RESEARCH ARTICLE

The distribution of coastal fish eDNA sequences in the Anthropocene

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Handling Editor: Aaron MacNeil

Abstract

Aim: Coastal fishes have a fundamental role in marine ecosystem functioning and contributions to people, but face increasing threats due to climate change, habitat degradation and overexploitation. The extent to which human pressures are impacting coastal fish biodiversity in comparison with geographic and environmental factors at large spatial scale is still under scrutiny. Here, we took advantage of environmental DNA (eDNA) metabarcoding to investigate the relationship between fish biodiversity, including taxonomic and genetic components, and environmental but also socio-economic factors.

Location: Tropical, temperate and polar coastal areas.

Time period: Present day.

Major taxa studied: Marine fishes.

Methods: We analysed fish eDNA in 263 stations (samples) in 68 sites distributed across polar, temperate and tropical regions. We modelled the effect of environmental, geographic and socio-economic factors on α- and β-diversity. We then computed the partial effect of each factor on several fish biodiversity components using taxonomic molecular units (MOTU) and genetic sequences. We also investigated the relationship between fish genetic α- and β-diversity measured from our barcodes, and phylogenetic but also functional diversity.

Results: We show that fish eDNA MOTU and sequence α- and β-diversity have the strongest correlation with environmental factors on coastal ecosystems worldwide. However, our models also reveal a negative correlation between biodiversity and human dependence on marine ecosystems. In areas with high dependence, diversity of all fish, cryptobenthic fish and large fish MOTUs declined steeply. Finally, we show that a sequence diversity index, accounting for genetic distance between pairs of MOTUs, within and between communities, is a reliable proxy of phylogenetic and functional diversity.

Main conclusions: Together, our results demonstrate that short eDNA sequences can be used to assess climate and direct human impacts on marine biodiversity at large scale in the Anthropocene and can further be extended to investigate biodiversity in its phylogenetic and functional dimensions.

KEYWORDS
coastal fish communities, environmental DNA, environmental factors, socio-economic factors, α- and β-diversity

1 | INTRODUCTION

Species and their habitats are under increasing threats worldwide (Díaz et al., 2019), but the biodiversity crisis is particularly acute in coastal ecosystems that provide well-being and socioeconomic benefits to billions of people globally (Williams et al., 2022). The ongoing decline of fish abundance (Edgar et al., 2023) and the loss of top predators have been widely reported (Pacoureau et al., 2021) with severe consequences on nature (e.g., Schiettekatte et al., 2022) and people (e.g., Mellin et al., 2022). However, the extent to which environmental and human pressures affect fish biodiversity and

community composition across spatial scales (local α-diversity and turnover β-diversity) are yet to be quantified globally.

Large-scale patterns of marine fish biodiversity are predominantly influenced by environmental factors (Vasconcelos et al., 2015). Sea surface temperature, which is inversely correlated with oxygen concentration, is the main determinant of fish species distribution (Lenoir et al., 2020) and fish trait composition (McLean et al., 2021). High temperatures increase metabolic and reproductive rates so promote speciation rates and ultimately species richness (Fine, 2015) while Quaternary climate refugia preserved marine species from extinction (Pellissier et al., 2014). Together with other

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factors (e.g., plate tectonics, Leprieur et al., 2016), past and current natural environmental gradients have structured fish assemblages across coastal bioregions (Parravicini et al., 2013; Zinke et al., 2018).

The increasing human footprint across oceans also has a major impact on fish distribution and biodiversity (O'Hara et al., 2021). Marine biodiversity decline and compositional shift following human pressure are predominantly linked to habitat degradation coupled with high fishing pressure, often leading to the local extirpation of specialist species (Stuart-Smith et al., 2021). Beyond taxonomic diversity erosion, increasing human footprint also had a major impact on fish functional and phylogenetic diversity (D'Agata et al., 2014) with consequences on ecosystem functioning (Duffy et al., 2016). Yet, the local extirpation of marine fish species, functional groups or evolutionary lineages, due to human pressure or climate change, remains challenging to assess since residual populations may persist without being detected owing to their rarity or modified behaviour. For example, 32.6% of chondrichthyan species (391 shark and ray species) are globally threatened with extinction (Dulvy et al., 2021) but some are elusive and remain unseen when using classical survey techniques such as visual census or baited cameras, giving a false signal of local extirpation (Boussarie et al., 2018).

Environmental DNA (eDNA) metabarcoding offers new perspectives for the assessment of marine biodiversity by collecting, sequencing and analysing small fragments of intra- and extracellular DNA released by organisms in their proximate environment (Miya, 2021). Environmental DNA has provided fish assemblage-wide scans in both temperate and tropical seas (Agersnap et al., 2022; Juhel et al., 2020) and can be less prone to false absences than classical surveys, particularly for elusive, rare and cryptobenthic species (Boussarie et al., 2018; Mathon et al., 2022). Thus, eDNA can be a powerful tool to reveal large-scale biodiversity patterns and their drivers. Yet, eDNA sampling is often local or regional (Valdivia-Carrillo et al., 2021; West et al., 2021) while genetic reference databases are notoriously incomplete (Marques, Milhau, et al., 2020) to assign eDNA sequences to known taxa preventing widespread biodiversity assessments.

Here, we take advantage of a large-scale eDNA sampling of coastal marine ecosystems across all oceans, including tropical, temperate and polar areas, to model the distribution of fish biodiversity according to geographic, environmental and socio-economic factors. We used the diversity of Molecular Operational Taxonomic Units (MOTUs) and of genetic sequences as alternatives to taxonomic diversity, hereafter called MOTU and sequence diversity, respectively. We hypothesize that (i) fish MOTU diversity is mainly shaped by the environment following the well-known latitudinal diversity gradient with a peak in the Coral Triangle (Bellwood & Hughes, 2001; Parravicini et al., 2013), (ii) fish MOTU diversity may decrease with intensifying human activities, at least for large fish (Edgar & Stuart-Smith, 2014), when local or regional extinction occurs, and (iii) human activities may also impact sequence diversity since some families are heavily targeted by fisheries and can be locally extirpated close to humans (Cinner et al., 2018) while other evolutionary lineages, such as cryptobenthic fishes, can thrive

in a human-dominated seascape (Boulanger et al., 2021; Loiseau et al., 2021). Last, since functional and phylogenetic diversity are important for ecosystem functioning but challenging to measure using eDNA metabarcoding without complete taxonomic assignment, we evaluate whether fish sequence diversity can be considered as a proxy for fish functional and phylogenetic diversity across space. If so, eDNA sequences could inform on various diversity aspects, even without species-level assignments.

2 | METHODS

2.1 | Environmental DNA collection

Environmental DNA (eDNA) samples of seawater were collected between the surface and 40 m deep, at 263 stations, in 68 sites, across 11 marine regions from the tropics to the poles (Figure 1). Four different sampling methods were used: (i) collection of 2 L of water in DNA-free sterile plastic bags on the surface water from a small boat and with close circuit rebreather diving (depths between 10 and 40 m) as close as possible to the substrate (Juhel et al., 2020); (ii) collection of 1 L of water in sterilized bottle, from the surface; (iii) 2-km long filtration transect with two replicates of $30 L \pm 15\%$ of water just under the surface; (iv) 2-km-long filtration of water along a transect, approximately 5 m above the substrate, using a long pipe, from the boat. Details on the filtration device and storing methods can be found in Supporting Information Method S1, Tables S1 and S2. For each sampling campaign, a strict contamination control protocol was followed in both field and laboratory stages (Valentini et al., 2016), and each water sample processing included the use of disposable gloves and single-use filtration equipment. Negative field controls were performed in multiple sites across all sampling locations and revealed no contamination from the boat or samplers.

2.2 | eDNA extraction, amplification and sequencing

Environmental DNA extractions were performed following the protocols by Juhel et al. (2020) and Pont et al. (2018). As we analysed our data using MOTUs as a proxy for species to overcome genetic database limitations, we chose to amplify only one marker. The teleo barcode, on the 12S mitochondrial rRNA gene (forward primer—ACACCGCCCGTCACTCT, reverse primer—CTTCCGGTACACTTACCATG [Valentini et al., 2016]) has been shown to be one of the most appropriate for fishes, owing to its high interspecific variability and its short size allowing the detection of rare and degraded DNA reliably (Collins et al., 2019; Kumar et al., 2022; Zhang et al., 2020). The primers were 5′ labelled with a unique eight-nucleotide tag (with at least three differences between tags) allowing the assignment of sequences to the respective samples during the sequence analysis. Tags for forward and reverse primers were identical for each sample. Twelve PCR replicates per sample were performed (Pont

(a)

(b)
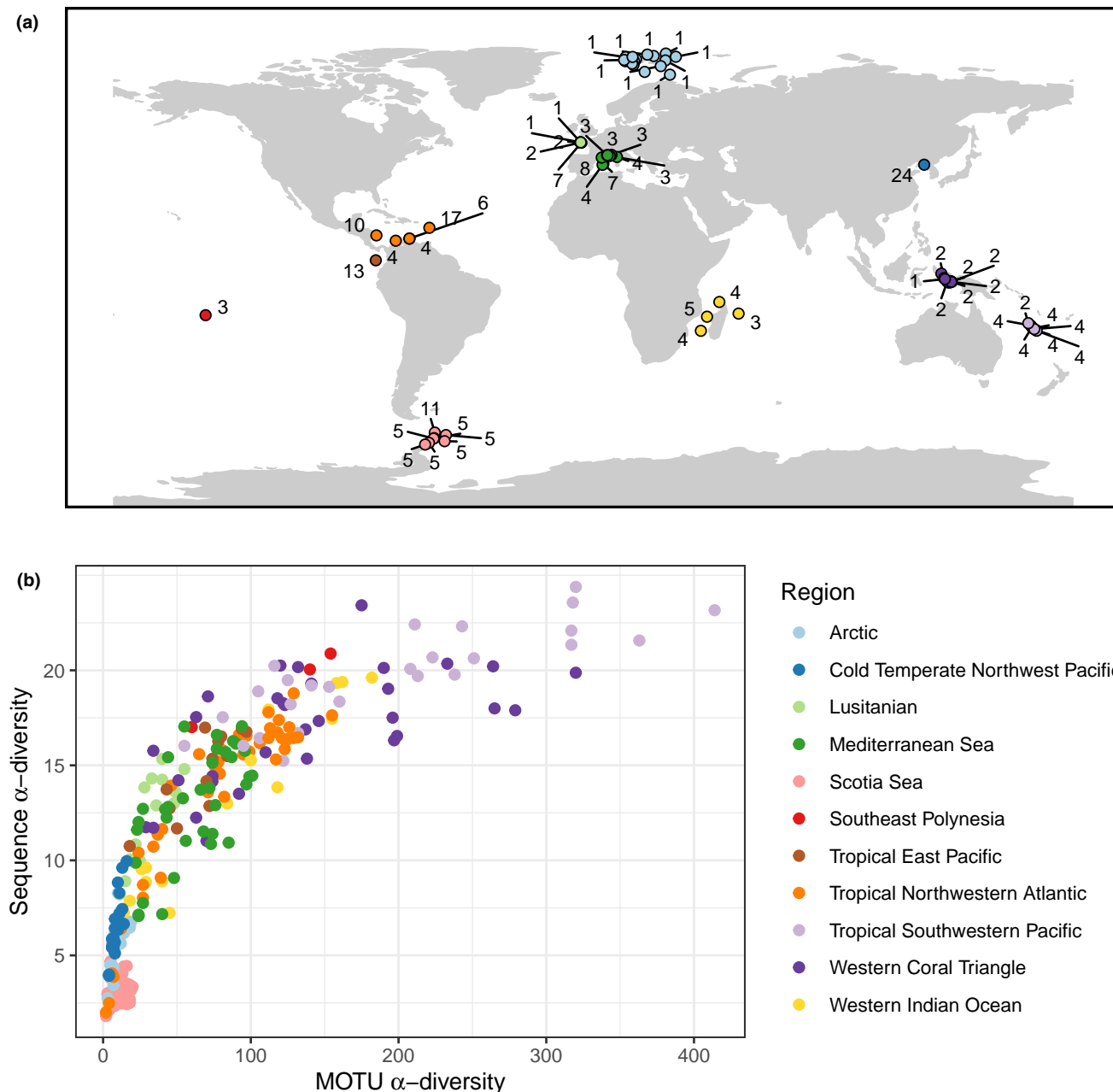
FIGURE 1 Sampling locations and patterns of α-diversity across coastal regions. (a) Map of the sampling sites, with the number of stations per site and (b) relationship between fish (α-diversity (number of molecular operational taxonomic or MOTUs per station) and sequence α-diversity (expressed as Hill number with genetic relatedness between MOTUs). The Spearman correlation between fish MOTU and sequence α-diversity is $\rho = 0.92$ ($p < 0.001$).

et al., 2018). Details on the extraction, amplification and sequencing can be found in Supporting Information Method S2. An average of 624,468 sequence reads were generated per sample.

2.3 | Bioinformatic analysis

Following sequencing, reads were processed using clustering and postclustering cleaning to remove errors and estimate the number of species using Molecular Operational Taxonomic Units (MOTUs)

(Marques, Guérin, et al., 2020). First, reads were assembled using *vsearch* (Rognes et al., 2016), then demultiplexed and trimmed using *CUTADAPT* (Martin, 1994) and clustering was performed using SWARM v.2 (Mahé et al., 2015) with $d = 1$, which corresponds to a maximum of 1 mismatch between neighbouring pairs of sequences within each cluster. Taxonomic assignment of MOTUs was carried out using the Lower Common Ancestor (LCA) algorithm *ecotag* implemented in the Obitools toolkit (Boyer et al., 2016) and the European Nucleotide Archive (ENA) as a reference database (release 143, March 2020), supplemented by our custom reference database,

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containing approximately 800 sequences. We discarded all observations with less than 10 reads and present in only one PCR replicate to avoid spurious MOTUs originating from a PCR error. Then, errors generated by index-hopping (MacConaill et al., 2018) were filtered using a threshold empirically determined per sequencing batch using experimental blanks (Taberlet et al., 2018). Tag-jumps (Schnell et al., 2015) were corrected by removing sequences with unmatching tags on the forward and reverse primers, and tolerating zero mismatch on tag sequences. An additional threshold removing all sequences with a frequency of occurrence <0.001 per MOTU and per library was implemented to clear all reads from the blanks. We then used the LULU algorithm (Frøslev et al., 2017) to clean MOTUs identified as erroneous based on sequence identity between MOTUs, abundances and patterns of co-occurrence, with an identity threshold of 84% (Marques, Guérin, et al., 2020). Details on the bioinformatic processes can be found in Supporting Information Method S3. The number of reads, MOTUs and species after each cleaning step are available in Supporting Information Tables S3 and S4.

2.4 | Explanatory factors

Diverse studies have shown that environmental conditions primarily shape fish community composition on coastal ecosystems (Parravicini et al., 2021; Zinke et al., 2018). We included sea surface temperature (SST), degree heating weeks (DHW), net primary productivity (NPP), and salinity (SSS), averaged over 1 and 5 years, collected with a variety of satellite and in-situ observations, optimal interpolations and ocean system models (as documented in Supporting Information Method S4 and Table S5).

In order to account for, and assess the impact of human populations on coastal ecosystems, we included some factors related to wealth, fisheries, economy and pollution. Those socio-economic factors included the Human Development Index of the sovereign country in 2019 (HDI); an index of marine ecosystem dependence (Selig et al., 2019); and an index of the human impact coined as gravity (Cinner et al., 2018). We calculated the gravity of a sampling station as the human population size divided by the travel time between the station and this population centre (in minutes). Total gravity is the sum of gravities in a buffer of 500 km around a station (Cinner et al., 2018) and is thus a proxy of pollution and habitat degradation.

Geography, such as the topography and localization, might also influence fish community composition and richness (Letessier et al., 2019). We thus included the bathymetry (measured directly on site with a sounder, or extracted from GEBCO_2020 Esri ASCII raster on a 15 arc-second interval grid), the depth of sampling (measured on site), the distance to shore (computed with the function *gDistance* from the "rgeos" package) and the distance to the Coral Triangle (calculated as the geographic distance from the sampling point to the centre of the Coral Triangle (longitude = 133.679826, latitude = −1.307436), using the function *pointDistance* from the 'raster' package). The Coral Triangle hosts the highest fish diversity due to the development of complex reef habitats in the Miocene and the

persistence of these habitats during the Quaternary climate change periods (Cowman & Bellwood, 2013; Pellissier et al., 2014). The distance to this refugia has been demonstrated to shape the traits structure and family richness in reef fishes (Parravicini et al., 2021) and can thus explain the variation of α- and β-diversity across oceans.

Sampling factors considered included the sample method (transect or point), and the total volume filtered per station.

To select only noncollinear explanatory factors, we computed the variance inflation factor (VIF), with the function *multicol* from the 'fuzzySim' package, and kept factors with a VIF < 10. Thirteen explanatory factors passed this threshold and were included in the models (Table 1). Factors with a large magnitude were $\log_{10}(x+1)$ transformed.

Maps of SST, gravity and marine ecosystem dependence can be found in Supporting Information Figures S1–S5.

2.5 | Statistical analyses

All statistical analyses were run at the station level, pooling reads from samples and PCR replicates. All analyses were run in R version 4.1.1. Details on statistical analyses can be found in Supporting Information Method S5.

2.5.1 | MOTU diversity

Fish MOTU diversity, expressed as the total number of distinct fish MOTUs, was calculated at each station, as well as the MOTU diversity of fish from large fish families ($n = 479$ MOTUs) and cryptobenthic families ($n = 539$ MOTUs). MOTU diversities were log-transformed. The selection of cryptobenthic MOTUs was made according to the definition of cryptobenthic families (Brandl et al., 2018), so families characterized by the high prevalence (>10%) of small-bodied species (<50 mm). To select the large fish MOTUs, we extracted the length of all fish species from FishBase, computed the mean but also the 5th and 95th quantiles for each family and order, and selected species belonging to families and orders with a 5th quantile superior to 20 cm. MOTU α-diversity corresponds to numbers of fish MOTUs per station and is independent of the taxonomic assignment which was only used to select the MOTUs belonging to cryptobenthic and large fish families.

2.5.2 | Sequence α-diversity

As opposed to MOTU diversity, which corresponds to the diversity of MOTUs identified within samples, sequence diversity is based on the diversity of nucleotidic composition within all MOTU centroid sequences composing a sample. To compute the sequence α-diversity for each station, we first computed the genetic distance between each pair of sequences with the function *dist.gene* from the package 'ape', which corresponds to the percentage of different

TABLE 1 Details of the explanatory factors retained in our models, and hypotheses associated with each factor.

Explanatory factor	Definition	Expectation
Degree Heating Weeks (DHW)	Daily temperature 1°C above the maximum monthly mean SST, over a 12 weeks period. Averaged over 1 year. Spatial resolution: 0.05°	Decrease in taxonomic and sequence diversity with increasing DHW due to thermal stress
Sea Surface Temperature (SST)	Daily values, averaged over 1 year. Spatial resolution: 0.05°	Increase in taxonomic and sequence diversity with increasing SST
Sea Surface Salinity (SSS)	Daily values, averaged over 1 year. Spatial resolution: 0.25°	Increase in taxonomic and sequence diversity with increasing SSS
Net Primary Productivity (NPP)	Standard Vertically Generalized Production Model. Monthly values, averaged over 1 year. Spatial resolution: 0.083°	Increase in taxonomic and sequence diversity with increasing NPP
Gravity	Human population size divided by the travel time between the station and this population centre, summed in a buffer of 500 km around a station	Decrease in taxonomic and sequence diversity with increasing gravity. Cryptobenthic species may suffer less from gravity increase than demersal and pelagic species that are more exploited.
Human Development Index (HDI)	Synthetic measure of life expectancy, education and wealth. Value for 2019	Increase in taxonomic and sequence diversity with increasing HDI
Marine Ecosystem Dependency	Nutritional, economic and coastal protection dependence on marine ecosystems at the country scale	Decrease in taxonomic and sequence diversity, especially for large fish, with increasing dependency
Distance to Coral Triangle	Geographic distance to the centre of the Coral Triangle, in km	Decrease in taxonomic and sequence diversity with increasing distance to CT
Distance to coast	Distance to the nearest coast, in m	Decrease in taxonomic and sequence diversity with increasing distance to coast
Bathymetry	Depth of the seafloor, at the sampling location, in m	Decrease in taxonomic and sequence diversity with increasing bathymetry
Depth of sampling	Depth of the water sampling	Increase in taxonomic and sequence diversity with sampling closer to the substrate (especially cryptobenthic diversity)
Sampling method	Method used for sampling: transect or point	Increase in taxonomic and sequence diversity with method transect since integrating broader water masses
Volume	Volume of water filtered at the station	Increase in taxonomic and sequence diversity with increasing volume

nucleotides between two sequences. We then applied the unified framework based on the generalization of Hill number to measure sequence diversity. Hill numbers have been recommended to produce reliable diversity assessments from molecularly characterized samples (Alberdi & Gilbert, 2019; Mächler et al., 2021). We used the function *alpha.fd.hill* from package 'mFD' (Magneville et al., 2022), with parameters $q=0$, which gives equal weight to all sequences, and τ as equal to the mean genetic distance (Chao et al., 2019).

2.5.3 | Modelling MOTU and sequence α-diversity

We investigated the relationship between fish MOTU and sequence diversity at each station and all explanatory factors with a generalized least square model (GLS) that considered the gaussian spatial autocorrelation between samples. A variance inflation factor (VIF) approach was used to identify and remove residual collinear factors (factors with VIF > 10). We tested for spatial autocorrelation in the model residuals using the Moran's index I. Standardized effect sizes

of each explanatory factor were extracted with the function *effectsize* from the 'effectsize' package. Partial relationships between response variables and each explanatory factor while controlling for all the other factors were visualized with the function *visreg* from the 'visreg' package. The same procedures were repeated for cryptobenthic and large fish MOTU α-diversity within stations. The volume filtered at the station and the sampling method were included as explanatory factors in the model to account for the heterogeneity in our sampling design and effort.

Sensitivity analyses were performed on 10 subdatasets after randomly removing 20% of the stations, to assess the robustness of our models, and after removing samples from polar regions (Scotia Sea and Arctic), to control for the influence of these extreme regions.

2.5.4 | Modelling β-diversity

The Jaccard dissimilarity index was computed between stations using fish MOTU composition (presence/absence) with the function

vegdist from package 'vegan'. Similarly, we computed the dissimilarity in sequence β-diversity between each pair of stations using the Hill number framework. The sequence β-diversity was calculated with the function *beta.fd.hill* from the 'mFD' package, with parameter $q = 0$ and tau = 'mean'.

We then performed a distance-based redundancy analysis (dbRDA) on the sequence β-diversity and MOTU β-diversity matrices. To account for spatial autocorrelation in our samples, we first computed distance-based Moran Eigenvectors Maps (dbMEM) with the function *dbmem* from the 'adespatial' package, which returned 15 dbMEM. We then ran the dbRDA on the full model, with all explanatory factors and the five main dbMEMs. Factors with $VIF > 10$ were removed and a final partial dbRDA was run with all selected explanatory factors, and with sampling factors and dbMEMs as conditional variables. Partial R^2 for each group of factors were obtained with the *varpart* function of the 'vegan' package.

2.5.5 | Functional and phylogenetic diversity

In order to assess whether eDNA sequence diversity can be used as a robust proxy of functional and phylogenetic diversity, we first explored the relationship between the pairwise sequence, phylogenetic and functional distances, and then applied the α- and β-diversity Hill number framework on sequence, functional and phylogenetic distances. For that purpose, we selected only the MOTUs assigned to the species level in our dataset ($n = 787$). We computed genetic pairwise distances for these species with the function *dist.gene* from package 'ape'. We computed the pairwise functional Gower distance based on functional traits extracted from fishbase, available for 685 of our species using the function *compute_dist_matrix* from package 'funrar'. Selected traits describe species functional roles in the ecosystem, and encompass body size (shape and length), habitat use (preferred habitat and substrate, depth range), feeding ecology (trophic group and diet) and behaviour (water column position, gregariousness) (Villéger et al., 2017). The pairwise phylogenetic distance between species was computed using the functions *fishtree_phylogeny* from the 'fishtree' package and *cophenetic.phylo* from the package 'ape', and the phylogeny from Rabosky et al. (2018). These distance matrices were compared using a mantel test, and by calculating the area under the curve (AUC) criterion, based on Somer's D statistic. AUC varies between 0 (no correlation) and 1 (identical matrices) and is computed with the functions *coranking*, *R_NX* and *AUC_ln_K* from package 'coRanking'.

We applied the α- and β-diversity Hill number framework for sequence, functional and phylogenetic diversity ($q = 0$ and τ equal to the mean genetic, functional or phylogenetic distance), using the functions *alpha.fd.hill* and *beta.fd.hill* from 'mFD' package, for sequence and functional diversities, and function *ChaoPD* from package 'entropart' for phylogenetic diversity. α-diversity indices were compared with a Pearson's correlation test, and the β-diversity matrices were compared with AUC and Mantel tests.

3 | RESULTS

3.1 | Biogeography of MOTU and sequence diversity

From the 584 seawater eDNA samples collected at 263 stations across 11 marine regions (Figure 1a), we found a total diversity of 2888 MOTUs, of which 2276 were assigned at least to the family level (539 MOTUs belong to cryptobenthic families and 479 to large fish families), and we identified 791 distinct fish species.

The regions with the highest detected fish diversity were Lengguru in the Western Coral Triangle (1145 MOTUs) and New-Caledonia in the Tropical Southwestern Pacific (917 MOTUs), followed by the Caribbean (Tropical Northwestern Atlantic, 452 MOTUs), the Scattered Islands (Western Indian Ocean, 357 MOTUs), the Mediterranean Sea (249 MOTUs), Southeast Polynesia (197 MOTUs) and the Tropical East Pacific (153 MOTUs). The lowest fish MOTU diversity was found in the Northeast Atlantic Ocean (Lusitanian, 96 MOTUs), the Yellow Sea (Cold Temperate Northwest Pacific Ocean, 42 MOTUs), the Antarctic Ocean (Scotia Sea, 40 MOTUs) and the Arctic Ocean (33 MOTUs).

Local or α-diversity ranged between 2 and 414 fish MOTUs per station (Supporting Information Figure S6). Cryptobenthic fish diversity ranged between 0 and 95 MOTUs per station (Supporting Information Figure S7). Large fish diversity ranged between 0 and 67 MOTUs per station, with 16% of stations having no MOTU belonging to large fish (Supporting Information Figure S8). Yet, the high variability in MOTU diversity among stations cannot be directly interpreted, partly due to the heterogeneity in the sampling design and effort that are accounted for in further analyses.

Sequence α-diversity in our stations ranged between 1.7 and 16.3 (Figure 1b, Supporting Information Figure S9). The highest values of sequence α-diversity were found in the Western Coral Triangle and Tropical Southwestern Pacific. The lowest sequence α-diversity was observed at the poles (Arctic and Scotia Sea) while temperate regions showed an intermediate level of sequence α-diversity. MOTU and sequence α-diversity were significantly and positively correlated (Spearman's $\rho = 0.92$, $p < 0.001$), indicating that richer stations are composed of more genetically differentiated sequences (Figure 1b).

3.2 | Modelling α-diversity patterns

The GLS model fitted on fish MOTU and sequence α-diversity both revealed high explanatory power, with adjusted R^2 of 0.81 and 0.78, respectively. Both responses were primarily related to environmental factors, then to geographic and socio-economic factors (Supporting Information Figures S10 and S11). The partitioning of R^2 (see Methods) showed that fish MOTU diversity was mainly linked to environmental factors ($R^2 = 0.32$), then to geographic ($R^2 = 0.21$), sampling ($R^2 = 0.14$) and socio-economic factors ($R^2 = 0.09$). Sequence α-diversity was also primarily related to environmental

factors ($R^2 = 0.36$), then to geographic ($R^2 = 0.18$), socio-economic ($R^2 = 0.11$) and sampling factors ($R^2 = 0.09$).

Most environmental factors showed a significant and positive relationship with MOTU and sequence α-diversity (Supporting Information Tables S6 and S7). MOTU α-diversity increased with sea surface temperature and salinity while sequence α-diversity increased with SST and NPP (Figure 2). Both MOTU and sequence α-diversity were significantly and negatively related to the distance to the shore and the distance to the Coral Triangle. Sequence α-diversity was positively related to the depth of sampling. Among the socio-economic factors, MOTU and sequence α-diversity were significantly and negatively related to marine ecosystem dependence while MOTU or sequence α-diversity showed no significant relationship with human gravity.

The GLS model was then fitted on cryptobenthic and large fish MOTU diversity and both showed high explanatory power ($R^2 = 0.71$ and 0.83, respectively). Both MOTU diversities were primarily associated with environmental factors, and then with geographic and socio-economic factors (Supporting Information Figures S12 and S13, Tables S8 and S9). Cryptobenthic and large fish MOTU diversity increased with SST and NPP (Figure 2). Both cryptobenthic and large fish diversity significantly decreased with distance to the shore and distance to the Coral Triangle. Only cryptobenthic MOTU diversity was positively related to the depth of sampling. Cryptobenthic and large fish diversity both decreased significantly with increasing

country's dependence on marine resources, but none was significantly related to human gravity (Figure 3). However, the combined effects of gravity and marine ecosystem dependence amplified the decrease of all fish and large fish MOTU diversity (Supporting Information Figure 14). Sensitivity analyses provided similar results (Supporting Information Figures S15 and S16).

3.3 | Modelling β-diversity patterns

The dbRDAs on MOTU and sequence β-diversity between stations showed a marked dissimilarity but with a low-to-moderate explanatory power ($R^2 = 0.13$ and 0.35 respectively) (Figure 4). MOTU β-diversity was related to environmental ($R^2 = 0.07$), socio-economic ($R^2 = 0.05$) and geographic factors ($R^2 = 0.03$) (Supporting Information Figure S17). Sequence β-diversity was mainly related to environmental ($R^2 = 0.26$) and geographic factors ($R^2 = 0.16$), then to socio-economic factors ($R^2 = 0.06$) (Supporting Information Figure S18). The Antarctic substantially differed from all other regions on the first axis of both dbRDAs, indicating a distinct fish MOTU and sequence composition from other regions. The second axis of the MOTU dbRDAs differentiated the Mediterranean temperate region from the East Pacific and the Caribbean, while all tropical regions were grouped together. Fish MOTU composition was more similar when considering the Atlantic, China and Arctic
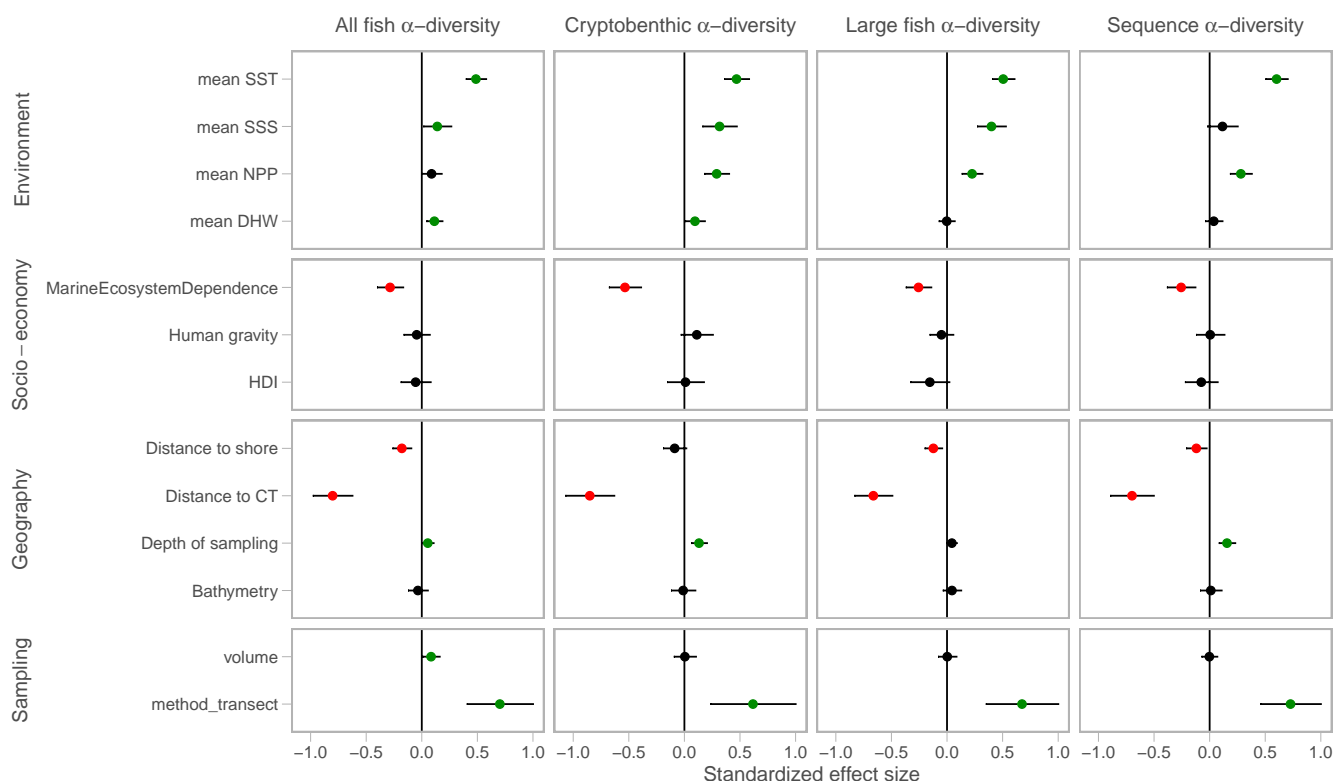
FIGURE 2 Effect size of factors in GLS models predicting the level of fish MOTU (Molecular Operational Taxonomic Unit) and sequence α-diversity, but also cryptobenthic (*n*=539 MOTUs) and large fish MOTU α-diversity (*n*=479 MOTUs). Segments indicate 95% confidence intervals. Red dots indicate significant negative effects and green dots indicate significant positive effects while black dots are for nonsignificant effects. All factors and their acronyms are presented in the Methods.
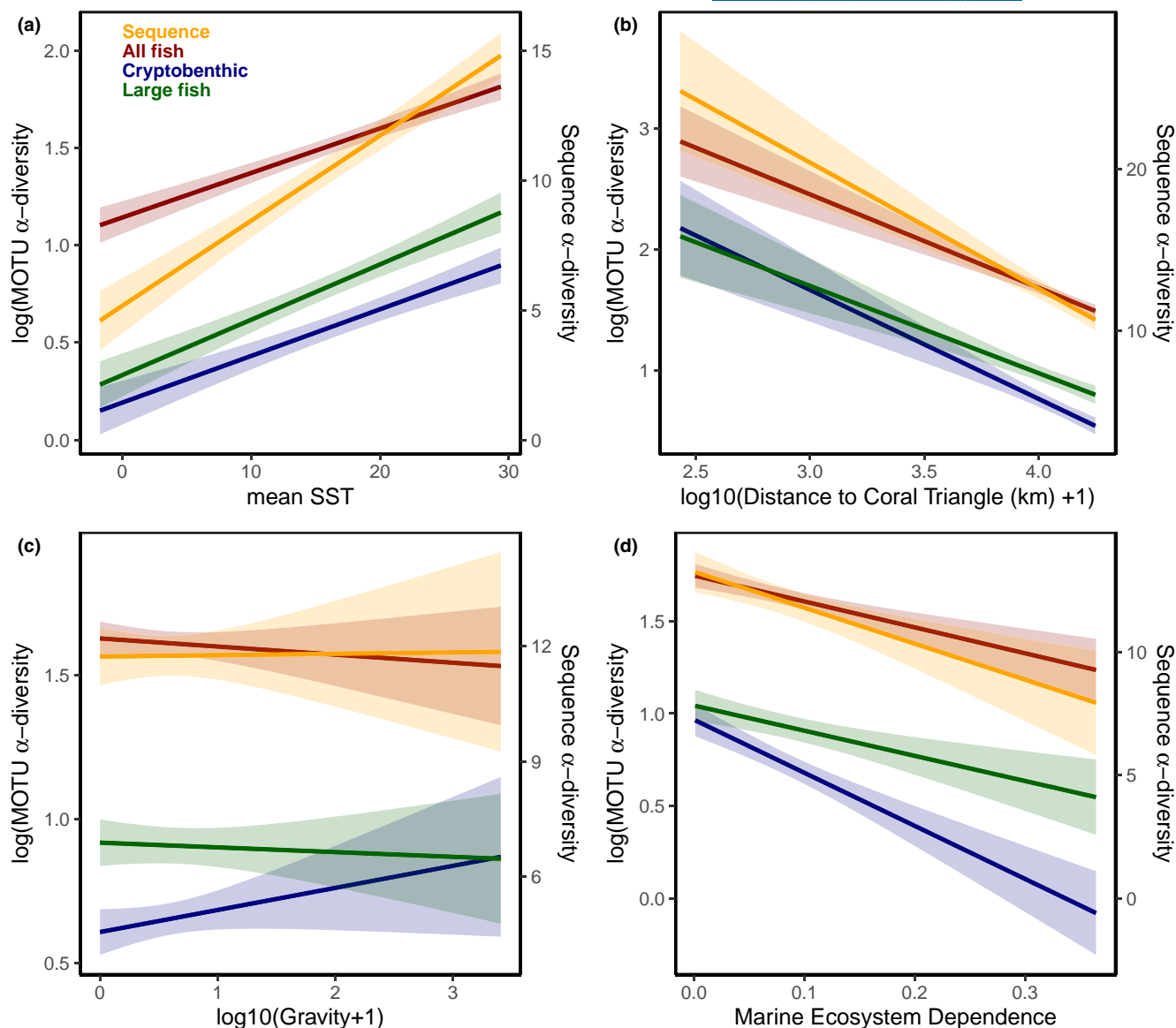
FIGURE 3 Partial regression plots showing the relationships between the α-diversity of all fish MOTUs (Molecular Operational Taxonomic Units) (red), large fish MOTUs (green, $n = 479$ MOTUs), cryptobenthic MOTUs (blue, $n = 539$ MOTUs) and all fish sequences (yellow, right y axis), and the four main factors conditioned on the median value of all other retained factors. Factors were (a) Sea Surface Temperature, (b) Distance to Coral Triangle, (c) Human Gravity and (d) Marine Ecosystem Dependence. The coloured shaded areas are the 95% confidence intervals of the relationships.

regions. The MOTU composition of the Caribbean and East Pacific regions was distinct from the other tropical stations.

The pattern of sequence β-diversity differed from that of MOTU β-diversity, with the second axis differentiating the Arctic from the tropics and temperate regions. Even though MOTU composition was similar between the Arctic and temperate regions, the sequence β-diversity was high, due to fewer species in the Arctic and a few very distant species. The Caribbean and East Pacific, however, had similar sequence composition in comparison with the other tropical regions, while the MOTU composition greatly differed. The factors showing the strongest relation with fish MOTU β-diversity were SST, NPP, marine ecosystem dependence and distance to the Coral Triangle (Supporting Information Table S10). Sequence β-diversity

between stations was mainly related to SST, SSS, bathymetry, marine ecosystem dependence and distance to the shore (Supporting Information Table S11).

3.4 | Sequence diversity as a proxy of functional and phylogenetic diversity

The sequence pairwise distance between assigned species pairs was significant and positively but weakly correlated with phylogenetic (mantel = 0.23, $p < 0.001$, AUC = 0.18) or functional distance (Mantel = 0.04, $p < 0.001$, AUC = 0.027) between these species pairs (Supporting Information Figure S19). In contrast, the sequence

(a) MOTU β–diversity **(b)** Sequence β–diversity
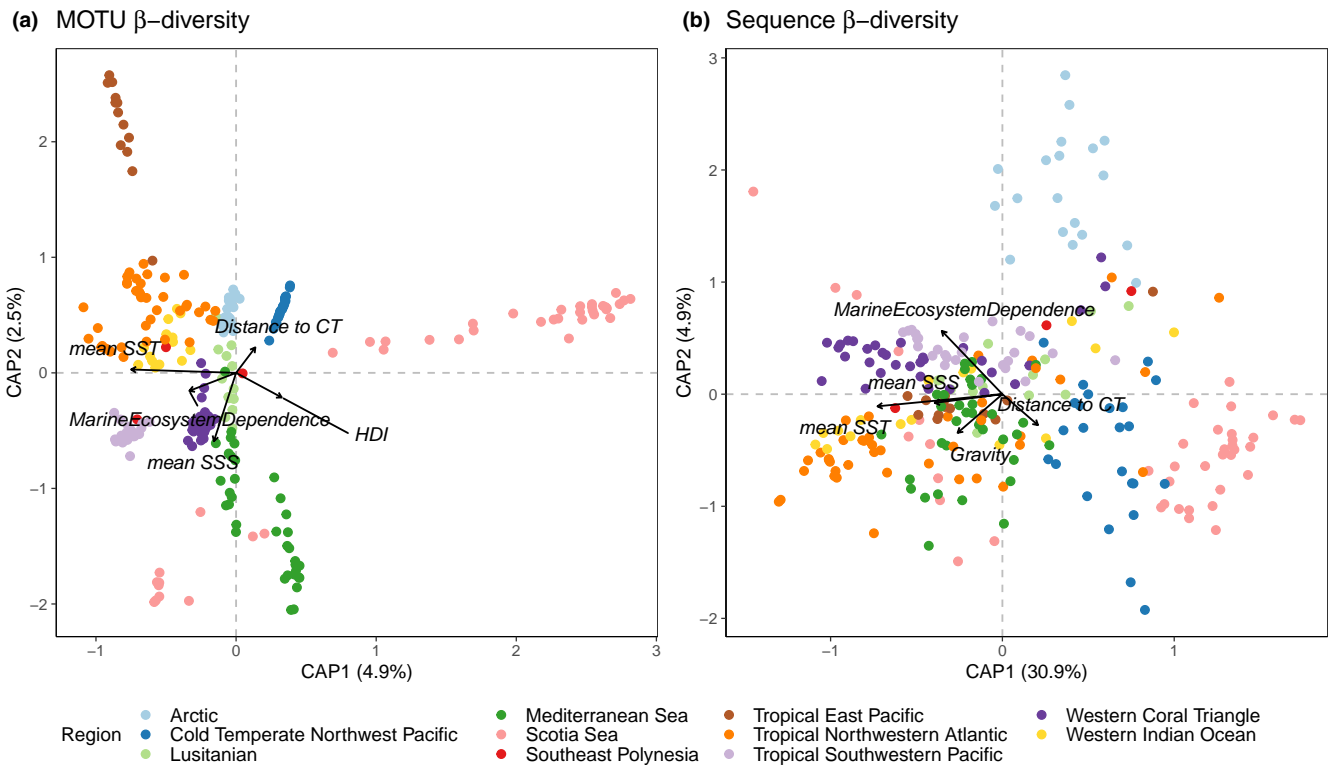
FIGURE 4 Distance-based redundancy analysis (dbRDA) showing the variation in fish (a) MOTU (Molecular Operational Taxonomic Unit) composition and (b) sequence composition between stations, according to 12 factors, with sampling factors and distance-based Moran Eigenvectors Maps (dbMEMs) as conditional variables. Stations are coloured by marine region and only the main factors are shown. Stations positions on the figures reflect their similarity in terms of MOTU composition or sequence composition, driven by the explanatory factors.

α-diversity was positively and strongly correlated with phylogenetic α-diversity (Pearson's correlation coefficient $r = 0.94$, $p < 0.001$) and to functional α-diversity (Pearson's $r = 0.91$, $p < 0.001$) (Figure 5). The sequence β-diversity between samples was also strongly correlated with phylogenetic (Mantel test $r = 0.91$, $p < 0.001$; AUC = 0.58) and functional β-diversity (Mantel test $r = 0.87$, $p < 0.001$; AUC = 0.55).

4 | DISCUSSION

Through the analysis of 584 eDNA samples distributed in 263 stations from the tropics to the poles, we show that environmental factors primarily shape fish MOTU, in accordance with our first hypothesis, but also sequence diversity. The diversity of large fish MOTU is affected by human pressures, in accordance with our second hypothesis, while other groups show contrasted patterns. We also reveal a negative relationship between eDNA sequence diversity and human pressures, suggesting that coastal fish diversity is, at least partly, shaped by human activities in accordance with our third hypothesis. We finally highlight that eDNA sequence diversity can be used as a reliable proxy of functional and phylogenetic diversity.

Our regional fish biodiversity estimates obtained with eDNA are close to those of several available regional checklists (Allen & Erdmann, 2009; Fricke et al., 2011), and to local biodiversity estimations with classical methods (Friedlander et al., 2020; Johannesen

et al., 2021). Yet, we detect species that are rarely reported in classical inventories such as the Greenland shark (*Somniosus microcephalus*) in the Arctic, the elegant firefish (*Nemateleotris decora*) in the Coral Triangle, or the Antarctic escolar (*Paradiplospinus antarcticus*). We also find strong significant correlations between the number of MOTUs and the number of species belonging to each family in the checklists (Supporting Information Figure S20). While direct and synchronized in-situ comparison between eDNA and other sampling methods would be necessary to confirm the effectiveness or superiority of eDNA in species inventories and to standardize its use at large scale, previous studies provide encouraging results with eDNA studies based on the 12S primer recovering regional fish diversity with few samples compared with traditional methods (Momota et al., 2022; Polanco Fernández et al., 2021; Valdivia-Carrillo et al., 2021).

MOTU diversity patterns display the expected fish species richness gradient from the Coral Triangle to the Caribbean (Parravicini et al., 2013) and the poles (Freeman & Pennell, 2021). The sequence α-diversity, capturing species genetic relatedness, follows the same gradients. The lowest sequence α-diversity is observed at the poles, where most fish MOTUs are close relatives, the highest diversity lies in the tropics, where MOTU richness was the highest with a large number of families and genera (Juhel et al., 2020), while temperate regions present intermediate values (Figure 1b). Some stations in the Yellow Sea and polar regions, where the MOTU richness is
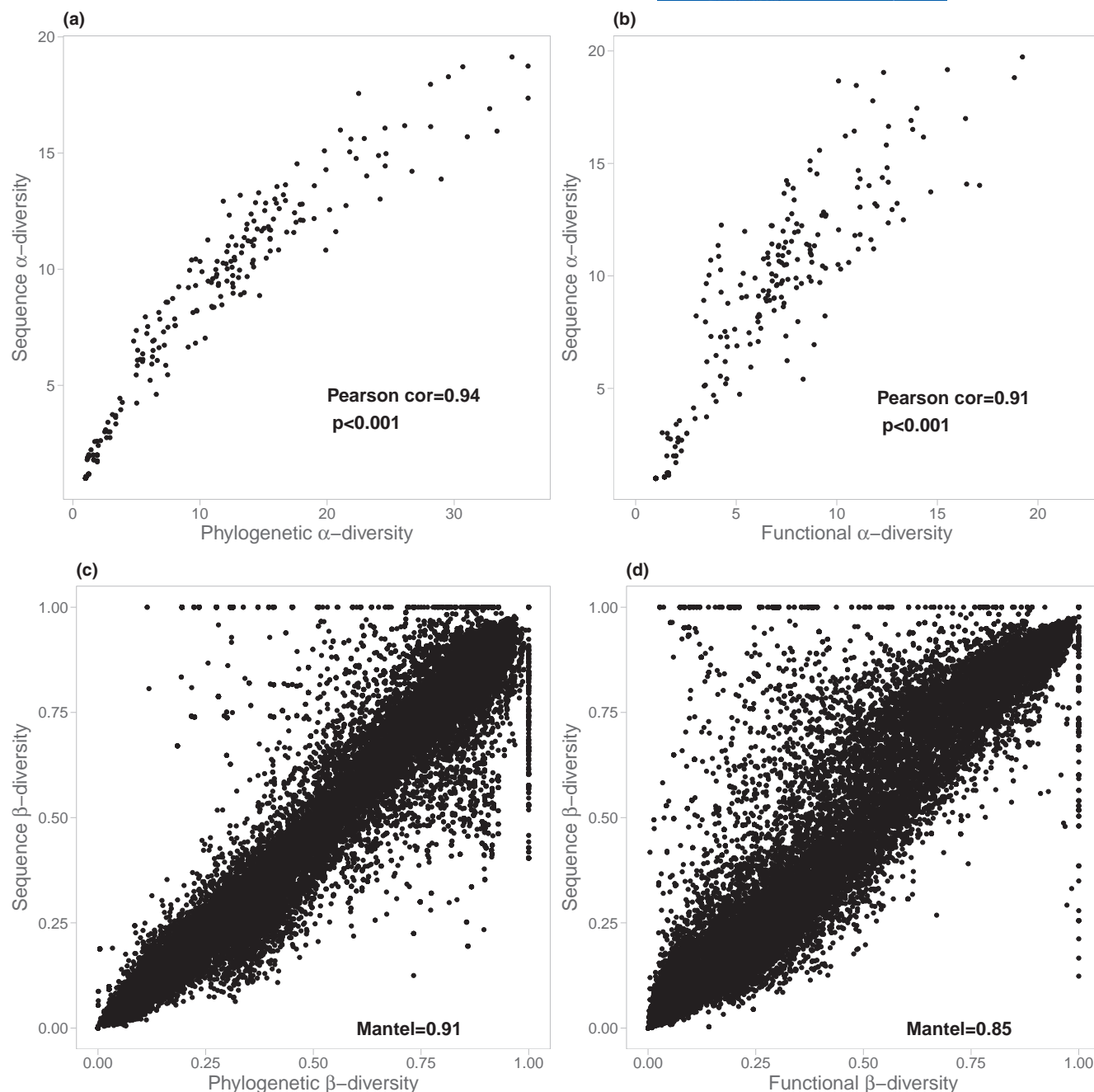
FIGURE 5 Correlation between fish sequence diversity and phylogenetic or functional diversity for all stations, considering only the 787 MOTUs assigned to the species level. (a) Phylogenetic and sequence α-diversity, (b) Functional and sequence α-diversity, (c) Phylogenetic and sequence β-diversity, and (d) Functional and sequence β-diversity.

the lowest, reveal, however, intermediate sequence α-diversity due to very distinct genera (e.g., *Lycodes*, *Liparis* and *Somniosus* in the Arctic).

The increase in MOTU and sequence α-diversity of marine fishes with increasing temperature can be related to the 'evolutionary speed' and 'climate stability' hypotheses (Manel et al., 2020). According to the 'evolutionary speed' hypothesis (Fine, 2015), high temperatures promote metabolic, reproduction and speciation rates, and ultimately increase species richness (Harmelin-Vivien, 2002), yet fish richness gradients worldwide do

not correlate with recent speciation rates (Rabosky et al., 2018). The 'climate stability' hypothesis posits that warmer areas in the tropics have experienced less historical variability in climatic conditions, whereas colder areas were highly unstable, leading to species diversity declines along temperature gradients (Mittelbach et al., 2007; Pellissier et al., 2014). This second 'climatic stability' hypothesis is supported by our fish MOTU and sequence α-diversity patterns which both decrease towards the poles and farther from the Coral Triangle. Owing to environmental niche conservatism (Gaboriau et al., 2019), closely related species or

entire lineages can be extirpated under climatic filtering while only a limited number of lineages are adapted to the extreme climatic conditions of the poles (Mittelbach et al., 2007).

Fish biodiversity is also related to human pressures, as indicated by the significant decrease in MOTU and sequence α-diversity in response to countries' dependence on marine resources (Figure 2). Human populations highly dependent on marine resources for food and income may use nonselective artisanal fishing methods (blast, trawling, poison) to catch even small or cryptobenthic species (Batista et al., 2014; Munro, 1996) leading to a deterioration of key habitats such as coral reefs and affecting the whole trophic spectrum (Fox et al., 2003). Fishing pressure could thus impact all fish size classes in countries highly dependent on marine resources, removing entire parts of the food web, and decreasing the genetic diversity of the remaining species pool. More specifically, the diversity of large-bodied fishes is negatively associated with human pressure (Figure 2). Species abundance and richness of sharks, jacks, groupers and snappers are known to decrease with increasing human population density (Dulvy et al., 2021), affecting top down control in overexploited ecosystems (McClure et al., 2020). As human pressures (e.g., nutrient and chemical release and habitat degradation) affect the most sensitive species, often belonging to the same evolutionary lineages or families (Cinner et al., 2018; Dulvy et al., 2021), we observe a greater decrease in sequence α-diversity than in MOTU diversity with increasing human pressure (Figure 3) as we hypothesized.

Geography is also significantly related to the distribution of fish eDNA sequences in the Antarctic, with MOTU composition and sequence β-diversity differing from all other regions (Figure 4). This result is coherent with previous studies showing that the Antarctic region was progressively isolated and cooled during the Cenozoic period by the opening of the Drake Passage and the development of the Antarctic Circumpolar Current (Crame, 2018). MOTU and sequence composition markedly differ between stations in the Drake passage and stations in the Antarctic peninsula, possibly due to the different environmental and oceanographic conditions. Antarctic marine fauna is therefore evolutionarily isolated and dominated by a few families of highly specialized benthic fishes. Indeed, of the 22 MOTUs identified in our Antarctic samples, 15 were unique to this region, among which species from the mostly endemic Nototheniidae, Zoarcidae and Liparidae families (Eastman, 2005), and the endemic Antarctic silverfish (*Pleuragramma Antarctica*).

Arctic fauna is similar to temperate faunas in terms of fish MOTU composition but distinct in terms of sequence β-diversity, which is also expected (Bluhm et al., 2011). A few fish MOTUs are shared between the Arctic and Atlantic, which can be explained by the connectivity between these regions due to currents from the Atlantic and the Pacific flowing into the Arctic Ocean, and species range shifts due to the ongoing Atlantification occurring in the Arctic (Ingvaldsen et al., 2021). The Arctic also contains some very distinct MOTUs belonging to Anarhichadidae, Cyclopteridae, Stichaeidae, Somniosidae or Zoarcidae for example, of which

several are adapted to cold waters or are endemic to the Arctic (Bluhm et al., 2011).

The Caribbean and East Pacific faunas also show distinct fish MOTU compositions compared with other tropical regions but similar sequence β-diversity patterns. The unique fauna composition of the Caribbean is well known and explained by a strong geographic barrier (i.e., Isthmus of Panama) and a limited suitable area for coral reefs during the past quaternary glaciation (Bender et al., 2017; Pellissier et al., 2014). Our study reveals a low sequence β-diversity between stations of tropical regions, suggesting that the high fish MOTU dissimilarity between these regions is due to close relative species. In other words, most fish species in the Caribbean and other tropical regions belong to the same evolutionary lineages.

The pairwise species genetic distances, computed only for the MOTUs assigned at the species level (~30% of the dataset), were positively but weakly correlated to the phylogenetic and functional pairwise distances for these same species pairs. On such a short barcode (~60 bp), several species can have the same sequence (Polanco et al., 2021) so a null pairwise genetic distance while they diverge in terms of phylogeny and traits. In contrast, a few species may show intraspecific variability, resulting in a positive genetic distance within the same species. While genetic distances are not good proxies for functional and phylogenetic distances, our results reveal that the sequence α- and β-diversity computed from these pairwise distances are significantly correlated with the corresponding phylogenetic and, to a lesser extent, functional α-and β-diversity. Therefore, sequence α- and β-diversity within and between stations represent good proxies for phylogenetic α- and β-diversity, which is not trivial given the length of our barcode. The relationship between sequence and phylogenetic α-diversity being asymptotic, the use of sequence diversity is potentially limited when phylogenetic diversity becomes high. This new finding offers potential perspectives for the use of short eDNA barcodes, without taxonomic assignment, to estimate phylogenetic and functional diversity and thus monitor ecosystem functioning (Duffy et al., 2016), evolutionary history (McLean et al., 2021), or environmental and human impacts (Trindade-Santos et al., 2020).

Since our study covers an extensive spatial scale, there are some limitations in terms of data collection or analysis. Our sampling design was not balanced among regions (Supporting Information Table S1), which can affect biodiversity estimates. We found a positive relationship between the number of detected MOTUs and the volume of seawater filtered indicating a species-area relationship (Figure 2). The models also found a significant effect of the sampling method. Sampling along transects retrieves higher MOTU and sequence diversity than sampling on points (Supporting Information Figure S21). Thus, we may have underestimated the diversity in the regions where we used punctual sampling and low water volume (i.e., Yellow Sea in China and Coral Triangle). Including the sampling information in our models ensures that these differences are controlled for when estimating the importance of other factors. The degradation of eDNA being fast in seawater (<48 h, Holman et al., 2021), we are confident that

the species detected were recently present. However, seasonal variation in the sampling of the different regions can also influence the level of α- and β-diversity, as eDNA is more detectable during summer, when species are more active (Troth et al., 2020).

Due to the incompleteness of available reference databases at the global scale (Marques, Milhau, et al., 2020), the assignment to the species level remained impossible for more than 70% of sequences. For this reason, we used MOTUs curated by a conservative bioinformatic pipeline (Marques, Guérin, et al., 2020). A conservative curation of MOTUs better reflects the true level of fish diversity (Sales et al., 2021) by decreasing the number of MOTUs representing the same taxa. Our conservative MOTU pipeline may, however, underestimate fish diversity of some cryptobenthic or rare fish groups that are more poorly represented in public databases, and of families with low taxonomic resolution (Supporting Information Figure S22). Combining eDNA with other sampling methods could provide a more exhaustive diversity inventory, as cameras or divers may detect some species not detected by eDNA (Juhel et al., 2022; Valdivia-Carrillo et al., 2021). Using multiple markers could be an alternative to overcome the incompleteness of genetic reference databases and the lack of primer resolution (Ruppert et al., 2019), but this approach would be much more expensive. Improving the accuracy of taxonomic assignment and completing genetic reference databases are thus urgently needed to improve estimates of large-scale biodiversity patterns (Marques, Milhau, et al., 2020) and local monitoring (Dalongeville et al., 2022).

From an extensive eDNA survey from the tropics to the poles, our study associates the distribution of eDNA sequences released by coastal fishes to environmental, geographic and human factors. As expected, the environment shows the strongest relationship to fish biodiversity, but human activities are also at play. Fish sequence diversity, reflecting species relatedness, strongly decreases with human pressures suggesting a strong environmental but also human filtering on coastal ecosystems. Furthermore, our study highlights that sequence diversity from eDNA metabarcoding is a robust indicator of human impact and a reliable proxy of phylogenetic and functional diversity, which are essential to ecosystem functioning. We recommend that eDNA monitoring should be considered in future conservation management plans.

AUTHOR CONTRIBUTIONS

DM, LP, SM and LM conceived the study. DM, LP, SM and LM contributed to the study design. LM, VM, CA, MA, FB, GBP, RH, JBJ, K, EM, GM, AP, HYS, LV, EB, JD, FH, NF, NG, PL, NL, KT, LV, IV XZ and WZ contributed to the acquisition of data. AV, TD, XZ and WZ supervised/conducted the eDNA extraction, amplification and sequencing. VA, EB, RH, LM, NF and LP contributed to the laboratory analyses for the reference database. PEG, VM and LM contributed to the bioinformatic analysis. LM and DM contributed to the statistical analysis and the creation of the figures. LM, DM, LP and SM contributed to the interpretation of the results. LM, DM and SM wrote the manuscript. All co-authors edited the manuscript. RH, SM, DM, LV, LP, KT, XZ and LP acquired funding to conduct the study.

CONFLICT OF INTEREST STATEMENT

Teleo primers and the use of amplified fragments for identifying fish diversity from environmental samples are patented by the CNRS and the Université Grenoble Alpes. This patent only restricts commercial applications and has no implications for the use by academic researchers. SPYGEN owns a licence for this patent. TD and AV are research scientists at SPYGEN.

DATA AVAILABILITY STATEMENT

All eDNA data (except from New-Caledonia) are available in open access in Zenodo: https://doi.org/10.5281/zenodo.7805935. New-Caledonia eDNA data are available from Zenodo upon request at: https://doi.org/10.5281/zenodo.6381130. The code used for the analyses is publicly available at: https://github.com/lmathon/Pole2Pole_eDNA. The bioinformatic pipeline used to analyse the metabarcoding data has been published in Marques, Guerin, et al. (2020).

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BIOSKETCH

Laetitia Mathon is a marine biologist and ecologist at CEFE, France. She is interested in the use of metabarcoding of environmental DNA to study the patterns of marine fish distribution across scales, and inform the conservation.

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: Mathon, L., Marques, V., Manel, S., Albouy, C., Andrello, M., Boulanger, E., Deter, J., Hocdé, R., Leprieur, F., Letessier, T. B., Loiseau, N., Maire, E., Valentini, A., Vigliola, L., Baletaud, F., Bessudo, S., Dejean, T., Faure, N., Guerin, P.-E. … Mouillot, D. (2023). The distribution of coastal fish eDNA sequences in the Anthropocene. *Global Ecology and Biogeography*, *00*, 1–17. https://doi.org/10.1111/geb.13698