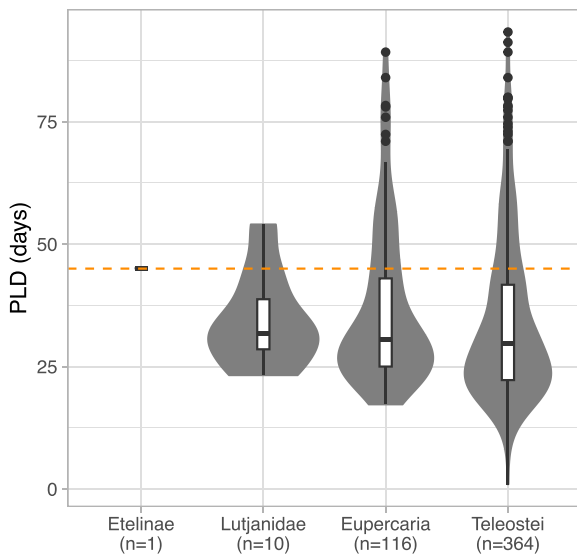


FIGURE 3 Violin plot showing pelagic larval duration (PLD) in days, for the different community delineations (Etelinae, Lutjanidae, Eupercaria and Teleostei). Numbers in brackets indicate the number of species present over the study sites for which trait values were collected from Luiz et al. (2013). The orange dashed line indicates the estimated minimum PLD for *Etelis coruscans* (Andrews et al., 2014).

Figure 4). No α -SGDC at any spatial scale or community delineation was detected (Figure S7).

3.4 | Drivers of β -SGDCs

To assess processes acting on both β -GD and β -SD, we implemented dbRDA with geographic distance (expressed as Moran's Eigenvector Maps) and environment (PCA axes) as explanatory variables (Figure S8). When the genetically differentiated Seychelles were excluded, we found that β -diversity patterns at both intraspecific (*E. coruscans*'s β -GD) and interspecific levels (Lutjanidae's β_{Jtu} -SD) were significantly associated with large-scale spatial structure (MEM1), but not with environment (Table 2). It is worth noting that these results are consistent with those found using the Mantel test and Procrustes analysis that evaluate the degree of association between β -GD (or β -SD) with geographic distance and environmental distance (Figures S9 and S10, Table S5). The only exception concerns the Etelinae community, for which we found a moderate but significant increase in species turnover with geographic distance (Figure S9, Table S5). When all sites were considered, dbRDA showed that the β -GD of *E. coruscans* was explained neither by spatial structure nor by environment (Table 2).

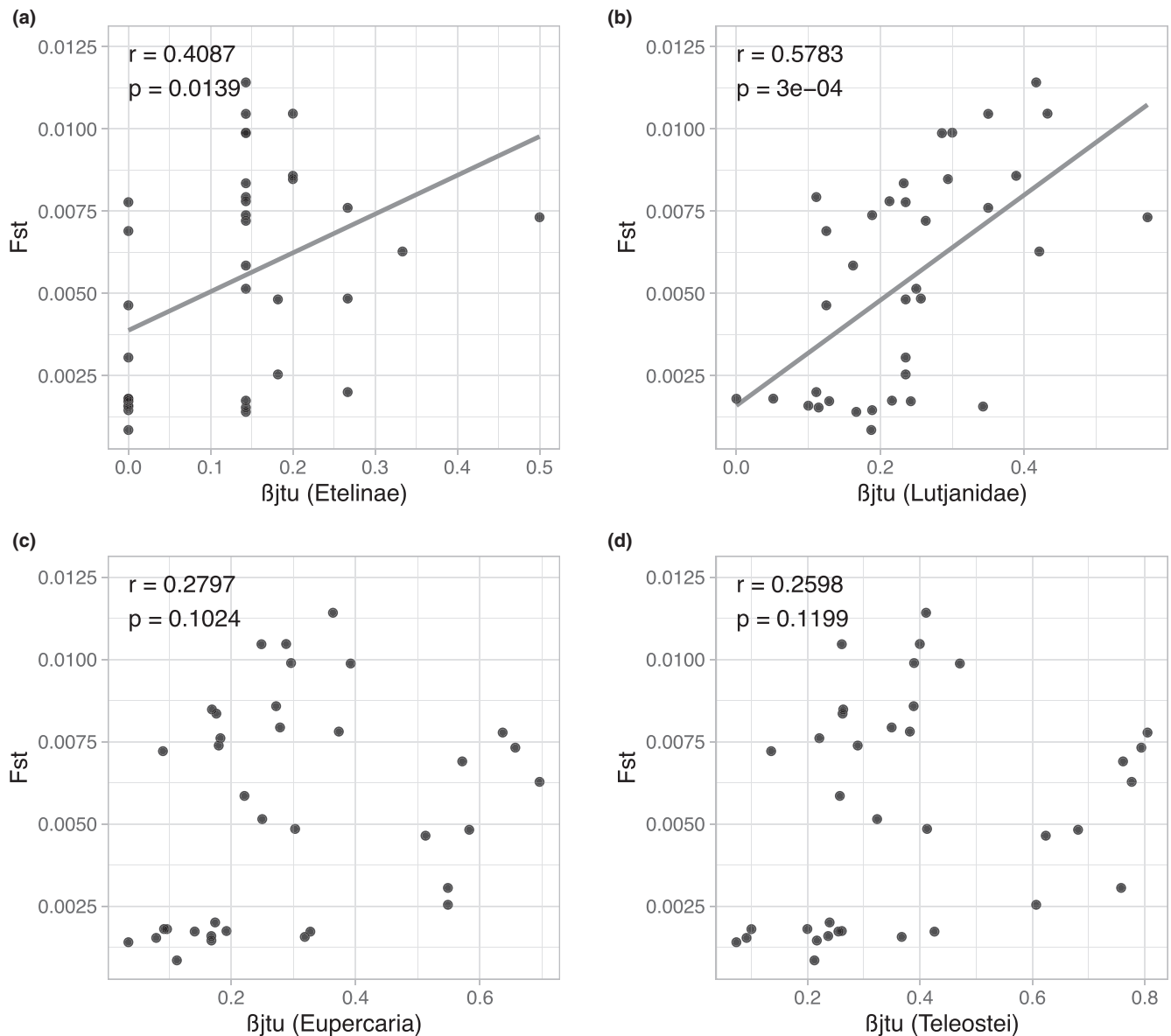


FIGURE 4 β -SGDCs between *Etelis coruscans* β -GD (measured as F_{ST}) and β -SD (measured as Jaccard turnover β_{jtu}), computed for different community delineations: (a) Etelinae, (b) Lutjanidae, (c) Eupercaria, (d) Teleostei, when excluding the Seychelles. The fitted line of a linear regression model is shown when Pearson's correlation coefficient is significant (Mantel test: $p < .05$).

For the positive and significant β -SGDCs (i.e., with the Etelinae and Lutjanidae communities), the covariance decomposition showed that half of the correlation between β -GD and β_{jtu} -SD was explained by geographic distance (Figure 5). Almost half of the correlation remained unexplained by our predictors, with residuals of β -GD and β_{jtu} -SD remaining significantly correlated at the family level (Lutjanidae), indicating that other processes may in part explain the β -diversity continuum.

4 | DISCUSSION

Here, we show that geographic distance is the main driver of genetic differentiation (β -GD) and spatial species turnover (β_{jtu} -SD) for a tropical submesophotic fish species (*E. coruscans*), its subfamily (Etelinae) and family (Lutjanidae), leading to a marked spatial covariation

between intra and interspecific β -diversities. However, this covariation is only found when considering the Central Indo-Pacific and Central Pacific regions. It is lost across the wider scale of the entire Indo-Pacific or when considering a taxonomic level higher than the family. This suggests that processes shaping the two levels of β -diversity are different at larger spatial or taxonomic scales. Contrary to our first expectation (E1), we also found no association between species and genetic α -diversities.

4.1 | No parallel gradient in genetic and species α -diversities

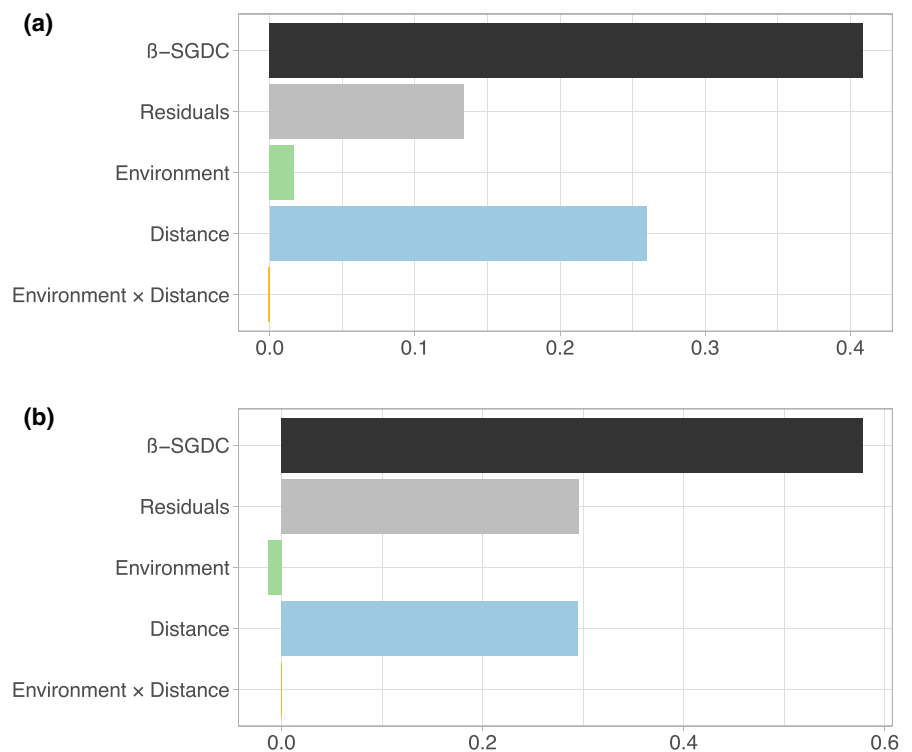
While all the defined communities recovered the well-known pattern of decreasing species richness from West to East of

TABLE 2 Models selected by distance-based redundancy analysis (dbRDA) for each β -diversity matrix as captured by F_{ST} for *Etelis coruscans* (genetic β -diversity), and β_{jac} and β_{jtu} for each community (species β -diversity).

	Model	R^2	Adjusted R^2	F	p -value
All sites	β_{jac} (Lutjanidae)~MEM1	.2605	.1680	2.797	.005**
	β_{jtu} (Lutjanidae)~MEM1	.4444	.3750	3.728	.01*
	β_{jac} (Eupercaria)~MEM1	.2423	.1476	2.558	.012*
	β_{jac} (Teleostei)~MEM1	.2190	.1214	2.244	.019*
Without Seychelles	F_{ST} ~MEM1	.8149	.7884	19.949	.003**
	β_{jtu} (Lutjanidae)~MEM1	.4596	.3824	3.302	.019*

Note: Response variables include the spatial structures captured by Moran's Eigenvector Maps (MEMs) and the first two environment-related PCA axes accounting for 95% of the total environmental variation (PC1 and PC2). Only statistically significant models are reported. Response variables that appeared in both genetic and species β -diversity models are underlined. Significance levels are indicated: * $p < .05$; ** $p < .01$.

FIGURE 5 β -SGDC covariance decomposition by geographic and environmental distance. β -SGDC (black bar) is the Pearson correlation coefficient between β -GD (F_{ST}) in *Etelis coruscans* and β_{jtu} -SD measured on (a) the Etelinae subfamily, or (b) the Lutjanidae family. Each of the other bars represents the effect of environmental distance (green bar), geographic distance (blue bar), or the covariation between both (orange bar), on this β -SGDC. Residuals (grey bar) correspond to the correlation between residuals of β -GD (F_{ST}) and β_{jtu} -SD that are not explained, that is, the effect of unmeasured variables. If one explanatory variable has a similar effect on β -GD and β -SD, these covariance components are positive, otherwise it is negative.



the Central Indo-Pacific and Central Pacific regions (e.g., Mora et al., 2003), there was no evidence of such a longitudinal gradient for *E. coruscans* genetic α -diversity. Thus, contrary to our first expectation (E1), no association was found between genetic diversity per se and species richness, irrespective of community delineation or spatial extent. Although some shallow coral reef fish species have been shown to exhibit a decline in genetic diversity across the Pacific Ocean (Messmer et al., 2012), there are exceptions (Matias & Riginos, 2018).

The absence of decline in *E. coruscans* α -GD across the Central Indo-Pacific and Central Pacific regions, even at the edge of its distributional range (i.e., Hawai'i), suggests that *E. coruscans* is either a

particularly dispersive species, or may have a different centres of origin than the central Indo-Pacific (Briggs, 1999). Further studies of nuclear α -GD for other mesophotic Lutjanidae species across the Indo-Pacific, including species with lower larval dispersal abilities and smaller body sizes than *E. coruscans*, could be used to evaluate whether SGDCs depend more on life history traits or evolutionary history for this taxonomic group. In addition, these analyses could be used to test predictions regarding the geographic origin of these species. Species that originated in the central Indo-Pacific region would be expected to exhibit a west-to-east decline in their genome-wide α -diversity, paralleling the gradient in tropical reef fish species richness.

4.2 | Dispersal governs Lutjanidae β -diversities across scales of biological organization

We detected a clear genetic clustering of the Seychelles (Figure 2), as previously observed with both microsatellite and mtDNA data for *E. coruscans* (Andrews et al., 2020). However, the observed genetic differentiation of the Seychelles relative to its distance from other sites suggests a more reduced gene flow relative to geographic distance than for the other sites. This highly restricted gene flow between the Eastern and Western Indian Ocean has previously been reported in shallow reef fish species (e.g., Fernandez-Silva et al., 2015; Huyghe & Kochzius, 2018) and has been attributed to the large area of open ocean, which provides few opportunities for stepping stone dispersal.

When the Seychelles was excluded from our analysis, we found patterns of isolation-by-distance in both genetic differentiation and species composition, adding evidence that dispersal might be the main driver of diversity structure across levels of organization in tropical fishes (Vilcot et al., 2023). This parallel effect of dispersal limitation on both genetic and species dissimilarities explains the continuum in β -diversity in Lutjanidae (Figure 5), as described in other systems (Blum et al., 2012; Fourtune et al., 2016; Odat et al., 2010; Papadopoulou et al., 2011; Robuchon et al., 2019; Sei et al., 2009; Watanabe & Monaghan, 2017). This is consistent with our second expectation (E2) and more generally with the predictions of neutral models of biodiversity (Antonovics, 1976; Hubbell, 2001), involving stochastic dispersal processes (Papadopoulou et al., 2011). Nevertheless, a non-negligible fraction of the covariation between species and genetic β -diversity remains unexplained (Figure 5), which suggests that other processes related to past environmental changes may have left an imprint on both SD and GD patterns, as shown in freshwater fishes (Robuchon et al., 2019). For Indo-Pacific tropical fishes, rapid sea-level changes during the Pleistocene strongly affected habitat availability, which in turn led to population fragmentation. For example, the exposure of the Sunda and Sahul shelves during sea-level lows left a pronounced genetic signature in many tropical marine species (reviewed in Ludt & Rocha, 2015).

Our results showed that the use of Jaccard's dissimilarity index to explore spatial patterns of species β -diversity did not allow the detection of a β -SGDC, regardless of the community and the spatial extent considered (Table S4). This widely used index in community ecology is known to be strongly affected by differences in species richness due to nestedness (Baselga, 2012), which is the case for tropical reef fishes of the Indo-Pacific (Mouillot et al., 2013). The use of the turnover component of the Jaccard's index (β_{JTU}) to evaluate the relative influence of dispersal limitation and environmental filtering in shaping species β -diversity patterns is therefore recommended (Baselga et al., 2022; Maxwell et al., 2022), as the processes leading to species nestedness and turnover may differ (e.g., Leprieur et al., 2011). Overall, our results suggest that the choice of the compositional dissimilarity index is critical when exploring β -SGDC patterns across a marked

species richness gradient, which requires special attention in future SGDC studies.

4.3 | β -SGDC is lost across the entire Indo-Pacific range

β -diversities measured here as genetic differentiation and species spatial turnover behaved differently at the scale of the whole Indo-Pacific, with the Seychelles on one end being more distinct in terms of genetic composition of *E. coruscans*, whereas Hawai'i on the other end was more distinct in terms of species composition. It supports our third expectation (E3) regarding a general discordance between genetic and species diversity patterns at the scale of the whole Indo-Pacific, as suggested by Crandall et al. (2019) based on phylogeographical data from 56 marine taxa.

In particular, the compositional break between the EIO and the WIO is not observed for any community. With the Seychelles showing lower genetic diversity, this supports a westward colonization of the genus *Etelis* (Andrews et al., 2016). Thus, the equilibrium in terms of gene flow and genetic drift might not be reached with the eastern range of *E. coruscans*, as it may be the case for most species in the Indo-Pacific (Hellberg, 2009). Intra- and interspecific diversity may also respond to colonization dynamics with different timing or to different extents (Landguth et al., 2010) so that dispersal may tend to homogenize species composition faster than genetic composition. As such, communities may be in equilibrium while populations are not, which could explain the discrepancy of diversity between levels of organization at larger spatial scales.

4.4 | β -SGDC is lost at higher taxonomic levels

After considering the spatial scale that showed evidence for a continuous spatial gradient of compositional dissimilarity (i.e., removing the Western Indian Ocean), we determined the taxonomic scale at which β -SGDC occurs as suggested in Lamy et al. (2017). We showed positive β -SGDCs at the subfamily and family levels, as evidenced for the family level in shallow reef fishes (Vilcot et al., 2023), but not when considering communities of higher taxonomic scales (Figure 4). These results are consistent with our fourth expectation (E4), namely that positive β -SGDCs should be observed if the focal species display a similar dispersal ability to those that composed the community, which is the case here for Lutjanidae, which have relatively low variability in PLD over the studied sites (Figure 3), in contrast to Eupercaria and Teleostei. The absence of β -SGDC when considering the order and class levels also suggests that evolutionary history associated with speciation, extinction and dispersal events is important to consider in future SGDC studies. Indeed, differential evolutionary histories among phylogenetically distant species may also imply distinct patterns of genetic differentiation at the population level (Matias & Riginos, 2018), which may therefore blur the relationship between species and genetic β -diversities at large

spatial scales. Finally, in this study we considered the taxonomic scale to delineate communities, but β -SGDC could also be explored with communities defined on the basis of the breath of ecological niche (i.e., specialist version generalist species) or considering the trophic level (Fargeot et al., 2023), which may provide new insights to the role of ecological processes in shaping β -SGDC patterns.

5 | CONCLUSION

We provide evidence that within-species genetic differentiation and within-family species dissimilarity in a mesophotic tropical reef fish covary spatially. This covariation was mainly explained by geographic distance, which suggests that dispersal limitation is a major process shaping β -diversity not only for shallow tropical reef fishes (Vilcot et al., 2023) but also for mesophotic reef fishes. However, other processes may also help explain β -SGDCs in mesophotic reef fishes such as historical patterns of colonization. Overall, our work provides evidence for a diversity continuum driven primarily by neutral processes in a mesophotic reef-associated fish species. Further studies including genetic data from more species are needed to determine whether these patterns are consistent across this taxonomic group (e.g., Vilcot et al., 2023 for shallow tropical reef fishes). To our knowledge, this is the first formal evidence that SGDCs depend on the community scale, such that the micro- to macroevolutionary continuum is lost as the community gets further from the focal species.

We encourage future research to integrate multiple spatial and community scales to better understand the underpinning processes that shape the spatial distribution of biodiversity across scales of biological organization. We also emphasize the use of compositional dissimilarity indices that control for species nestedness (Baselga, 2012), particularly when there are large differences in species richness between sites. The assessment of community variability on traits relevant to the processes studied can also be of great interest in evaluating a diversity continuum. All of these works are needed to improve our understanding of processes across scales and their impacts on biodiversity (Overcast et al., 2023).

AUTHOR CONTRIBUTIONS

M. Vilcot, F. Leprieur and S. Manel designed the research study. M. Vilcot conducted data analyses. N. Faure contributed to the data analyses. K.R. Andrews and B.W. Bowen contributed specimens. M. Vilcot wrote the first draft. N. Faure, K.R. Andrews, B.W. Bowen, F. Leprieur and S. Manel contributed at the writing stage. All authors critically read and approved the final version of the manuscript.

ACKNOWLEDGEMENTS

This work was supported by Agence Nationale de la Recherche (grant no. ANR-18-CE02-0016 SEAMOUNTS). For specimen collections we thank V. Moriwake and E.G. Grau at the University of Hawai'i; C. Kelley, S. Pooley, M. Seki and R. Moffitt at the U.S. NOAA Pacific Islands Fisheries Science Center; C.B. Wakefield, A.J. Williams and

S.J. Newman at James Cook University and the Western Australian Fisheries and Marine Research Laboratories, as well as Laurent Vigliola at Institut de Recherche pour le Développement (IRD) for New Caledonia sampling. Specimen collections were funded in part by the University of Hawai'i Sea Grant College Program, the Seaver Institute and the Australian Agency for International Development, the French Oceanographic Fleet and IRD. Collection in New Caledonia were performed under permits to Laurent Vigliola by the Government of New Caledonia (permits No. 2019_733/GNC, 2020_503/GNC, 2021_489/GNC), the Northern Province of New Caledonia (permit No. 609011-39/2020/DEPART/JJC) and the Southern Province of New Caledonia (permit No. 716-2021/ARR/DDDT). We thank Lila Desgarnier for assistance with sorting and preparing samples. We are also grateful to Philippe Jarne and Thomas Lamy for helpful discussions and to the two reviewers for constructive feedback that greatly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

SNP and presence data used in this paper are available on Zenodo at <https://doi.org/10.5281/zenodo.11202673>, except for SNP data from the SEAMOUNTS project which are available at <https://doi.org/10.5281/zenodo.11201065>. Scripts to replicate this study are available on GitHub at https://github.com/mvilcot/etelis_SGDCs.

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How to cite this article: Vilcot, M., Faure, N., Andrews, K. R., Bowen, B. W., Leprieur, F., & Manel, S. (2024). Neutral processes and taxonomic scale drive beta species–genetic diversity correlations in a submesophotic tropical reef fish. *Molecular Ecology*, 33, e17423. <https://doi.org/10.1111/mec.17423>