





















































# Dispersal limitation, environmental filtering, and historical contingencies explain the patterns of taxonomic and phylogenetic turnover in Amazonian freshwater fish faunas, but only poorly their functional traits turnover

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Identifying the main taxonomic, phylogenetic and trait dimensions of beta diversity, and evaluating their prospective drivers, advances our understanding of patterns and processes involved in the evolution of biological assemblages. Using comprehensive databases on the distribution, phylogeny, and morphological traits of Amazonian freshwater fishes, we analyzed turnover beta diversity patterns of these three dimensions to evaluate prospective historical and contemporary drivers using multiple regression on distance matrices. We found mean taxonomic beta diversity about two times higher than mean phylogenetic and six times higher than species traits beta diversity, and coincident spatial patterns in Taxo $\beta$ sim and Phylo $\beta$ sim dimensions, whereas Trait $\beta$ sim seemed more diffuse and heterogeneous across space. We find prominent influence of sub-basins geographic distances, habitat harshness and water color types on the taxonomic and phylogenetic dimensions of beta diversity, together with smaller individual effects of current temperature and habitat types, historical sub-basins connections and marine incursions, and sampling effort. By contrast, Trait $\beta$ sim was weakly explained only by sampling effort and current sub-basins hydro-morphological conditions. These results point to leading effects of dispersal limitation, environmental filtering and historical contingencies in explaining Amazonian fish assemblages taxonomic and phylogenetic beta diversity patterns, but not functional traits turnover.

**Keywords:** Amazon basin, Beta diversity metrics, Environmental filtering, Fish assemblages, Historical events.

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Identificar as principais dimensões taxonômica, filogenética e de atributos da diversidade beta, e avaliar seus possíveis fatores determinantes, aprimora nossa compreensão dos padrões e processos envolvidos na evolução das assembleias biológicas. Utilizando bancos de dados abrangentes sobre a distribuição, filogenia e atributos morfológicos dos peixes de água doce amazônicos, analisamos os padrões de substituição de espécies dessas três dimensões para avaliar seus potenciais determinantes históricos e contemporâneos usando regressão múltipla em matrizes de distâncias. Observamos que a diversidade beta taxonômica média foi cerca de duas vezes maior que a diversidade beta filogenética média e seis vezes maior que a diversidade beta baseada em atributos das espécies, com padrões espaciais coincidentes nas dimensões Taxo $\beta$ sim e Phylo $\beta$ sim, enquanto a Trait $\beta$ sim apresentou-se mais difusa e heterogênea no espaço. Nós encontramos a influência proeminente das distâncias geográficas entre sub-bacias, da severidade do habitat e dos tipos de cor da água nas dimensões taxonômica e filogenética da diversidade beta, junto com efeitos individuais menores da temperatura atual, tipos de habitat, conexões históricas entre sub-bacias, incursões marinhas e esforço amostral. Em contraste, a Trait $\beta$ sim foi pouco explicada, sendo influenciada apenas pelo esforço amostral e pelas condições hidromorfológicas atuais das sub-bacias. Esses resultados apontam para efeitos predominantes da limitação de dispersão, filtragem ambiental e contingências históricas na explicação dos padrões de diversidade beta taxonômica e filogenética dos agrupamentos de peixes amazônicos, mas não na substituição de atributos funcionais.

**Palavras-chave:** Assembleias de peixes, Bacia Amazônica, Eventos históricos, Filtragem ambiental, Métricas de diversidade beta.

## INTRODUCTION

Determining the drivers of variation in species composition between assemblages (*i.e.*, taxonomic beta diversity, Taxo $\beta$ ) is key to understanding the distribution of biodiversity across space and time. Taxonomic beta diversity is linked to important ecological mechanisms, such as environmental filtering (Leibold, Chase, 2018), species dispersal limitation (Hubbell, 2001; Wu *et al.*, 2017; Leibold, Chase, 2018; Guilherme *et al.*, 2022), biotic interactions (Graham, Fine, 2008) and historical contingency (Leprieur *et al.*, 2011; Fitzpatrick *et al.*, 2013; Dias *et al.*, 2014; Fluck *et al.*, 2020; Wu *et al.*, 2017). In addition to taxonomic beta diversity, phylogenetic and functional traits beta diversity (Phylo $\beta$  and Trait $\beta$ , respectively) have been adopted as complementary biodiversity dimensions (Graham, Fine, 2008; Swenson *et al.*, 2011; Leprieur *et al.*, 2012; Villéger *et al.*, 2013; Brum *et al.*, 2017). While Taxo $\beta$  measures species composition dissimilarity among assemblages (Whittaker, 1960), the two other dimensions measure the changes in lineages and species functional traits, respectively, providing insights into the evolutionary history and environmental conditions that shape assemblages (Graham, Fine, 2008; Weinstein *et al.*, 2014; Penone *et al.*, 2016). Although these three beta diversity measures are correlated due to phylogenetic constraints (Cadotte *et al.*, 2009; Swenson

*et al.*, 2011; Fritz, Rahbek, 2012; Weinstein *et al.*, 2014; Fluck *et al.*, 2020), each metric may add distinct information on the causal mechanisms involved in shaping assemblage formation (Mcgill *et al.*, 2006; Graham, Fine, 2008; Weinstein *et al.*, 2014; Penone *et al.*, 2016; Brum *et al.*, 2017; Mazel *et al.*, 2017; Villéger *et al.*, 2017, 2013; Lu *et al.*, 2019; McLean *et al.*, 2021). Thus, analyzing these three beta diversity dimensions together, and highlighting the drivers affecting each of them, may advance our understanding of patterns and processes involved in the evolution of biological assemblages.

The Amazon Basin is a major biodiversity hotspot (Antonelli *et al.*, 2018), containing, among others, the highest freshwater biodiversity on earth (Tisseuil *et al.*, 2013). This is notably true for Amazonian freshwater fishes which represent ~15% of all freshwater fish species described worldwide (Jézéquel *et al.*, 2020a; Tedesco *et al.*, 2017a). Much of this diversity is thought to be associated with major geological landscape events that took place between 30–7 Ma, as suggested by a continental-scale study using the entire South American freshwater fish fauna (Cassemiro *et al.*, 2023). Compared to other large riverine ecosystems worldwide, the Amazon Basin is still relatively well preserved (Reis *et al.*, 2016) but is facing rising anthropogenic threats, including damming, deforestation and climate change, that may potentially endanger its exceptional fish fauna in the near future (Reis *et al.*, 2016; Pelicice *et al.*, 2017; Albert *et al.*, 2020, 2023; Herrera-R *et al.*, 2020; Frederico *et al.*, 2021; Couto *et al.*, 2024; Correa *et al.*, 2025). Basin-wide approaches to understand the mechanisms underlying the origin and maintenance of Amazonian fish diversity patterns are thus urgently needed to organize evidence-based policy development and conservation planning (Socolar *et al.*, 2016; Jézéquel *et al.*, 2020b; Dagosta *et al.*, 2021; Flecker *et al.*, 2022; Caldas *et al.*, 2023).

Despite recent advances describing Amazonian fish diversity patterns and diversification (Dagosta, Pinna, 2017, 2019; Boschman *et al.*, 2023; Cassemiro *et al.*, 2023), only two studies covering the entire Amazon drainage basin have attempted so far to quantitatively analyze its basin-wide fish diversity drivers. The first one showed prominent influences of current and past climatic conditions, habitat size, and natural fragmentation on Amazonian sub-basins species richness, but also highlighted an independent West-East gradient of decreasing species richness, suggesting a center of fish diversity located westward and a colonization eastward from this center not yet achieved (Oberdorff *et al.*, 2019). Based on the same framework, the second study showed, in particular, that Western Amazon sub-basins were more phylogenetically clustered but less phylogenetically diverse compared to Eastern Amazon ones, suggesting deeper evolutionary divergences among taxa located to the East, and more recent radiations in the Western sub-drainages (Salgueiro *et al.*, 2022). Based on these findings and integrating the West-East gradient of decreasing richness (Oberdorff *et al.*, 2019), Salgueiro *et al.* (2022) concluded that Western Amazon was an evolutionary “cradle” of biodiversity (*i.e.*, location with unusually high rates of recent speciation), in line with the accelerating net diversification rates during the last 20 Ma (mainly in Western Amazon) found by Cassemiro *et al.* (2023) and Boschman *et al.* (2023). Taken together, results from Salgueiro *et al.* (2022), Cassemiro *et al.* (2023), and Boschman *et al.* (2023) suggest that Western Amazon is the most important source of fish lineages for the Amazon Basin.

Here, we analyze how historical and contemporary ecological factors interact to generate modern patterns of taxonomic, phylogenetic and functional traits beta diversity

across the Amazon Basin. Given the large spatial grain (*i.e.*, sub-basins) and geographical extent (*i.e.*, the whole Amazon Basin) of our study and the limited dispersal capacity of species, we expect spatial distance (*i.e.*, dispersal limitation), and to a lesser extent environmental filtering, to be the most important drivers of taxonomic beta diversity (Barton *et al.*, 2013). On the other hand, we expect phylogenetic changes in lineages across sub-basins (*i.e.*, turnover) to be highly dictated by the geological and historical events that occurred in the basin over the last 20 Ma (Boschman *et al.*, 2023; Cassemiro *et al.*, 2023). Finally, we anticipate functional (*i.e.*, species morphological traits in our case, but see Olden *et al.*, 2025) beta diversity to be notably dictated by current drivers such as differences in hydrological habitat types between sub-basins.

## MATERIAL AND METHODS

**Biological data.** Fish data were retrieved from the AmazonFish project ([www.amazon-fish.com](http://www.amazon-fish.com)), which offers the most complete fish distribution database available for the entire Amazon drainage basin (Jézéquel *et al.*, 2020a). Briefly, occurrence fish records were compiled (and are regularly updated) by mobilizing and integrating all information available in published articles, books, gray literature, online databases, worldwide museums and Universities, and expeditions conducted during the project. All occurrence records were validated by freshwater fish specialists and taxonomists (for details on data construction, see Jézéquel *et al.*, 2020a,b). The database currently contains 300,000 georeferenced records for 2,500 valid native freshwater fish species from 514 genera and 56 families. As we were interested in riverine organisms, we excluded species from the genus *Orestias* because they are mostly restricted to lakes in the Andean highlands (Scott *et al.*, 2020).

Here, our defined fish assemblages consist of 2,392 species presence/absence in each of our 97 sub-basins. The corresponding point data containing the geographic coordinates of all georeferenced records and the information sources can be freely downloaded from the AmazonFish website at [https://figshare.com/articles/dataset/A\\_database\\_of\\_freshwater\\_fish\\_species\\_of\\_the\\_Amazon\\_Basin/9923762](https://figshare.com/articles/dataset/A_database_of_freshwater_fish_species_of_the_Amazon_Basin/9923762). The choice of this large spatial grain was motivated by the heterogeneous distribution of sampling effort within the basin, limiting the possibilities to work at smaller spatial grains (Oberdorff *et al.*, 2019). The full method for sub-basins delineation and dataset construction are detailed in (Oberdorff *et al.*, 2019; Jézéquel *et al.*, 2020a,b), respectively. Briefly, we classified our sub-drainage basins based on the HydroBASIN framework (Lehner, Grill, 2013) and combined different HydroBASIN levels to retain only sub-basins >20,000 km<sup>2</sup> to optimize sampling effort (Oberdorff *et al.*, 2019). According to (Jézéquel *et al.*, 2020b) all but nine of these 97 sub-basins have >60% of completeness estimated based on Chao 2 richness estimators (*i.e.*, Demini, Paru\_Este, Jari, Jamanxim, Grande, Tapua, Apurimac1, Ucayali2, Curaray; see fig. S1 from Oberdorff *et al.*, 2019). A sub-basin with completeness ratio >0.6 is considered well surveyed (Troia, McManamay, 2016). The nine sub-basins having < 60% of completeness may thus generate potential biases in turnover values linked to insufficient sub-basin sampling effort. However, including or excluding these nine under-sampled sub-basins from analyses (see below) did not change the overall results so that we decided to discuss results obtained for the whole dataset (*i.e.*, 97 sub-basins).

We obtained phylogenetic information on Amazonian fishes from the supertree established by (Rabosky *et al.*, 2018). The backbone of this ultrametric supertree consists of 11,638 species with genetic data available, a calibration process including 130 fossil points, and the insertion of 19,888 species based on a stochastic polytomy resolution algorithm (Rabosky, 2020). In the Amazon Basin, we found 635 species for which genetic data were available and 1451 for which inclusion was based on the polytomy algorithm, resulting in 2086 fish species in the final pruned tree (~87% of Amazonian species). As the supertree consists of 100 samples from the posterior distribution (Rabosky *et al.*, 2018; Rabosky, 2020), we relied our analyses on each one of the 100 samples and estimated their mean dissimilarity values over all phylogenetic pruned trees. To confirm results obtained from this phylogenetic information, we further calculated the phylogenetic beta diversity metrics with a newly compiled, comprehensive phylogeny of Neotropical freshwater fish taxa based exclusively on DNA sequences (Casemiro *et al.*, 2023) and containing 1,111 species from our AmazonFish dataset. As phylogenetic beta diversity index calculated with both phylogenies were highly correlated (Mantel  $r = 0.90$ ;  $p < 0.001$ ; Fig. S1) and our results were similar whatever the phylogenetic information used, we discuss below only those stemming from Rabosky's phylogeny (*i.e.*, 2086 species), but also provide those obtained using the 1,111 species available in the phylogeny from Casemiro *et al.* (2023).

Fish species functional traits were gathered from the database developed by Brosse *et al.* (2021) and concerned exclusively morphological attributes related to species body size and body shape. The body shape of species was described using nine unitless measures (*i.e.*, body elongation, eye vertical position, relative eye position, oral gape position, relative maxillary length, body lateral shape, pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling) linked to species' locomotion and food acquisition (see fig. 1 from Brosse *et al.*, 2021). The data set used here included 1,661 fish species for which trait information was consistently available (>69% of our Amazonian fish species pool). To summarize, the calculation of the three beta diversity metrics was performed on distinct pool of species for each facet (*i.e.*, taxonomic: 2,392 species; phylogenetic: 2,086 species; functional: 1,661 species).

**Current, past and spatial predictors.** Large scale biodiversity patterns can be explained by a range of ecological and historical drivers (Ricklefs, 2004; Brown, 2014), and most of these drivers also apply for freshwater fishes at large spatial scales (Hugueny *et al.*, 2010). These drivers can be summarized under climate/productivity, area/environmental heterogeneity, historical/evolutionary, and spatial hypotheses (Ricklefs, 2004; Hugueny *et al.*, 2010; Brown, 2014). Data sources and definitions of the drivers used in this study are presented in detail in (Oberdorff *et al.*, 2019), and we only provide here a brief overview of each of them. All predictors described below were extracted for each of the 97 sub-drainage basins, providing a single mean value for each variable, and subsequently transformed into dissimilarity matrices (see below).

**Current environmental predictors.** To estimate the effects of climate and productivity, we used the annual mean and seasonality (Coefficient of Variation of intra-year monthly values calculated as the standard deviation divided by the mean) of temperature (Temp), precipitation (Prec), actual evapotranspiration (AET), potential

evapotranspiration (PET), net primary productivity (NPP), solar radiation (SolRad), run-off (RO), and the lowest (or highest) value of minimum (or maximum) temperature of the coldest (or warmest) month from WorldClim (version 1). These variables measure the mean current climatic condition, the seasonal climatic variability and the energy availability within each sub-drainage basin.

Habitat size and diversity were estimated using the surface area of the sub-drainage basin (km<sup>2</sup>; Area), the network density (*i.e.*, length of the riverine network divided by the surface area of the sub-basin, a measure of habitat availability for fishes; NetwD), the land cover heterogeneity (*i.e.*, the proportion of native land cover classes within each sub-drainage basin; VegCover), and the soil heterogeneity (*i.e.*, the proportion of each soil type within each sub-drainage basin; SoilCover). Finally, we used the hydromorphological heterogeneity (*i.e.*, the proportion of river hydromorphological types within each sub-basin; HydromorphoTypes). This last variable is derived from a recently developed classification scheme defining homogenous geomorphological river types throughout the Amazon Basin (Jézéquel *et al.*, 2022). Each river type, based on similar processes and river form characteristics (*e.g.*, channel planform, islands, bars, river bed dominant substrates size), is supposed to partly reflect hydrological constraints for biological assemblages (*e.g.*, Chessman *et al.*, 2006).

Amazonian waters were divided into three distinct biogeochemical water types or “colors”, differentiated by sediment composition, geochemistry and optical characteristics: *whitewaters* have an Andean origin (*e.g.*, the Madeira River and the Amazon mainstem), characterized by their usually low transparency due to large amounts of sediment particles and a neutral pH (pH ~6–8.5); nutrient poor *blackwaters* mostly draining the Precambrian Guiana shield (*e.g.*, the Negro River) characterized by their brownish color and acidic waters (pH < 5); and nutrient-poor, low-sediment, high-transparency and slightly acidic *clearwaters* (pH ~ 5.3–7.2) mostly draining the Brazilian and Guianas shields (*e.g.*, the Tapajós and Xingu Rivers) (Ríos-Villamizar *et al.*, 2020). Fish assemblages respond to water types (*e.g.*, Bogotá-Gregory *et al.*, 2020), hence we classified sub-basins according to their main water type as detailed in (Venticinque *et al.*, 2016) (see also fig. S2 from Oberdorff *et al.*, 2019). The three water color types were coded as categorical variables (coded as black, white and clear water (see *Predictors of dissimilarity matrices*)).

We further estimated the fragmentation and the isolation of sub-drainage basins, both key drivers of freshwater fish diversity at large spatial scale (Dias *et al.*, 2013; Tedesco *et al.*, 2017b), by using the number of waterfalls (>30 m) within each sub-basin using data from Lehner, Grill (2013), the sub-basin elevation (mean, and range; ElevMean and ElevRange), the proportion of the sub-basin surface with terrain slope above 15% (Csup15) and the proportion of the sub-basin surface above 1,000 m in altitude (ElevProp1000) (Oberdorff *et al.*, 2019).

The number of sampling sites divided by the surface area of each sub-basin was also included in our models to further control for a potential sampling effort effect (SamplingEffort).

**Historical factors.** We included variables related to the Amazon Basin geological history from distinct time periods. We identified the sub-basins potentially belonging or not to the Pebas system at ~23 Mya (Hoorn *et al.*, 2010), the surface area of each

sub-basin under sea water considering a sea-level rise of 25m during recent Pleistocene marine incursions (<1 Mya, Miller *et al.*, 2005), and the Quaternary climate stability within the sub-basin (from ~21 kyr to present; the strongest climatic shift in recent history, Sandel *et al.*, 2011). We used Quaternary climate reconstructions of mean, max and min annual temperatures and precipitations at the Last Glacial Maximum (LGM; 21 kyr) from three General Circulation Models (CCSM, MIROC, and MPI; three independent initiatives from distinct research communities to estimate past, present and future Earth climate metrics) and calculated the difference between current and LGM mean values to describe climate stability (Diff\_CurrentLGM).

We used the distance of each of the sub-drainages to the current Amazon river mouth (km) and the longitudinal position (downriver-upriver) of the principal tributary hosting a sub-basin to represent the position of each of the sub-drainages within the Amazon River network (see Oberdorff *et al.*, 2019 for a detailed explanation).

**Spatial predictors.** Watercourse distance is known to better represent the connections between sites in a riverine network than does the Euclidean spatial distance (Grant *et al.*, 2007; Tonkin *et al.*, 2018; Larsen *et al.*, 2021). Therefore, we calculated the watercourse distance (km) between each of our sub-drainages to represent the path to current fish dispersal. In this way, the watercourse distance matrix represents the distance (km) between each pair of sub-drainages following the dendritic configuration of the Amazon Basin.

### Statistical analyses

**Biological dissimilarity matrices.** To quantify the taxonomic, phylogenetic and functional beta diversity, we used the pure turnover component of the Sørensen dissimilarity index for all three facets (*i.e.*, the Simpson dissimilarity,  $\beta_{sim}$ ). The Sørensen dissimilarity index ( $\beta_{Sor}$ ) can be partitioned into two components: pure turnover (*i.e.*,  $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) (Baselga, 2010, 2012). As, in our case,  $\beta_{sim}$  represented a larger fraction of the  $\beta_{Sor}$  than  $\beta_{sne}$  (see results), we chose here to discuss only results obtained from the former. However, results obtained using  $\beta_{sne}$  are given for information.

The  $\beta_{sim}$  for taxonomic data (*i.e.*, Taxo $\beta_{sim}$ ) quantifies  $\beta$ -diversity due to pure turnover (replacement) of species between sub-basins, independently of their respective differences in species richness (Baselga, 2010, 2012). It is calculated as Taxo $\beta_{sim} = \min(b,c) / (a + \min(b,c))$ , where  $a$  is the number of species shared by the two concerned sub-basins,  $b$  is the number of species unique to one sub-basin and  $c$  is the number of species unique to the other sub-basin.

Taxonomic dissimilarity has been extended to phylogenetic and functional (*i.e.*, species traits) data (Leprieur *et al.*, 2012; Villéger *et al.*, 2013). To quantify the pure turnover component of phylogenetic dissimilarity of sub-basins assemblage, we used the Phylo $\beta_{sim}$  metric which is analogous to Taxo $\beta_{sim}$  with shared and unique species being replaced by shared and unique branch lengths on the phylogenetic tree (Leprieur *et al.*, 2012).

Finally, we adopted a similar framework to calculate the functional dissimilarity between assemblages (Trait $\beta_{sim}$ ) (Villéger *et al.*, 2013). We used species body size and the nine continuous morphological body ratios (centered and reduced so that they all have zero mean and unity standard deviation) available in Brosse *et al.* (2021)

to compute four Principal Components axes in order to construct the species traits multidimensional space. We used four axes summarizing 71% of variability of the total morphological matrix and giving a good representation of functional spaces (low mean residual variation; 0.61; see Tabs. S2, S3; Figs. S4, S5) without excessively increasing the computation time requested to calculate trait volumes for higher dimensions (Maire *et al.*, 2015). The morphological dissimilarity metric (*i.e.*, Trait $\beta$ sim) between two assemblages was calculated as the proportion of unshared convex hull volume between a pair of sub-basins after controlling for their size differences in the morphological space (Villéger *et al.*, 2013). All metrics were calculated using the *vegan* (Oksanen *et al.*, 2022), *betapart* package (Baselga, Orme, 2012), and *picante* (Kembel *et al.*, 2010) packages. Taxo $\beta$ sim, Phylo $\beta$ sim and Trait $\beta$ sim metrics vary from 0 (total similarity in assemblage taxonomic or phylogenetic or species traits composition between two sub-basins) to 1 (total dissimilarity in assemblage taxonomic or phylogenetic or species traits composition between two sub-basins).

**Matrices of predictors.** Predictors were log-transformed, when necessary, to minimize potential effects of extreme values (see Oberdorff *et al.*, 2019). We further standardized all metrics so that they all had mean zero and 0.5 standard deviation (Gelman, 2008); this procedure is key to homogenize their scales and ranges, and assures each variable to have the same weight when computing the dissimilarity predictor matrices. Then, we applied the Euclidean distance, a common approach to deal with continuous environmental variables, to calculate each of the predictor dissimilarity matrices. As the water type variable was categorical with three levels (Tab. 1), we constructed a pairwise binary matrix coding pairs of sub-basins of the same water type as 1, and 0 when different. We calculated the similarity matrix of Pebas past connection/disconnection by coding 1 for pairs of sub-basins both connected to Pebas, and 0 for all other configurations. As spatial watercourse distance was a pairwise matrix (watercourse distance between two sub-basins), no pairwise calculation was further needed. We finally calculated fourteen matrices representing major ecological, historical and evolutionary hypotheses in order to estimate their independent effects on fish assemblage dissimilarities (Tab. 1).

Prior to modeling, we assessed multicollinearity among all predictor distance matrices using the Variance Inflation Factor (VIF). Although there are no canonical rules of thumb, VIF values <10 are usually considered as acceptable and indicate low collinearity among predictors (Dormann *et al.*, 2012). As none of our predictor distance matrices presented VIF values >10, all predictors were included simultaneously in our modeling framework.

**Concordance among metrics and mapping.** We first performed Pearson' correlation among vectorized Taxo $\beta$ sim, Phylo $\beta$ sim, and Trait $\beta$ sim matrices to estimate correlations between all assemblage beta diversity metrics. As we were dealing with pairwise distance matrices, we mapped spatial assemblage dissimilarity by calculating the mean dissimilarity values of a focal sub-drainage over all pairwise combinations with the other sub-drainages (*i.e.*, calculating mean values over rows of the pairwise matrices), allowing therefore to visualize the spatial patterns of the three beta diversity facets. In order to improve visualization, we also performed Non-Metric Multidimensional Scaling analysis (NMDS) on each individual dissimilarity matrix and

**TABLE 1** | All predictors used to construct each dissimilarity matrix and their corresponding explanation group. Some predictors have been transformed ( $\log[x+1]$  or arcsin of the square root) to improve distribution of values along their gradients (predictors are named following the adopted transformation). Standardized predictor means predictors have been centered (mean = 0) and reduced (sd = 0.5) to give them equal weight prior distance matrix computation. Variance Inflation Factor (VIF) values are shown for all resulting pairwise matrices.

Predictors	Combined variables	Matrix calculation; dissimilarity/similarity	Group	VIF
D_Energy	AET (min, max, annual, cv), PET (min, max, annual, cv), NPP (mean, sd, cv)	Euclidean distance of standardized predictors; dissimilarity	Current environment	8.4
D_Water	Precipitation (min, max, annual, cv), Runoff (mean)	Euclidean distance of standardized predictors; dissimilarity	Current environment	2.4
D_Temp	Temperature (min, max, mean, cv), Solar Radiation (mean, cv)	Euclidean distance of standardized predictors; dissimilarity	Current environment	6.2
D_HabitatSize	NetworkDensity, SurfaceArea_log	Euclidean distance of standardized predictors; dissimilarity	Current environment	1.1
D_HabitatType	VegType (relative proportion), SoilType (relative proportion)	Euclidean distance of binded VegCover and SoilCover categories; dissimilarity	Current environment	1.3
D_HabitatHarsh	Csup15, ElevMean_log, ElevRange_log, ElevPropBasin-Above1000m_asin_sqrt	Euclidean distance of standardized predictors; dissimilarity	Current/Historical	2.2
D_Fragmentation	NumberWaterfall_log	Euclidean distance of standardized predictor; dissimilarity	Current/Historical	1.1
D_Position	DistanceRiverMouth, PositionCodeAlongWestEast	Euclidean distance of standardized predictors; dissimilarity	Current/Historical	2.6
D_WaterColor	WaterColor (categories black, clear, white)	Same water color = 1, Distinct water color = 0; similarity	Current environment	1.2
D_SampEff	Density of sampling points_log (log[NumSamplingPoints/Subdrainage surface area])	Euclidean distance between standardized predictor; dissimilarity	Current environment	1.2
D_CurrentLGM	Difference between Current and Past temp (min, max, mean), precip (min, max, annual)	Euclidean distance of standardized predictors; dissimilarity	Historical	1.5
D_MarineInc	Proportion (%) of Surface area below 25m_log	Euclidean distance of standardized predictor; dissimilarity	Historical	1.8
D_PastConnect	Connected/not Connected to Pebas system	Two sub-basin connected to Pebas = 1, only one connected or no connections to Pebas = 0; similarity	Historical	1.5
D_HydromorphoType	Relative proportion of riverine hydrological habitats (%)	Euclidean distance between relative proportion of hydrogeomorphology riverine categories; dissimilarity	Current environment	1.4
D_Spatial	Spatial distance	WaterCourse pairwise distance among sub-drainages (km); dissimilarity	Space	2.8

used the scores of the two resulting axes as Red Green Blue (RGB) color parameters for each map. As a result, sub-basins with similar species composition are represented with similar colors on the maps (Fig. S6).

**Drivers of fish assemblage dissimilarities.** As usually done, we modeled the pairwise dissimilarity (*i.e.*, Taxo $\beta$ sim, Phylo $\beta$ sim, Trait $\beta$ sim) against all the dissimilarity matrices related to current climate and environmental factors, historical and geological events, and spatial distance between sub-drainage basins (Tab. 1) using Multiple Regression on Distance Matrices (*i.e.*, ordinary MRM based on Gaussian error distribution; *i.e.*, MRM\_lm) (Lichstein, 2007), which are equivalent to partial Mantel analysis. However, due to the properties of dissimilarity values (*i.e.*, bounded between 0 and 1 and their relationship with predictors often involving non-linear trends), we also adopted the MRM approach based on Generalized Linear Models with Binomial error distribution (*i.e.*, MRM\_glm, performed with ecodist package and MRM function), as MRM\_glm models appear more suitable for our response variables. As results obtained using the two approaches were very similar, we chose to provide both of them for transparency. These analyses allow us to estimate the independent effects of predictors current, historical and

spatial effects while controlling for those peculiarities. The statistical significance was assessed with permutation of the response matrix, using the frequency at which 3999 null simulated coefficients were higher and/or lower than the observed coefficients. All analyses and graphics were performed under R environment (R Development Core Team, 2022), modeling routines were implemented in the *ecodist* package (Goslee *et al.*, 2007) and all codes are available as Appendix files and at <https://github.com/mversutdias/AmazonFISHBetaDiversity.git>.

## RESULTS

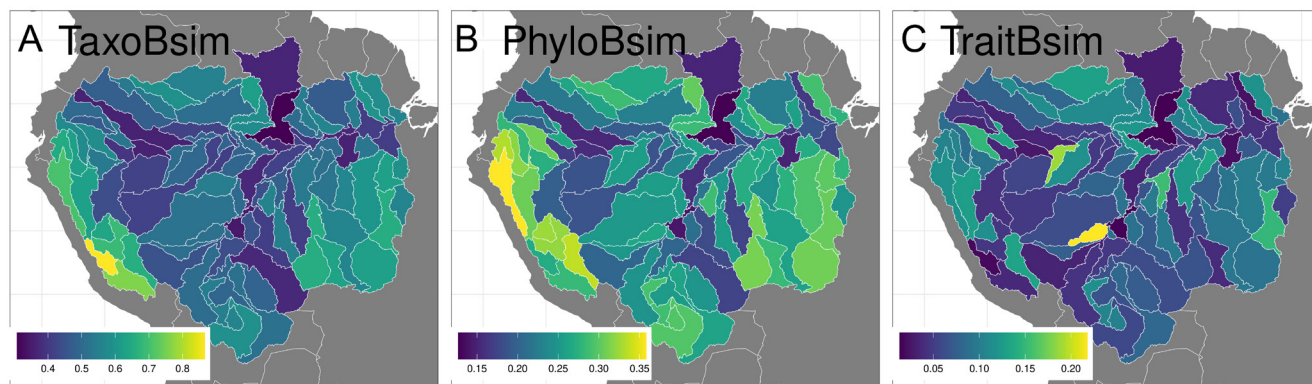
Over all pairwise combinations, the turnover component is higher than the nestedness for taxonomic (mean  $\text{Taxo}\beta_{\text{sor}} = 0.66$ , range = 0.22–1.00,  $\text{sd} = 0.16$ ; mean  $\text{Taxo}\beta_{\text{sim}} = 0.51$ , 0.03–1.00,  $\text{sd} = 0.18$ ; mean  $\text{Taxo}\beta_{\text{sne}} = 0.15$ , 0.00–0.77,  $\text{sd} = 0.13$ ) and phylogenetic metrics (mean  $\text{Phylo}\beta_{\text{sor}} = 0.42$ , range = 0.13–0.95,  $\text{sd} = 0.15$ ; mean  $\text{Phylo}\beta_{\text{sim}} = 0.24$ , 0.01–0.69,  $\text{sd} = 0.11$ ; mean  $\text{Phylo}\beta_{\text{sne}} = 0.17$ , 0.00–0.89,  $\text{sd} = 0.16$ ). The nestedness component was higher than the turnover component for trait beta diversity (mean  $\text{Trait}\beta_{\text{sor}} = 0.38$ , range = 0.02–1.00,  $\text{sd} = 0.23$ ; mean  $\text{Trait}\beta_{\text{sim}} = 0.08$ , 0.00–0.70,  $\text{sd} = 0.09$ ; mean  $\text{Trait}\beta_{\text{sne}} = 0.30$ , 0.00–1.00,  $\text{sd} = 0.26$ ).

**Geographical patterns in the three beta diversity facets.** Mean taxonomic beta diversity among sub-basins ( $\text{Taxo}\beta_{\text{sim}} = 0.51$ ) is around two times higher than mean phylogenetic beta diversity ( $\text{Phylo}\beta_{\text{sim}} = 0.24$ ) and six times higher than species traits beta diversity ( $\text{Trait}\beta_{\text{sim}} = 0.08$ ). Using all pairwise distance values, all three beta diversity dimensions are positively and significantly related to each other, but correlations vary a lot among metrics (Tab. 2). Using mean pairwise dissimilarity values for each focal sub-basin (*i.e.*, mean dissimilarity values over rows in matrices),  $\text{Taxo}\beta_{\text{sim}}$  and  $\text{Phylo}\beta_{\text{sim}}$  dimensions show coincident spatial patterns of low dissimilarity levels at the center (and along the river mainstem) of the Amazon Basin and higher dissimilarity at its periphery, Andean sub-basins displaying the highest dissimilarity values together with sub-basins located in the southeastern part of the basin (Figs. 1A, B). The  $\text{Trait}\beta_{\text{sim}}$  pattern is more diffuse and heterogeneous across space, with highest assemblage dissimilarity values found, for instance, in sub-basins located in the northern part of the basin (*e.g.*, upstream parts of the Negro River) (Fig. 1C; see also Fig. S6).

**Factors explaining patterns in the three beta diversity facets.** MRM\_glm and ordinary MRM models show Pseudo- $R^2$  and  $R^2$  ranging from 8 to 54% of explained variance. Our multiple MRM\_glm models reveal a significant and prominent positive influence of geographic distance between sub-basins on the taxonomic and phylogenetic dimensions of beta diversity (Tab. 3; Fig. 2). In addition to geographic distance,  $\text{Taxo}\beta_{\text{sim}}$  increases with dissimilarity in habitat harshness and habitat types (*i.e.*, soil and vegetation cover), and decreases in Amazonian sub-basins having the same chemical water type. The model also suggests negative effects of the historical connection to the Pebas system, of marine incursions, and a positive effect of mean current temperature on  $\text{Taxo}\beta_{\text{sim}}$ , but these last three effects are only marginally significant. Besides geographic distance,  $\text{Phylo}\beta_{\text{sim}}$  is negatively related to dissimilarity in sampling effort, water

**TABLE 2** | Pearson correlation among all pairwise indices of fish beta diversity in the Amazon 97 sub-drainages. All correlation values are significant at  $p < 0.001$ .

	Taxo $\beta$ sim	Phylo $\beta$ sim	Trait $\beta$ sim
Taxo $\beta$ sim	-	-	-
Phylo $\beta$ sim	<b>0.89</b>	-	-
Trait $\beta$ sim	<b>0.36</b>	<b>0.56</b>	-

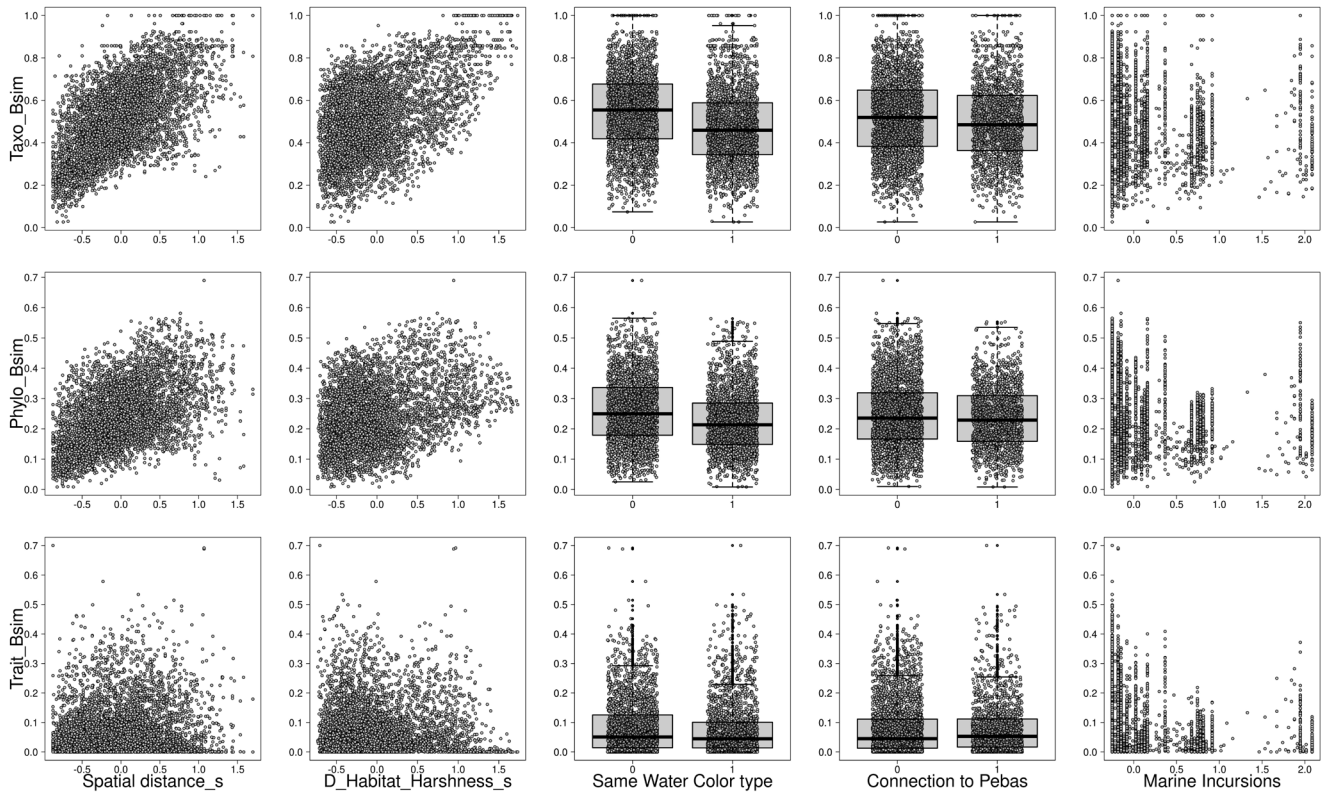


**FIGURE 1** | Spatial mapping of mean (a) taxonomic (Taxo $\beta$ sim), (b) phylogenetic (Phylo $\beta$ sim), and (c) functional (Trait $\beta$ sim) beta diversity dimensions. The values within sub-drainages are mean dissimilarity values calculated over all pairwise combinations targeting each of the 97 sub-basins analyzed. As they are all dissimilarities, all values are bounded between 0 and 1.

type, and positively related to dissimilarity in habitat harshness. These effects suggest high phylogenetically dissimilar assemblages in sub-basins having distinct degree of harshness; whereas phylogenetically similar assemblages are found in sub-basins of the same water type and having high differences in sampling effort. Sampling effort and hydromorphological types significantly affect Trait $\beta$ sim patterns. This suggests trait assemblage dissimilarity decreases with increasing difference in sampling effort, whereas trait dissimilarity is high when differences in rivers' hydromorphological type increase between sub-basins.

Ordinary MRMs (MRM\_lm) for the three beta diversity dimensions retain the same variables as MRM\_glm but also highlight supplementary significant effects of historical connection to the Pebas system, of marine incursions (Fig. 2), Quaternary (D\_CurrentLGM) and differences in current temperature (D\_Temp) on sub-basins taxonomic dissimilarity (Taxo $\beta$ sim). Assemblages in two sub-basins connected to the Pebas system are overall less taxonomically dissimilar (more similar) than their counterparts, while sub-basins having been subject to increasing levels of past marine incursions are overall less dissimilar to other sub-basins. Phylo $\beta$ sim is related to the same predictors detected with MRM\_glm (D\_HabitatHarsh, D\_HabitatWaterCol, D\_SampEff), but D\_CurrentLGM and D\_PastConnect also show marginally significant effects similar to Taxo $\beta$ sim (Tab. 3). Sampling effort and riverine hydromorphology were detected again as the only significant predictors for Trait $\beta$ sim (Tab. 3). Results obtained are similar when using a recently published Neotropical freshwater fish

phylogeny (Cassemiro *et al.*, 2023) instead of the one proposed by Rabosky *et al.* (2018) (Tabs. S7, S8) or when excluding pairwise dissimilarity from the 9 under-sampled sub-basins (Tab. S9). See also results for  $\beta_{sne}$  component (Tab. S10).



**FIGURE 2 |** Relationships between fish dissimilarity facets from the Amazon sub-basins pairs and the most important predictors identified in Tab. 2.

**TABLE 3** | Observed coefficient estimates from Multiple Regression on distance Matrices (MRM) models using Binomial (MRM\_glm) and Gaussian (MRM\_lm) error distribution on taxonomic, phylogenetic and trait beta diversity from the Amazon River basin. Pseudo-R<sup>2</sup> is defined as (Null Deviance - Residual Deviance) / Null deviance. \*\*p< 0.01; \*p< 0.05; † 0.05<p<0.10.

Dissimilarity predictors	MRM_glm			MRM_lm		
	Taxoβsim	Phyloβsim	Traitβsim	Taxoβsim	Phyloβsim	Traitβsim
(Intercept)	<b>0.07**</b>	<b>-1.16**</b>	<b>-2.51**</b>	<b>0.51**</b>	<b>0.24**</b>	<b>0.08**</b>
D_Energy	-0.16	-0.21	-0.39	-0.04	-0.04†	-0.03
D_Water	-0.02	0.02	0.11	0.00	0.00	0.01
D_Temp	0.37†	0.15	-0.14	<b>0.08*</b>	0.03	-0.01
D_HabitatSize	-0.06	0.05	0.06	-0.01	0.01	0.00
D_HabitatType	<b>0.15*</b>	0.09	0.02	<b>0.04**</b>	0.02†	0.00
D_HabitatHarsh	<b>0.40**</b>	<b>0.25**</b>	0.15	<b>0.09**</b>	<b>0.05**</b>	0.01
D_Position	0.14	0.03	0.04	0.03	0.01	0.01
D_HabitatFragment	0.02	-0.02	-0.13	0.00	0.00	-0.01
D_HabitatWaterCol	<b>-0.20**</b>	<b>-0.12*</b>	-0.07	<b>-0.05**</b>	<b>-0.02**</b>	-0.01
D_SampleEff	-0.07	<b>-0.25**</b>	<b>-0.58**</b>	-0.02	<b>-0.04**</b>	<b>-0.04**</b>
D_MarineInc	-0.24†	-0.13	-0.29	<b>-0.06*</b>	-0.02	-0.02
D_CurrentLGM	0.17	0.13	0.22	<b>0.04*</b>	0.02†	0.01
D_PastConnect	-0.22†	-0.13	-0.09	<b>-0.05*</b>	-0.02†	-0.01
D_HydromorphoType	-0.03	0.03	<b>0.16*</b>	-0.01	0.01	<b>0.01*</b>
D_Spatial	<b>0.54**</b>	<b>0.40**</b>	0.20	<b>0.13**</b>	<b>0.07**</b>	0.01
Null deviance	675.58	289.24	452.78	-	-	-
Residual Deviance	324.39	186.92	409.81	-	-	-
Pseudo-R <sup>2</sup> (%)	52.00	35.37	9.49	-	-	-
F statistic	-	-	-	<b>364.50**</b>	<b>174.88**</b>	<b>26.23**</b>
R <sup>2</sup> (%)	-	-	-	<b>54.00**</b>	<b>36.00**</b>	<b>8.00**</b>

## DISCUSSION

By analyzing, for the first time, three fish beta diversity dimensions among 97 sub-basins covering the whole Amazon Basin, our study unravels the role of several drivers and associated processes that act together to shape diversity patterns in this hyperdiverse basin.

**A leading effect of dispersal limitation by geographic distance on taxonomic and phylogenetic beta diversity patterns.** Regardless of the models retained (*i.e.*, MRM\_glm or MRM\_lm), taxonomic (Taxoβsim) and phylogenetic beta diversity (Phyloβsim) dimensions are most-strongly related to geographic distance. This result is controlled for and independent of the other potential drivers used in the modeling, suggesting that species dispersal limitation by space strongly influences patterns of assemblage turnover among sub-basins as already detected for fish in other regions (Albert *et al.*, 2011; Craig *et al.*, 2020) and for several other taxonomic groups (Dambros *et al.*, 2016, 2020; Fluck *et*

*al.*, 2020). Despite the fact that riverine fishes, with the exception of migratory species, are considered poor dispersers (Rodríguez, 2002; Comte, Olden, 2018), the Amazonian fish fauna is in addition largely dominated by small-bodied species evenly distributed among the richest families (Dagosta, Pinna, 2019; Albert *et al.*, 2020). Given the large spatial grain used in our study (*i.e.*, sub-basins), the huge geographical area of the Amazon Basin (~6 million km<sup>2</sup>, excluding the Tocantins Basin), and considering that small-sized fishes display lower dispersal abilities than their larger counterparts (Jenkins *et al.*, 2007; Radinger, Wolter, 2013; Giam, Olden, 2018), it is not surprising that dispersal limitation by geographic distance strongly drives the variation in these two beta diversity facets (Rodrigues-Filho *et al.*, 2018). Moreover, as the metric Phylo $\beta$ sim is sensitive to turnover among recently diverged lineages (Leprieur *et al.*, 2012) and two times lower than Taxo $\beta$ sim, the increase in assemblage phylogenetic dissimilarity with spatial distance also suggests recent allopatric diversification processes, rather than adaptive radiation in distant sub-basins and maintenance of these neo-endemic species in these sub-basins due to their usually smaller body size and consequent limited dispersal capacities (Tedesco *et al.*, 2012).

According to metacommunity theory (Leibold, Chase, 2018), the spatial distribution of assemblages in a region is determined by the rate of dispersal of organisms and the environmental heterogeneity of habitat patches (Ricklefs, 2007). Beta diversity is often thought to be driven by environmental heterogeneity (Soininen *et al.*, 2018) because different conditions among patches lead to distinct species using different niche opportunities due to their distinct habitat requirements (*i.e.*, environmental filtering, Chase, Leibold, 2003). However, under the neutral model (Hubbell, 2001), dispersal limitation restricts species occurrence in different patches, resulting in spatially structured beta diversity patterns independent of environmental distance (Leibold, Chase, 2018). In practice, the relative importance of environmental conditions and dispersal as factors affecting species geographic ranges shifts from stronger environmental filtering to stronger dispersal limitation while changing from smaller to larger regional scales (Antonelli *et al.*, 2018; Benone *et al.*, 2020; Yunoki, 2023). Considering the large spatial grain involved (sub-basins >20,000 km<sup>2</sup>), that most Amazonian fishes are presumably poor dispersers (see above) and the high taxonomic beta diversity among sub-basins, we argue that at this spatial grain, dispersal limitation contributes strongly to the formation of Amazonian fish species assemblages (Albert *et al.*, 2020), leading assemblages dissimilarity to increase with increasing geographic distance, and this independently of any environmental distance. In contrast, we found only a slightly positive influence of current temperature and habitat types on the Taxo $\beta$ sim dimension, which may come from the fact that the analyzed sub-basins, given their size, broadly include most climatic conditions and types of habitat found in the Amazon Basin (Jézéquel *et al.*, 2022).

**Environmental filtering through habitat types and habitat harshness also drives taxonomic, phylogenetic and to a lesser extent functional beta diversity patterns.** Besides geographic distance, our models depict a significant effect of habitat harshness (*i.e.*, high elevation streams/rivers with steep gradients, cold climatic conditions and high hydrological variability) on assemblage taxonomic and phylogenetic turnover among sub-basins. This environmental harshness strongly constrains dispersal (Oberdorff *et al.*, 2019) and drives deterministic selection over evolutionary times, leading to a reduced

number of species filtered from the regional species pool, and possessing biological traits that allow them to cope with these specific environmental conditions (Datry *et al.*, 2016). Consequently, in sub-basins harboring these habitats (mainly in the Andes and cratonic shields), fish assemblages display more distinct species composition and distinct lineages compared to other sub-basins (Fig. S6), leading to higher taxonomic and phylogenetic turnover between pairs of sub-basins. Assemblage composition changes produced by environmental harshness have previously been noticed locally in the Amazon Basin (*e.g.*, Datry *et al.*, 2016; Herrera-R *et al.*, 2020). High taxonomic beta diversity is also found among sub-basins draining different types of soil and habitat cover, suggesting that these habitat types exercise a significant filtering process on the compositional structure of fish assemblages (Lo *et al.*, 2020), usually affecting differentially species depending on their biological traits (*e.g.*, trophic traits; Arantes *et al.*, 2017).

We also find high taxonomic and phylogenetic beta diversity among sub-basins draining distinct water chemistry types, independently of the other considered drivers. According to our dataset, 83 genera and 258 species are found exclusively in *whitewaters*; 59 genera and 342 species are found exclusively in *clearwaters*; and 39 genera and 150 species are found exclusively in *blackwaters*. This suggests that differences in biogeochemical water types between sub-basins of the Amazon River act as filters to species dispersal and may also provide effective barriers to gene flow between populations leading to speciation processes and finally accumulation of distinctive fish assemblages between sub-basins. Both processes, *i.e.*, filter to dispersal (*e.g.*, Saint-Paul *et al.*, 2000; Winemiller *et al.*, 2008; Yunoki, Velasco, 2016; Bogotá-Gregory *et al.*, 2020; Borges *et al.*, 2023) and regulation of genetic exchanges between populations (*e.g.*, Cooke *et al.*, 2012; Beheregaray *et al.*, 2015; Pires *et al.*, 2018), have already been highlighted for fish assemblages inhabiting different water color types of the Amazon Basin.

Finally, one of our models also highlights a weak, though significant, positive effect of hydro-geomorphological river types on assemblages functional (species morphological traits) beta diversity. This pattern suggests that rivers' hydro-geomorphology do act as an environmental filter, influencing the morphological trait distribution (*i.e.*, the structure of the morphological space) of sub-basins fish assemblages through variations in habitat structural complexity (*e.g.*, Lamouroux *et al.*, 2002; Bower *et al.*, 2021), and independently of any phylogenetic signal (*i.e.*, morphological traits divergence among assemblages occupying habitats of distinct hydromorphological conditions). However, as previously said, the effect noticed is rather weak, despite a morphologically hyperdiverse Neotropical freshwater fish fauna (especially the Amazonian fauna) (Toussaint *et al.*, 2016). The fact that our functional beta diversity metric (exclusively based on morphological traits) showed very low mean values and very low spatial variability (Fig. 1) may be partly due to the large grain size used in our study but is consistent with earlier findings obtained for tropical reef fishes (Maxwell *et al.*, 2022). On the other hand, the Amazonian ichthyofauna has ancient origins, and many clades of Amazonian fishes had achieved modern phenotypes by the early Neogene [ $\sim 23$  million years (Ma) ago], when the aquatic system was mostly fluvio-lacustrine (Hoorn *et al.*, 2010; Albert *et al.*, 2020). It is thus likely that most of the diversification of species forms has been preferentially driven in this enduring, stable environment. The establishment of the transcontinental Amazon River during the last 10 Ma due to the uplift of the Andes, did not change drastically hydrological constraints for fishes as most

of the basin (except the Andean Foreland) is represented by lowland areas with a flat topography (Jézéquel *et al.*, 2022). In that, our results may plead for an overall historical and current non-binding physical environment for species morphological adaptation in the basin and suggest that the majority of morphological traits are shared among sub-basin assemblages. Furthermore, within the whole Amazon Basin, the trait composition of species-poor sub-basin assemblages is found to be nested within the trait composition of species-rich ones, as  $\beta_{\text{sne}}$  was much more influential than  $\beta_{\text{sim}}$  in explaining overall beta diversity patterns of functional (morphological) traits (see results).

**Historical contingencies also matter for explaining taxonomic and phylogenetic beta diversity patterns.** Independently of the effects of other considered drivers, assemblages in sub-basins historically connected to the Pebas system tend to be overall less taxonomically and phylogenetically dissimilar than their counterparts. This result is in phase with the well accepted historical hypothesis proposing the presence of a megawetland known as the Pebas system occupying western Amazonian during the Miocene and separated from a much smaller fluvial eastern Amazonia system by the Purus Arch (Hoorn *et al.*, 2010; Shephard *et al.*, 2010). Isolation of these two systems during millions of years before the Amazon River assumed its modern course toward the Atlantic (Campbell *et al.*, 2006; Hoorn *et al.*, 2010; Latrubesse *et al.*, 2010; Oberdorff *et al.*, 2019) may have generated two centers of diversification of the current Amazonian fish fauna by favoring independent diversification processes resulting in a pattern of high phylogenetic and high taxonomic beta dissimilarities between sub-basins located on both sides of this historical barrier.

A marginally significant (MRM\_glm) or significant (MRM\_lm) negative effect of Pleistocene marine incursion (<1 Ma ago, magnitude ~25 m) (Miller *et al.*, 2005) on sub-basins taxonomic beta diversity patterns was also revealed by our models; fish assemblages in sub-basins having experienced increasing marine incursion (measured here as the percentage of area of sub-basins having suffered from marine incursions) are overall less dissimilar to other sub-basins. A parsimonious hypothesis is that this recent marine incursion has eliminated freshwater habitats in the low-lying areas of the lower and central Amazon (see also fig. S4 from Oberdorff *et al.*, 2019), leading to populations extirpation of lowland freshwater fish species that homogenized fish assemblages in these concerned sub-basins. This last hypothesis is reinforced by the significant negative relationship we found between the nestedness component of taxonomic beta diversity and our Pleistocene marine incursion variable (see Tab. S10).

At last, one of our two models (MRM\_lm) highlights a supplementary positive effect of Quaternary climate variability (LGM) on sub-basins taxonomic and phylogenetic beta diversity patterns (also only marginally significant for the latter), suggesting that assemblages in sub-basins having undergone strong climatic variations since the LGM are more taxonomically and phylogenetically distant than their counterparts. This different history of climate evolution between sub-basins may have increased extinction rates in sub-basins where climatic variations were high (Cheng *et al.*, 2013) and, on the contrary, increased speciation rates in sub-basins having experienced stable climatic conditions through time (Tedesco *et al.*, 2012).

**A significant effect of sampling effort on the functional and phylogenetic facets of beta diversity.** After controlling for all other factors, our models highlight that both functional and phylogenetic assemblage dissimilarities decrease with increasing difference in sampling effort between sub-basins. A previous study using the same fish species occurrence database already noticed a positive and significant effect of sampling effort on our sub-basins species richness (Oberdorff *et al.*, 2019). Together, these results support the view that assemblages in under-sampled sub-basins most often represent a subset of species found in better sampled sub-basins (*i.e.*, species found in under-sampled areas are usually the most widespread ones, decreasing functional and phylogenetic sub-basins assemblage dissimilarities). Sampling gaps are pervasive in the Amazon, irrespective of the studied biological group, and are overall explained by difficulties to access some regions and/or remoteness of these regions from research infrastructure (Carvalho *et al.*, 2023; Herrera-R *et al.*, 2023).

To conclude, our large-scale analysis of spatial variation in the fish species assemblages inhabiting the Amazon sub-drainages provides insight into the processes structuring present-day fish assemblages. By analyzing three beta diversity facets (*i.e.*, taxonomic, phylogenetic and functional), our results indicate that, at the spatial grain (97 sub-basins) and geographical extent (whole Amazon Basin) of this study, dispersal limitation by geographic distance is the major process shaping taxonomic and/or phylogenetic differences in fish assemblages composition between sub-drainages. However, we further noticed that taxonomic and phylogenetic beta diversity patterns also arise due to contemporary environmental constraints (*i.e.*, environmental filtering) and to historical events, whereas functional turnover is only weakly linked to sampling effort and current sub-basins hydro-geomorphology. Finally, our results show that the Amazon Basin still suffers from incomplete knowledge on species spatial distribution, biological traits and phylogenetic information even though we used the most complete and up-to-date information currently available for these 3 biodiversity facets (Rabosky *et al.*, 2018; Jézéquel *et al.*, 2020a; Brosse *et al.*, 2021; Casemiro *et al.*, 2023). There is thus an urgent need to address these gaps by increasing field surveys in currently under-sampled areas (Jézéquel *et al.*, 2020b; Carvalho *et al.*, 2023).

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### ETHICAL STATEMENT

Not applicable.

### DATA AVAILABILITY STATEMENT

The corresponding point data containing the geographic coordinates of all georeferenced records and the information sources can be freely downloaded from the AmazonFish website at [https://figshare.com/articles/dataset/A\\_database\\_of\\_freshwater\\_fish\\_species\\_of\\_the\\_Amazon\\_Basin/9923762](https://figshare.com/articles/dataset/A_database_of_freshwater_fish_species_of_the_Amazon_Basin/9923762). All codes are available as Appendix files and at <https://github.com/msversutdias/AmazonFISHBetaDiversity.git>.

### AI STATEMENT

ChatGPT and DeepSeek has been used for preparing Bibliography list following NI standards.

### COMPETING INTERESTS

The authors declare no competing interests.

### SUPPLEMENTARY MATERIAL

Supplementary material S1

Supplementary material S2

Supplementary material S3

Supplementary material S4

Supplementary material S5

Supplementary material S6

Supplementary material S7

Supplementary material S8

Supplementary material S9

Supplementary material S10



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