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Functional responses to deforestation in fish communities inhabiting neotropical streams and rivers

Isabel Cantera[1*], Céline Jézéquel[2], Tony Dejean[3], Jérôme Murienne[2], Régis Vigouroux[4], Alice Valentini[3] and Sébastien Brosse[2]

Abstract

Background Deforestation is a widespread disturbance for neotropical freshwater ecosystems. While biodiversity declines have been associated with deforestation, its functional consequences for stream and river fish faunas remain poorly understood. In this study, we explored how deforestation affects the different facets of the functional structure of fish communities inventoried using environmental DNA metabarcoding in 64 river and 35 stream sites of French Guiana. Specifically, we investigated how functional richness, divergence, evenness and identity of fish faunas are affected by deforestation.

Results We showed that anthropogenic disturbances in French Guiana are modifying the functional diversity of freshwater fish communities. These disturbances not only affected the amount of functional traits held by the communities but also the identity of the traits and the internal structure of the functional space. Consequently, different facets of the functional diversity supported by fish assemblages were altered. In streams, deforestation did not affect the overall diversity of traits but reduced functional redundancy, underlined by a shift in functional identity towards assemblages dominated by pelagic detritivores. In contrast, river fish faunas experienced a decline in functional richness, paired with shifts in functional identity and a loss of fish species with extreme functions.

Conclusions The response to deforestation differed between streams and rivers, but it supports the hypothesis that deforestation is linked to functional changes in fish assemblages. By diminishing the range of the functions in rivers or by jeopardizing the redundancy of functions in streams, deforestation could severely hamper the functioning and stability of neotropical freshwater ecosystems.

Keywords eDNA, Traits, Functional space, Richness, Divergence, Evenness, Identity, Gold mining

Introduction

Ecosystems are facing increasing and unprecedented anthropogenic impacts that erode the diversity of biological communities (Barnosky et al. 2011). Quantifying biodiversity responses to anthropogenic disturbances is fundamental, as biodiversity maintains the functionality of ecosystems (Tilman et al. 2006; Naeem et al. 2012) and supports the multitude of ecosystem services vital for human societies (Cardinale et al. 2012).

Biodiversity is a multi-faceted concept, with each facet providing complementary information (Le

*Correspondence:
Isabel Cantera
isa_cantera@hotmail.com
[1] Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 26, 20133 Milan, Italy
[2] Laboratoire Evolution et Diversité Biologique, UMR5174 - Université Paul Sabatier, CNRS, IRD, 118 Route de Narbonne, 31062 Toulouse, France
[3] SPYGEN, Savoie Technolac - BP 274, 17 Rue du Lac Saint-André, 73375 Le Bourget-du-Lac Cedex, France
[4] HYDRECO, Laboratoire Environnement de Petit Saut, B.P 823, 97388 Kourou Cedex, French Guiana, France

Bagousse-Pinguet et al. 2019). Taxonomic diversity corresponds to the number of species occurring in a community, whereas the functional facet captures the variety of morphological, ecological, behavioral, and physiological traits among species within a community (Villéger et al. 2017). In the last decades, mismatches between taxonomic and functional diversities under human impacts pinpointed that these facets can respond differently to anthropogenic disturbances (Devictor et al. 2010; Su et al. 2021; Coutant et al. 2023). Functional diversity has been recognized as an appropriate and sensitive tool to assess the impact of anthropogenic activities on natural ecosystems, because functional traits mediate the interaction between an organism and its abiotic and biotic environment (Mouillot et al. 2013). Functional traits are thus more closely linked to ecosystem processes than taxonomic diversity (Loreau et al. 2001; Cadotte et al. 2011; Naeem et al. 2012; Mori et al. 2013). Indeed, functional changes were reported to be more pronounced than taxonomic changes as a result of disturbances, regardless of the ecosystems or taxa considered (Flynn et al. 2009). For instance, the introduction of non-native fish to rivers across the world over the past two centuries has resulted in functional changes ten times higher than taxonomic changes (Toussaint et al. 2018). Likewise, ocean acidification has led to functional diversity losses twice as high as taxonomic diversity losses in benthic marine communities (Teixidó et al. 2018). As a result, functional changes better relate alterations in community structure to changes in ecological processes that maintain ecosystem functions, representing a relevant tool to quantify the depth of human impacts on natural ecosystems. Determining how functional diversity responds to anthropogenic activities is thus essential for conservation.

The functional diversity of communities can be represented in a multidimensional space constructed by ordinating species based on trait distances and using multivariate analyses (Villéger et al. 2008). In this multidimensional space, axes correspond to functional traits or synthetic traits that summarize several raw traits. Hence, species are positioned according to their trait values within the functional space, and communities are represented in terms of the functional features of both the entire community and the component species (Mouillot et al. 2013). Within the multidimensional functional space, several indices describe the functional diversity of a given community based on the distribution of species in the functional space (see Villéger et al. 2008, 2010 and Mouillot et al. 2013 for more details):

i) Functional richness is the multidimensional volume occupied by the community within the global functional space. It represents the range of traits supported by the species co-occurring in a community.
ii) Functional divergence measures the degree of divergence of the species from the barycenter toward the edges of the functional space belonging to a community. It reflects the influence of species with the most extreme trait values in the functional space of a community.
iii) Functional evenness describes the internal structure of the functional space of a community and how traits are supported by the species within this space. It measures whether species are evenly distributed within the functional space (most of the traits have high redundancy) or packed in a specific location (ensuring redundancy for the traits represented by this location but leaving other traits without redundancy).
iv) Functional identity measures the average position of a community along each axis of the multidimensional space. It reflects the general patterns of traits supported by the species co-occurring in a community.

These indices provide different information about the functional diversity (amount and complexity) supported by a community. For instance, coral reef fish communities exhibit high trait diversity but low evenness, as species were packed into a few trait combinations, leaving the majority of traits without redundancy (Mouillot et al. 2014; D'agata et al. 2016). Similarly, the global freshwater fish fauna is strongly uneven but with limited divergence, as most species are concentrated toward the center of functional space. This indicates that the functional diversity of continental freshwater fish fauna is sustained by a few species with extreme functional traits, making regional functional diversity highly sensitive to the extinction of species with extreme functional traits (Su et al. 2019). Therefore, changes in species composition of communities due to human disturbances can affect differently the facets of functional structure according to the functional characteristics of the locally extirpated/introduced species (Villéger et al. 2010). For instance, the introduction of non-native species is known to increase functional richness by providing new traits to the communities, but it also increases functional divergence by reinforcing the influence of species with extreme traits, resulting in a global shift in the functional identity of communities (Toussaint et al. 2018).

While there is considerable knowledge about the multifaceted functional effects of species invasions, reports on the impact of environmental changes (e.g., deforestation and associated disturbances) on the functional structure of Amazonian faunas are limited (but see Leitão et al. (2018), for heavily deforested Brazilian streams). Yet, rivers and streams in the Amazonian region (*sensu lato,* including Guiana Shield and Amazon River drainage) host the most diverse freshwater fish fauna on earth (~20% of global fish species diversity, Lévêque et al. 2008). In addition, these ecosystems provide significant goods and services, with many local populations relying on rivers and streams for food acquisition and drinking water (Castello et al. 2013). Despite their high value, freshwater ecosystems in the Amazonian region have received little attention in terms of management compared to terrestrial ecosystems (Castello and Macedo 2016; Leal et al. 2020). Besides facing threats common to other freshwater ecosystems, such as deforestation and pollution from human settlements, damming, overharvesting, intensified agriculture and livestock (Vörösmarty et al. 2010; Carpenter et al. 2011), Amazonian streams and rivers are highly threatened by unprecedented levels of mining, logging, oil and gas extraction. These activities are polluting freshwater systems, altering physico-chemistry and disrupting hydrology and connectivity (Castello et al. 2013; Castello and Macedo 2016). It is crucial to define how the different facets of fish functional diversity in Amazonian rivers and streams respond to anthropogenic activities.

Figure 1A represents the functional structure of a hypothetical undisturbed community within the global functional space (constructed by ordinating all the species present in a set of sites according to their trait distances). The other panels compare undisturbed communities (blue) with disturbed ones (yellow) (Fig. 1B–D). We propose the following four non-exclusive

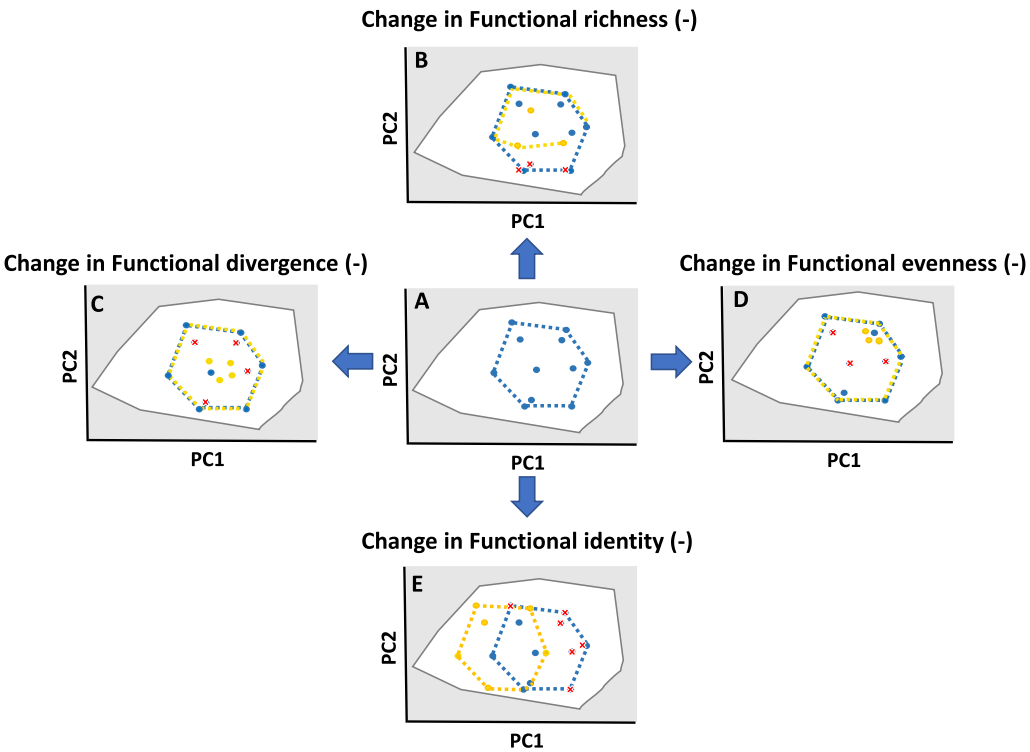

Fig. 1 Illustration of the potential human impacts on functional structure. The functional spaces of a undisturbed community (blue solid line, **A**) and disturbed ones (yellow dashed lines) are compared. The global functional space is represented by the white area. Species are represented with dots. Blue dots correspond to species that are not affected by the disturbance, red crosses represent species sensitive to disturbance and yellow dots indicate species favoured by the disturbance. Note that, in all cases, species richness remains constant between the undisturbed (blue) and the disturbed (yellow) communities. Four non-exclusive differences with the functional space of a hypothetical undisturbed community (**A**) are proposed. **B** Hypothesis i: lower functional richness due to the absence of species with extreme traits (and the presence of more generalist species located in the center of the functional space). **C** Hypothesis ii: lower functional divergence due to the presence of generalist species located toward the center. **D** Hypothesis iii: lower functional evenness due to higher redundancy of species favoured by disturbance and lower redundancy of species sensitive to the disturbance. **E** Hypothesis iv: different functional identity of the disturbed community due to the presence of species with distinct traits compared to the undisturbed community, causing a shift in the functional structure toward lower values of axis 1

hypotheses describing the impacts of deforestation on the functional structure of streams and rivers:

i) Disturbed communities should exhibit a lower range of traits (lower functional richness) compared to non-deforested ones (Fig. 1B).
ii) Disturbed communities should have lower functional divergence from the barycenter of the community's functional spaces due to a gain in generalist species located toward de center of the functional spaces (Fig. 1C).
iii) Disturbed communities should experience higher trait packing in some parts of the functional space compared to non-deforested ones, resulting in lower functional evenness in the distribution of the species within the functional space and leaving some traits without redundancy (Fig. 1D).
iv) Disturbed communities should harbour distinct functional traits compared to the non-deforested ones, resulting in different functional identity values along the axes (Fig. 1E).

We applied this framework to assess the impacts of deforestation on the functional structure of 99 freshwater fish communities inhabiting rivers (64 sites) and streams (35 sites) across French Guiana (Northern Amazonian region, Fig. 2). Local fish assemblages were inventoried using environmental DNA metabarcoding (eDNA). This method allows for efficient assembly of standardized fish community data for comprehensive studies without impacting the environment and has been proven effective in characterizing species-rich ecosystems, such as Guianese streams and rivers (Cilleros et al. 2019; Jerde et al. 2019; Cantera et al. 2019). We assessed stream and river communities separately to ensure environmental and faunistic homogeneity of the fish assemblages across sites.

Materials and methods

Sampling

From 2016 to 2018, a total of 99 sites were sampled during the dry season (September–November) across French Guiana (Fig. 2, Additional file 1: Table S1). The study area has a homogeneous equatorial climate and is covered by dense, uniform lowland primary rainforest (Hansen

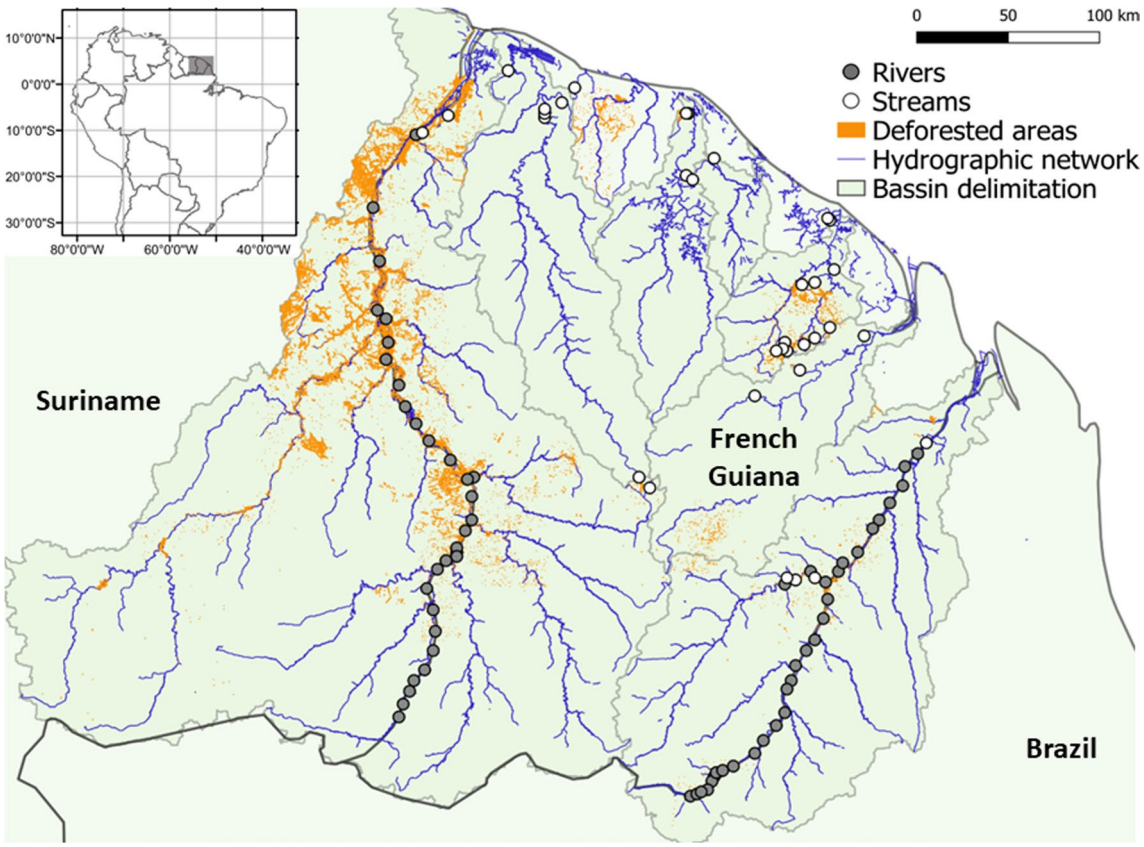

Fig. 2 Study area indicating the 99 fish sampling sites. Gray and white circles represent the sampling sites in rivers ($N = 64$ sites) and streams ($N = 35$ sites), respectively. The highlighted grey area in the inset map shows the location of the study area in South America

et al. 2019). The altitude spans from 0 to 860 m above sea level, and annual rainfall ranges from 2000 mm in the southwest to 3600 mm in the northeast. French Guiana is intersected by a dense river network, comprising seven large river basins. Within these basins, typical Amazonian freshwater fauna inhabit, including more than 400 described fish species that exhibit a wide array of forms (Planquette et al. 1996; Le Bail et al. 2012). These river basins share 50% of the species, while the remaining half consist of species endemic to specific basins (Le Bail et al. 2012). These distribution patterns stem from a mixture of different species pools arising from the intricate biogeographical history of the neotropical region (Cilleros et al. 2016) and Guineans basins (de Mérona et al. 2012). Four non-native freshwater species are established in French Guiana, but their distribution is still limited to a few coastal rivers (Brosse et al. 2021), and non-native species were not recorded in our study sites.

eDNA was filtered from the water at 64 river sites along the main channel and the large tributaries of the Maroni and Oyapock rivers and 35 stream sites across 8 river basins. The stream sites were less than 10 m wide and 1-m deep (Strahler orders 1–3), while river sites were wider than 20 m and deeper than 1 m (Strahler orders 4–8) (Strahler 1957). Such distinction between streams and rivers is frequently used to characterize these two environments (or freshwater ecosystems) for which the fauna and environmental conditions markedly differ (Dedieu et al. 2015; Allard et al. 2016; Cilleros et al. 2017). Sampling sites were selected to consider both undisturbed sites and sites under human disturbances, such as urbanization, agriculture, and gold mining.

Following the protocol of Cantera et al. (2019), we collected eDNA by filtering for 30 min per site one replicate for stream sites and two replicates for river sites. Our eDNA protocol was proved to need a lower sampling effort to adequately measure the site's species richness in streams than in rivers in the same region (Cantera et al. 2019), as the latter ecosystem hosts more species given that larger areas are expected to offer more niches and ecosystem space. One replicate detected, on average, 87% of the site's expected species richness in streams, while two replicates detected around 77% of the site's expected richness in rivers (Cantera et al. 2019). Moreover, the method was shown to provide similar or more complete inventories to those derived from gill-netting in large rivers within the study region (Cantera et al. 2019) and to describe local fish communities within a spatial signal comparable to that of capture-based methods describing fish communities over a few hundred metres (Cantera et al. 2022b).

A peristaltic pump (Vampire Sampler; Burkle GmbH, Bad Bellingen, Germany) and single-use tubing were used to pump the water into a single-use filtration capsule (VigiDNA, 0.45 µm; filtration surface 500 cm^2, SPYGEN, Le Bourget-du-Lac, France). The tubing input was placed a few centimetres below the water surface in zones with high water flow as recommended by Cilleros et al. (2019). Sampling was performed in turbulent areas with rapid hydromorphologic units to ensure optimal eDNA homogeneity throughout the water column. To avoid eDNA cross-contamination among sites, the operator remained on emerging rocks downstream from the filtration area. At the end of filtration, the capsule was emptied, filled with 80 mL CL1 preservation buffer (SPYGEN), and stored in the dark before the DNA extraction.

Laboratory procedures and bio-informatic analyses

The DNA extraction was performed using the protocol described in Pont et al. (2021) and the samples were tested for inhibition by qPCR following the protocol in Biggs et al. (2015). The DNA amplifications were performed in a final volume of 25 µL, including 1 U of AmpliTaq Gold DNA Polymerase (Applied Biosystems, Foster City, CA), 10 mM of Tris–HCl, 50 mM of KCl, 2.5 mM of $MgCl_2$, 0.2 mM of each dNTP, 0.2 µM of "teleo" primers (Valentini et al. 2016), 0.2 µg/µL bovine serum albumin (BSA; Roche Diagnostics, Basel, Switzerland) and 3 µL of DNA template. The "teleo" primers (Valentini et al. 2016) (forward: 3′-ACACCGCCCGTCACTCT-5′; reverse: 3′-CTTCCGGTACACTTACCATG-5′) were used as they efficiently discriminated local fish species (Cilleros et al. 2019; Cantera et al. 2019). Human blocking primer was added to the mixture for the "teleo" primers (5′-ACC CTCCTCAAGTATACTTCAAAGGAC-C3-3′) at final concentrations of 4 µM. Twelve PCR replicates were performed per field sample. The forward and reverse primer tags were identical within each PCR replicate. The PCR mixture was denatured at 95 °C for 10 min, followed by 50 cycles of 30 s at 95 °C, 30 s at 55 °C, and 1 min at 72 °C, and a final elongation step at 72 °C for 7 min. This step was conducted in a dedicated room for DNA amplification kept under negative air pressure and physically separated from the DNA extraction rooms under positive air pressure. The purified PCR products were pooled in equal volumes to achieve an expected sequencing depth of 500,000 reads per sample before DNA library preparation.

Sixteen libraries were prepared using the Metafast protocol, a PCR-free library protocol at Fasteris, Geneva, Switzerland (https://www.fasteris.com/metafast). Seven libraries were sequenced on an Illumina HiSeq 2500 (2×125 bp) (Illumina, San Diego, CA, USA) with a HiSeq SBS Kit v4 (Illumina) and nine were sequenced on a MiSeq (2×125 bp) (Illumina) with a MiSeq Flow Cell Kit Version3 (Illumina). Sequencing was performed

according to the manufacturer's instructions at Fasteris. Cantera et al. (2022a) found that the number of species between replicates sequenced on the same platform and those sequenced on different platforms did not differ in the river sites used here. Similarly, a previous study on 16S rRNA amplicon has shown that the samples were not influenced by the Illumina sequencing platform used (Caporaso et al. 2012).

To monitor for contaminants, 21 negative extraction controls were performed; one control was amplified twice. All of them were amplified and sequenced by the same methods as the samples and in parallel to them. For the negative extraction controls, 252 amplifications were prepared (21 negative controls). Twelve negative PCR controls (ultrapure water; 12 replicates) were amplified and sequenced in parallel to the samples. Thus, for the PCR negative controls, there were 144 amplifications.

The reference database from Cantera et al. (2022b) containing 265 Guianese fish species was used. The GenBank nucleotide database was consulted, but it contained little information on the Guianese fish species. The sequence reads were analysed with the OBITools package according to the protocol described by Valentini et al. (2016). Briefly, the forward and reverse reads were assembled with the *illuminapairedend* programme. The *ngsfilter* programme was then used to assign the sequences to each sample. A separate data set was created for each sample by splitting the original data set into several files with *obisplit*. Sequences shorter than 20 bp or occurring less than 10 times per sample were discarded. The *obiclean* program was used to identify amplicon sequence variants (ASVs) that have likely arisen due to PCR or sequencing errors. It uses the information of sequence counts and sequence similarities to classify whether a sequence is a variant ("internal") of a more abundant ("head") ASV (Boyer et al. 2016). Sequences labelled by the *obiclean* programme as "internal" and probably corresponding to PCR errors were discarded. After this step, we matched the ASV with the reference database to obtain the taxonomic assignation for each ASV. The *ecotag* programme was then used for the taxonomic assignment of molecular operational taxonomic units (MOTUs). The taxonomic assignments from *ecotag* were corrected to avoid overconfidence in assignments. Species-level assignments were validated only for $\geq 98\%$ sequence identity with the reference database. Sequences below this threshold were discarded.

Measuring deforestation gradients using GIS data

For each fish sampling site, we calculated the percentage of deforested surfaces upstream from each site. In freshwater systems, disturbances may accumulate because of the downstream transfer of matter and pollutants (Pringle 2001; Cantera et al. 2022a). Hence, the upstream sub-basin drainage network of each site was considered to measure deforestation. The sub-basins were delineated by applying a flow accumulation algorithm to the SRTM global 30 m digital elevation model (NASA 2013). For streams, upstream sub-basin areas were delineated at a distance of 0.5 km upstream from each sampling site, because deforestation occurred in the immediate vicinity of the sites, and none of the sites experienced deforestation farther than 0.5 km upstream from the site. For river sites, deforestation was much more extended over the sub-basin located upstream from the sites, and considering deforestation over an upstream distance of 30 km was found to be the appropriate spatial extent to measure deforestation impacts on fish diversity in the rivers sampled in this study with the same eDNA protocol (Cantera et al. 2022a).

At each sampling site, we summed upstream deforested surfaces from Landsat satellite image data sets. Forest loss surfaces were obtained from the Global Forest Change data set (Hansen et al. 2013), which identifies areas deforested between 2001 and 2017 on a 30 m spatial scale. To incorporate deforested areas before 2000, tree canopy cover data for that year were also used. Except for river courses, all pixels with $< 25\%$ canopy closure were regarded as deforested. Finally, surfaces deforested by gold mining activity in French Guiana, Suriname, and Northern Brazil were included (Rahm et al. 2015; WWF 2016). We merged those data sets to create an integrative disturbance variable of human-mediated environmental disturbances (including gold mining, logging, agriculture, and human settlements) that quantifies the percentages of deforested surfaces around the sampling sites. Reforestation was not considered here, because forest recovery following deforestation was rare due to a continuous and progressive spatial extension of human activities (Rahm et al. 2015). Moreover, in the sites where human disturbance stopped, forest recovery remained limited due to a drastic loss of soil fertility after forest removal. The absolute deforested surfaces are dependent on the surface area measured at each spatial extent (0.5 km for stream sites or 30 km for river sites), making the absolute value of deforestation dependent on the spatial extent considered. Similarly, within each spatial extent, the considered upstream area varies with the shape of the river, making again the absolute deforestation surface dependent on the area considered (Cantera et al. 2022a). For this reason, deforestation was calculated by summing the deforested surfaces located in the upstream sub-basin area delineated at a distance of 0.5 km (for stream sites) or 30 km (for river sites) upstream from each sampling site and divided by the upstream sub-basin area. All the spatial analyses were performed on ArcGIS 10.8.

Measuring functional indices

To measure the functional indices for each community, we assigned traits to the detected species using the most detailed morphological and ecological traits available. For the morphological traits, 9 measurements were made using side-view pictures collected over the past decade to compute 9 unitless ratios (hereafter, traits) reflecting food acquisition and locomotion (Villéger et al. 2017; Toussaint et al. 2018) (Additional file 2: Table S2). The morphological traits were measured for as many individuals as possible (1–20 depending on the species) and the averages of all measurements per species were used. Intraspecific variability in morphological traits was not considered, because a study using the same trait data set demonstrated that it was negligible compared to the among-species functional variation (Toussaint et al. 2018). The maximum body length of each species obtained from FishBase (www.fishbase.org) represented the maximum body size for the species and was regarded as a synthetic functional trait (Villéger et al. 2017). The qualitative traits, which are related to trophy, behavior (motility, territoriality and gregariousness), and habitat preference (substratum and position in the water column) (Additional file 2: Table S2), were selected and collected from FishBase (www.fishbase.org) and the literature (Planquette et al. 1996; Le Bail et al. 2000).

The 10 morphological traits (continuous) and the 6 ecological (categorical) traits were combined to build functional spaces. Gower's trait distances between species were calculated for each ecosystem. This parameter considers categorical and continuous traits, standardizes them, and handles missing data. The distance matrices were ordinated into multidimensional spaces by a principal coordinate analysis (PCoA), which generates coordinates for all species within the ordinations (i.e., global functional spaces). Based on the position of species within the multidimensional functional space of each ecosystem, four functional indices were calculated to describe the functional structure of fish communities (see Introduction) using the function multidimFD available online (http://villeger.sebastien.free.fr/Rscripts.html). See Villéger et al. (2008) and Mouillot et al. (2013) for more details. To calculate functional indices, the first three PCoA axes for streams and the first four PCoA axes for rivers were retained. This configuration maximized functional space quality (Maire et al. 2015) and minimized data loss, as sites must have more species than the number of axes selected to compute functional richness (the minimum number of species detected per site was 4 in streams and 30 in rivers). Functional richness, evenness and divergence indices range from 0 to 1. Higher values of the indices reflect higher volume occupation of the community and thus higher diversity of traits (Functional richness), greater regularity of species distribution (Functional evenness) within the functional space and higher divergence from the center of the functional space (Functional divergence). Trait composition was assessed using the functional identity index, which is the mean position of the community in each ordination axis and calculated as the average PCoA scores of the species present in a community. This index reflects trends on the identity of most common traits displayed by the all the species present in a community.

Data analysis

Linear Mixed Models were used to test if deforestation significantly affects the functional structure of fish communities. For both stream and river ecosystems, the position in the upstream–downstream gradient influences environmental conditions (Vannote et al. 1980). To test the effect of deforestation while controlling possible environmental variations within each ecosystem, we included the upstream–downstream gradient in the models using the log-transformed distance of the sampling site to the source in meters, considering that it increases from upstream to downstream. For each functional index (response variables), we built a specific model in which the upstream–downstream and deforestation gradients were scaled fixed variables. Basin identity was included as a random effect, to control for the regional differences in species taxonomic identity (Le Bail et al. 2012). The models were built using the *lmer* function from the lme4 package (Bates et al. 2015) in R (R Core Team 2023). Models were built separately for river and stream sites (see Introduction). The variance explained per model was calculated using a coefficient of determination (R^2) with the *r.squaredGLMM* function in the *MuMIn* package. Furthermore, we used Moran's *I* test to check if the residuals of our models did not show patterns of spatial autocorrelation (i.e., $P > 0.05$) using the *ape* package (Table 1). For the model of functional identity along the PCoA axis 2 in the rivers, the residuals exhibited significant spatial autocorrelation ($P < 0.001$). Hence, we controlled for this effect by including a spatial lag variable as a predictor in those models. The spatial lag variable was calculated as the average value of functional identity along the PCoA axis 2 in neighboring locations using the *spdep* package. Finally, to control for the potential impact of species richness on the relationships between the functional diversity and deforestation, we used null models to exclude the effects of taxonomic richness on each functional index (Gotelli and McCabe 2002). To this aim, observed values of each functional index were

Table 1 Results of the linear mixed models testing the effects of deforestation and the upstream–downstream gradient on the functional indices in stream and river ecosystems

Ecosystem	Functional index	Independent variables	Slope	*P*	R^2_M	R^2_C	Moran's I *P*
Streams	Functional richness	Deforestation gradient	− 0,02	0.481	0.39	0.39	0.3
		Upstream–downstream gradient	**0,11**	**< 0.001**			
	Functional divergence	Deforestation gradient	0,00	0.91	0.09	0.24	0.19
		Upstream–downstream gradient	− 0,01	0.076			
	Functional evenness	Deforestation gradient	**− 0,01**	**0.029**	0.14	0.14	0.17
		Upstream–downstream gradient	0,00	0.64			
	Functional identity along PCoA axis 1	Deforestation gradient	**− 0,01**	**0.002**	0.25	0.25	0.18
		Upstream–downstream gradient	0,00	0.947			
	Functional identity along PCoA axis 2	Deforestation gradient	− 0,01	0.303	0.18	0.18	0.55
		Upstream–downstream gradient	**0,01**	**0.019**			
	Functional identity along PCoA axis 3	Deforestation gradient	0,00	0.269	0.09	0.09	0.25
		Upstream–downstream gradient	− 0,01	0.155			
Rivers	Functional richness	Deforestation gradient	**− 0,08**	**< 0.001**	0.53	0.54	0.5
		Upstream–downstream gradient	0,00	0.722			
	Functional divergence	Deforestation gradient	**− 0,01**	**0.013**	0.12	0.2	0.1
		Upstream–downstream gradient	**0,01**	**0.008**			
	Functional evenness	Deforestation gradient	0,00	0.791	0	0.66	0.26
		Upstream–downstream gradient	0,00	0.766			
	Functional identity along PCoA axis 1	Deforestation gradient	**0,01**	**< 0.001**	0.09	0.64	0.61
		Upstream–downstream gradient	0,00	0.107			
	Functional identity along PCoA axis 2	Deforestation gradient	0,00	0.9	0.36	0.36	< 0.001
		Upstream–downstream gradient	0,00	0.4			
	Functional identity along PCoA axis 3	Deforestation gradient	**0,00**	**0.043**	0.68	0.68	0.62
		Upstream–downstream gradient	**0,01**	**< 0.001**			

For each index (response variable), a specific mixed model was built with basin identity included as a random effect. Marginal R^2 (R^2_M) accounts for the variance explained only by fixed variables, while conditional R^2 (R^2_C) accounts for the variance explained by the entire model. Significant effects ($P < 0.05$) were highlighted in bold. Moran's I *P* values indicate if the residuals of the models show patterns of spatial autocorrelation (i.e., $P < 0.05$)

compared to the ones obtained by randomizing the matrix 999 times while keeping the number of detected taxa per community fixed. We then calculated standardized effect size (SES) values as the difference between the observed values and the mean of randomly generated values divided by the standard deviation of the 999 null values. We ran the same models with standardized effects sizes (SES) of the functional indices, as response variables (Additional file 2: Table S5). If we observed significant effects of deforestation on a functional index but not for its respective SES, it means that the effect of deforestation is mainly due to changes on species richness.

To define how deforestation impacts on functional indices translates into changes in trait composition and identify the traits that were significantly affected by deforestation, functional spaces were constructed separately for stream and river ecosystems. Communities were located within those functional spaces according to their functional identity values along the key PCoA axes. Then, traits were fitted into the PCoA ordination using the function *envifit* from the vegan package to identify correlation strengths (measured using a determination coefficient, R^2) between traits and the ordination axes. Traits having high R^2 correspond to strong predictors of the ordination axis. In addition, *P* values were calculated by comparing if the observed R^2 values were significantly higher than permuted R^2 values, based on 999 random permutations of the data. To quantify the contribution of the continuous traits, they were transformed onto vectors with its direction according to the correlation type with the axes (positive or negative) and the length of the vectors proportional to the strength of the correlation between the axis and the trait (R^2 values). For categorical variables, average ordination scores were computed for each category of the traits to locate the different categories within the functional spaces.

Results

At stream sites, the percentage of deforested surfaces ranged from 0% to 77% (mean = 17%, SE = 4.1), while at river sites, it was in the range of 0–6.6% (mean = 1%, SE = 0.2) (Additional file 1: Table S1). eDNA sampling

allowed the detection of 184 fish species across the 99 sampling sites, with 119 species and 158 species detected at stream and river sites, respectively (Additional files 3 and 4: Tables S3 and S4). Species richness per site ranged from 4 to 56 (mean = 26, SE = 2) and from 30 to 90 (mean = 57, SE = 1.8) for stream and river sites, respectively.

The fish communities of both streams and rivers showed functional changes along the upstream–downstream gradient, with significant increases in functional richness ($P < 0.001$, Table 1) observed for stream fish faunas. This increase on functional richness was linked with an addition of traits due to increases in the number of species, as the SES values of functional richness were not significantly linked with the upstream–downstream gradient ($P = 0.4$, Additional file 2: Table S5). In rivers, functional changes were mainly attributed to increases in functional divergence toward the downstream areas ($P = 0.008$, Table 1), even after controlling for species richness difference between sites ($P = 0.002$, Additional file 2: Table S5).

In streams, deforestation was significantly associated with decreases in the functional evenness of fish communities ($P = 0.03$), regardless of species richness changes ($P = 0.03$, Additional file 2: Table S5), while functional richness and functional divergence were not significantly affected by deforestation (Table 1, Fig. 3). Nevertheless, after controlling for species richness differences between sites, the SES values of functional richness decreased with increasing deforested surfaces (Additional file 2: Table S5), meaning that species richness differences are hiding a pervasive effect of deforestation on functional diversity.

In rivers, deforestation was significantly associated with decreases in functional richness ($P < 0.001$) and, to a lower extent, with decreases in functional divergence ($P = 0.01$) of fish communities (Table 1, Fig. 3). After accounting for species richness differences, the decrease in functional richness with deforestation remained evident, while the decrease of functional divergence might be mostly related to decreases in species richness (Additional file 2: Table S5).

The trait composition in fish communities, as illustrated by the functional identity of communities on the axes of the PCoAs, showed shifts linked to deforestation in both streams and rivers. For stream sites, deforestation had a significant effect on functional identity values along the first axis of the PCoA ($P = 0.002$, slope = − 0.014), whereas the site position in the upstream–downstream gradient affected fish community position on the second axis of the PCoA (Table 1). Decreasing scores along the PCoA1 axis with deforestation were independent from species richness changes, while increasing scores along

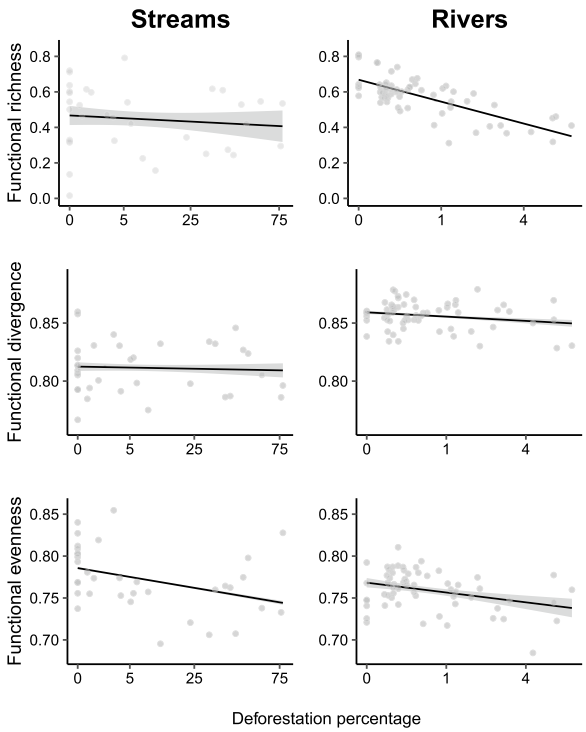

Fig. 3 Effects of the percentage of deforested surfaces on functional richness, functional evenness and functional divergence in stream (left, $N = 35$) and river ecosystems (right, $N = 64$). Fitted values of the mixed models are shown with solid lines (see Table 1 for significant effects). Grey shades represent the 95% confidence intervals. For each index (response variable), a specific mixed model was built with basin identity included as a random effect

the PCoA2 of downstream communities were linked with changes on species richness (Additional file 2: Table S5). As shown in Fig. 4A, fish assemblages from deforested sites experienced a functional shift toward negative values on the PCoA1 axis. These functional changes were significantly linked to most morphological and ecological traits, as all the traits except maximum body length and pectoral fin size were significantly related to the ordination (Table 2). The first axis of the functional space primarily reflected differences between benthic and pelagic species (Fig. 4C). Benthic species associated with hard substrates and having a sedentary behavior had positive PCoA1 values, whereas pelagic and benthopelagic species with mobile, gregarious, and non-territorial behavior had negative PCoA1 values. Among the morphological variables, eye vertical position, and body elongation were highly and positively correlated with the PCoA1, while the eye size was highly and negatively correlated with this axis (Fig. 4E). Highly deforested communities (negative PCoA1 scores, Fig. 4) tend to have fewer elongated species with relatively small eyes positioned toward the top of the head. These species mainly belong to the

Table 2 Contribution of each trait to the axes of the functional spaces constructed using Principal Components Analysis on 16 traits for stream and river fish communities

Trait	Category	Rivers			Streams			
		P	R^2	Axis 1	*P*	R^2	Axis 1	Axis 3
Relative eye size (Ed/Hd)	NA	**0.001**	**0.32**	− 1	**0.001**	**0.31**	− 0.82	− 0.58
Relative barbel length (Bbl/Bl)	NA	**0.01**	**0.11**	0.76	0.09	0.04	0.93	− 0.36
Oral gape position (Mo/Bd)	NA	**0.001**	**0.56**	− 0.73	**0.001**	**0.14**	− 1	0.09
Relative maxillary length (Jl/Hd)	NA	**0.001**	**0.23**	− 0.5	**0.01**	**0.08**	− 0.42	0.91
Eye vertical position (Eh/Bd)	NA	**0.001**	**0.71**	0.98	**0.001**	**0.6**	1	0.01
Pectoral fin vertical position (PFi/Bd)	NA	**0.001**	**0.53**	0.01	**0.001**	**0.16**	0.91	− 0.42
Pectoral fin size (PFl/Bl)	NA	0.48	0.02	0.54	**0.001**	**0.12**	0.53	− 0.85
Caudal peduncle throttling (CFd/CPd)	NA	**0.001**	**0.3**	− 0.25	**0.001**	**0.2**	− 0.88	0.47
Body elongation (Bl/Bd)	NA	**0.001**	**0.3**	0.94	**0.001**	**0.17**	0.88	0.47
Maximum body length	NA	0.14	0.05	0.57	**0.001**	**0.22**	0.08	1
Preferred substrate	Hard	**0.001**	**0.22**	0.11	**0.001**	**0.22**	0.07	0.05
Preferred substrate	None			− 0.07			− 0.08	0.06
Preferred substrate	Soft			− 0.07			− 0.04	− 0.09
Motility	Migratory	**0.001**	**0.4**	− 0.06	**0.001**	**0.4**	− 0.09	0.06
Motility	Mobile			− 0.16			− 0.15	0.02
Motility	Sedentary			0.08			0.12	0
Gregariousness	Solitary	**0.001**	**0.35**	0.04	**0.001**	**0.35**	0.07	0.05
Gregariousness	Gregarious			− 0.08			− 0.1	− 0.02
Water column position	Benthic	**0.001**	**0.64**	0.13	**0.001**	**0.64**	0.11	0.01
Water column position	Benthopelagic			− 0.15			− 0.14	0.02
Water column position	Demersal			0.05			0.12	0.01
Water column position	Pelagic			− 0.16			− 0.16	− 0.03
Territorial	No	**0.001**	**0.34**	− 0.05	**0.001**	**0.34**	− 0.07	0.01
Territorial	Yes			0.06			0.16	0
Guild	Carnivore	**0.001**	**0.43**	0.1	**0.001**	**0.43**	0.08	0.03
Guild	Detritivore			− 0.17			− 0.17	− 0.05
Guild	Herbivore			0.18			0.07	0.07
Guild	Invertivore			− 0.07			− 0.07	− 0.05
Guild	Omnivore			0.06			0.08	0.06
Guild	Piscivore			− 0.03			− 0.03	0.09

Only the axes significantly related to deforestation were included (i.e., PCoA 1 for streams and PCoA 1 and PCoA 3 for rivers, see results). The determination coefficients (R^2) of the correlation between each trait and the ordination, as well as the direction cosines of the continuous variables and the mean position of categorical traits on the two first axes of the PCoA are also provided. The *P* values indicate the significance of R^2, which were calculated by randomly permuting the data ($N = 999$ permutations) and determine if the observed R^2 were higher than the permuted R^2 values

(See figure on next page.)

Fig. 4 Functional spaces constructed with the axes significantly impacted by deforestation in streams ($N = 35$; **A**, **C**, **E**) and rivers ($N = 64$; **B**, **D**, **F**) (Table 1). **A**, **B** Location of the fish communities within the functional space based on functional identity values along PCoA axes; deforestation intensity at each site is indicated by varying shades of blue to brown. **C**, **D** Mean average position of each category of qualitative traits, where the mean position represents the average of PCoA scores for all species belonging to a given category. **E**, **F** Correlation between morphological continuous traits and PCoA axes; line segments indicate the direction and the strength of the correlation. Only traits that are significantly related to the ordination are shown (Table 2). See Table 2 for the meaning of abbreviations of the functional traits and Additional file 2: Table S2 for the ecological significance of the traits. The triangles correspond to the position of the species within the functional space (streams: 119 species and rivers: 158 species)

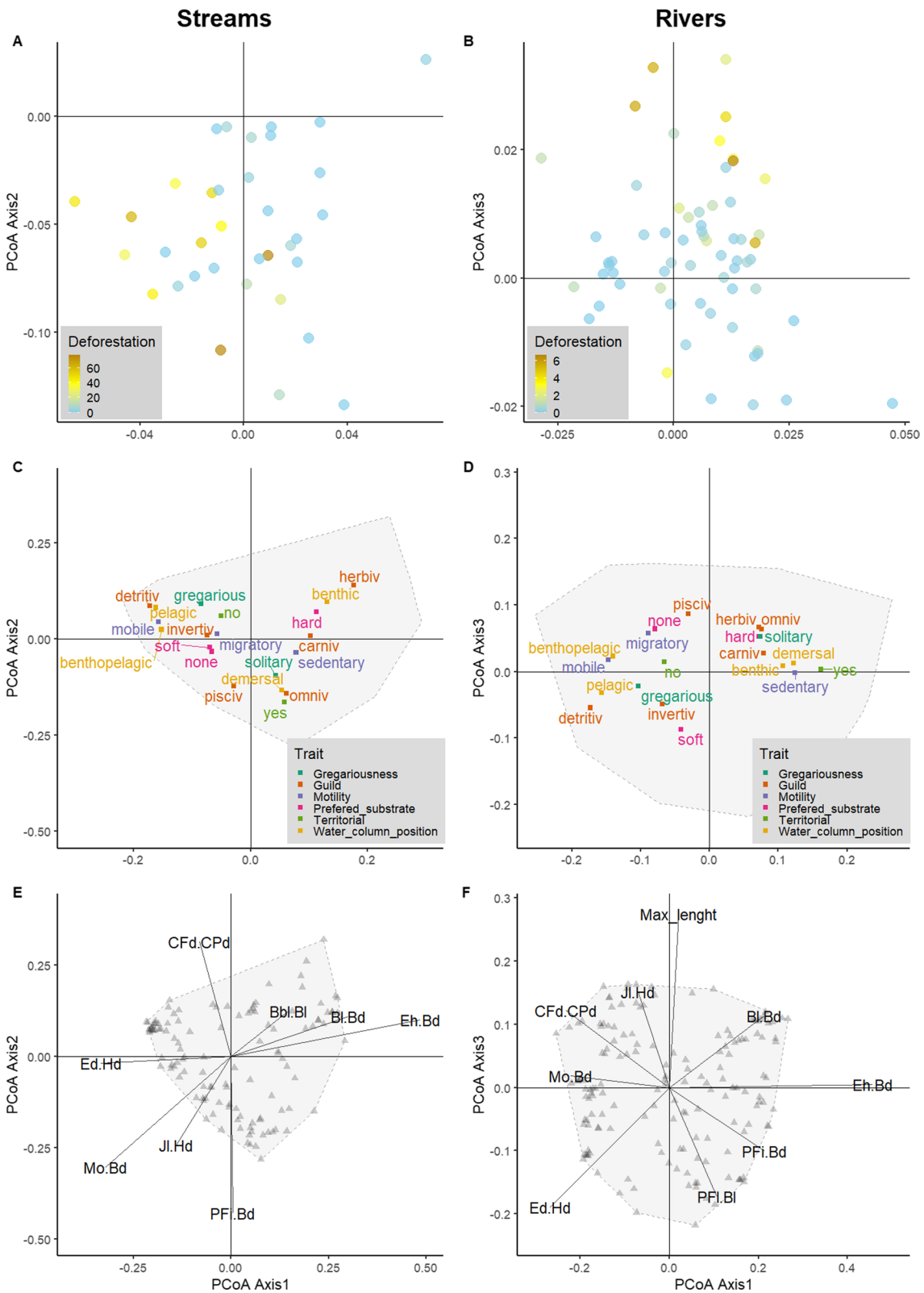

Fig. 4 (See legend on previous page.)

Loricariidae family, which are benthic algae feeders. Furthermore, under high deforestation levels, communities were characterized by a dominance of pelagic detritivores (Additional file 5: Table S6).

For river sites, deforestation was significantly associated with the functional identity of fish communities along the PCoA1 axis and, to a lower extent, along the PCoA3 axis (Table 1). As the intensity of deforestation increased, functional identity values increased along those axes (Fig. 4B, Table 1). Since deforestation was not related to the PCoA2 axis, the functional space of river communities was represented by the PCoA1 and PCoA3 axes to relate changes in functional identity induced by deforestation with traits (Fig. 4B, D, F). The effect of deforestation along the PCoA3 axis was coupled with functional changes due to the upstream–downstream gradient ($P=0.043$, Table 1) and resulted mostly from species richness changes, as the effect of deforestation on SES values was not significant ($P=0.27$, Additional file 2: Table S5). In opposition, the deforestation effect on the PCoA1 axis was independent from the upstream–downstream gradient ($P=0.11$, Table 1) and from species richness changes ($P<0.001$, Additional file 2: Table S5). All the traits except relative barbel length were significantly related to the ordination (Table 2). Similar to streams, the PCoA1 axis was mainly characterized by differences between benthic and pelagic species (Fig. 4D). Benthic species associated with hard substrates and having sedentary, solitary, and territorial behavior had positive PCoA1 values, whereas pelagic and benthopelagic species with mobile, gregarious, and non-territorial behavior had negative PCoA1 values. The most discriminant morphological variables in the ordination were eye vertical position, oral gape position and maximum body length (Fig. 4F). Highly deforested river sites were characterized by a lack of pelagic and mobile species that feed on detritus and invertebrates, but also by an over-representation of large fish species that are piscivorous, herbivorous, or omnivorous compared to non-deforested sites (Additional file 6: Table S7).

Discussion

Amazonian rivers and streams are highly diverse but are facing multiple and increasing human pressures that are affecting their biodiversity (Castello et al. 2013). Here, we showed that anthropogenic disturbances in French Guiana are modifying the functional diversity of freshwater fish communities. These disturbances affect not only the amount of functional traits but also their identity and the internal structure of the functional space. Following Mouillot et al. (2013), we hypothesized that the communities disturbed by deforestation face harsh conditions that filter out some functions. These disturbed communities should exhibit more ecologically similar traits than undisturbed ones, leading to a decline in functional richness, an over-representation of generalist species at the expense of extreme functional strategies (decline in functional divergence) and a packing of species toward a few functions (decline in functional evenness) due to an overall shift of functional composition toward advantageous attributes in disturbed environments (effects on functional identity). While not all four facets were consistently sensitive to deforestation, our observations in both streams and rivers fitted with our predictions for at least two out of the four facets, but the functional facets affected by deforestation differed between streams and rivers.

In streams, deforestation had no significant impact on overall trait diversity (functional richness) and did not increase the ratio between generalist and specialized species (no effect in functional divergence). However, we detected a decline of overall trait diversity when controlling for species richness difference between sites. This indicates a net loss in traits due to deforestation in the richest sites. Despite these observed effects in overall functional richness, and although deforestation strength can be important in small streams (> 30% of our sites experienced > 20% of upstream deforestation), functional redundancy within assemblages still ensures streams against net losses in traits. This resilience occurs, because the most impacted traits also tend to be the richest in species within stream communities (see Fig. 4E). Nonetheless, abrupt negative responses to deforestation could arise once biotic insurance is exhausted, as reported by Brejão et al. (2018) for Amazonian fish communities subjected to deforestation strengths exceeding 20%. In addition, in disturbed sites we reported a shift toward distinct traits compared to those encountered in undisturbed sites. This change in the functional identity of fish communities inhabiting disturbed stream sites confirms our hypothesis iv (see Fig. 1F). It indicates a shift from communities dominated by benthic species toward communities dominated by pelagic detritivores, probably because pelagic species are more mobile than benthic species and can thus move between disturbed and undisturbed areas, without being permanently constrained to the former. A similar trend was observed in marine fish communities, where pelagic species are less impacted by global warming than benthic species, because pelagic species can actively seek areas with optimal thermal regimes (McLean et al. 2019). In our stream study sites, deforestation was mainly due to gold mining, which is known to drastically affect the physical structure of stream bottoms through reductions in bottom complexity and bed stability (Hammond et al. 2007; Leitão et al. 2018). This

disproportionately affects species associated with the benthic compartment, causing a decline in catfish species from the Loricariidae family that feed on benthic algae (Allard et al. 2016). Moreover, logging and gold mining were reported to increase the turbidity and fine particle siltation in streams (Hammond et al. 2007; Brosse et al. 2011; Dedieu et al. 2014), negatively impacting algal growth (Tudesque et al. 2012) and reducing food availability for algae feeders. Therefore, the anthropogenic activities assessed here are strengthening environmental filters related to food and physical habitat availability (Cantera et al. 2023), thereby explaining the shift in trait composition along the deforestation gradient. Furthermore, the shift in trait dominance was associated with a decline in functional evenness. This means that species are disproportionally packed in zones of the functional space related to the pelagic compartment and the detritivore feeding guild, whereas other traits are still present but are less redundant among species, thereby reducing ecosystem insurance and making these traits vulnerable to further local species extirpations (Yachi and Loreau 1999). Consequently, the functional alterations reported here for disturbed streams deserve to be considered as an early warning of potentially more drastic functional changes if deforestation strengthens.

River sites experienced lower levels of deforestation intensity than streams (from 0% to 6.6%, mean = 1%), with multiple small sized deforested areas scattered throughout the river basins. As shown by Cantera et al. (2022a), deforestation impacts the fish fauna over long distances (up to 30 km) and local fish faunas are linked to the deforested surfaces scattered from the vicinity of the site to 30 km upstream. Despite reduced and scattered deforested surfaces, the functional richness of fish assemblages in deforested sites is negatively affected, with an average loss of more than 20% compared to sites with minimal deforestation (Cantera et al. 2022a). Such net loss in functional traits is paired with a decline in functional divergence, meaning that extreme functional strategies are the most impacted by deforestation. Extreme strategies are poorly redundant in freshwater fishes (Su et al. 2019), explaining why the local loss of a few species with extreme functional traits can lead to marked declines in functional richness. Nonetheless, contrary to streams, we did not find direct significant effects of deforestation on the functional evenness of river fish communities, but this can be related with the differences in species richness between sites, as when controlling for richness differences, functional evenness showed significant declines in deforested sites. Therefore, deforestation affects not only the internal structure of the functional space (decrease in functional evenness) but also targets the boundaries of community's functional space (decrease in functional richness and divergence). This observation reflects that deforestation effects in rivers lead to the complete disappearance of ecological strategies supported by functionally unique species. Those species correspond to benthic species feeding on detritus and invertebrates that are probably negatively affected by the siltation and turbidity generated by the deforestation associated with gold mining activities. Finally, small sized river fish species appeared more sensitive to deforestation than large species, a trend that converges with the functional vulnerability in neotropical fishes, where small fish species are among the most threatened, possibly because they have low dispersal abilities and are often endemic from restricted areas (Carmona et al. 2021). In contrast, large species are more mobile, widespread and occur in a wide diversity of habitats, which might explain the potentially lower sensitivity to disturbances. This point still deserves to be considered with caution, because most of the deforestation reported here is related to the gold mining rush experienced by the Guiana shield over the last decades (Hammond et al. 2007; Dezécache et al. 2017). Consequently, there might be a time lag between the disturbance and the local disappeareance of large species with longer lifespans than small species. A particular attention should be given to the future of Guianese fish faunas that might experience further functional changes through deforestation.

Study limitations

Fish diversity was inventoried in 99 sites across French Guiana, encompassing different levels of deforestation. eDNA metabarcoding was employed to gather broad-scale fish inventories that would be challenging to assemble using traditional methods. The eDNA approach has emerged as a powerful tool to efficiently characterize freshwater communities, particularly in remote and difficult to sample areas (Zinger et al. 2020; Yao et al. 2022). The method has been shown to provide realistic fish inventories and to be more sensitive than the traditional capture and observation methods, as shown by a recent meta-analysis (Fediajevaite et al. 2021), but also by field measurements on the study area (Cilleros et al. 2019; Cantera et al. 2019). Still, some challenges remain, such as the uncertainty of the spatial representation of the method (Yao et al. 2022). eDNA can be transported downstream, especially in large and rapidly flowing rivers (Pont et al. 2018). The exact measure of distance detection is complex to infer in natural conditions (Barnes et al. 2014). While broad distance detections were suggested (Deiner et al. 2016), most studies characterizing eDNA spatial patterns of aquatic taxa showed shorter distances (Jane et al. 2015;

Civade et al. 2016; Nakagawa et al. 2018; Cantera et al. 2022b; Jo and Yamanaka 2022). For instance, a recent experimental cage study showed that eDNA concentrations become strongly reduced 2 km downstream from the emission source (Van Driessche et al. 2022). Specifically, in the rivers sampled in this study, eDNA provided fish spatial patterns comparable to those of local samples using capture methods (Cantera et al. 2022b).

Using an extensive and comprehensive local reference database allowed to attain species-level identifications instead of MOTUs or wider taxonomic assignations, which is often the case in eDNA studies in under-studied areas, such as neotropical rainforests (Zinger et al. 2020). This enabled us to assign 16 morphological and categorical traits to the detected species. However, the eDNA approach does not provide local measurements of morphological characteristics, such as body length and weight, which are susceptible to vary among populations of the same species in response to environmental conditions. Accounting for such intraspecific variation in functional traits will provide unique insights on the effects of deforestation on functional diversity (Violle et al. 2012), such as local morphological adaptations to deforestation. Achieving this goal would require to couple eDNA collection with in situ specimen collection, which is currently challenging. Furthermore, intraspecific haplotype variability can also be inferred from eDNA (Yao et al. 2022), which can be used to assess genetic diversity impacts of deforestation, allowing to get population and community insights from the same water sample.

Conclusions

Overall, the functional structure of freshwater fish communities in the studied sites was affected by deforestation that changed the functional identity of disturbed fish communities in both stream and river sites, validating one of our hypotheses (hypothesis iv, Fig. 1E). Nevertheless, the deforestation effects on the other facets of functional diversity of fish communities differed between rivers and streams. The functional richness and divergence of fish communities were significantly eroded by deforestation in river sites (validating hypotheses i and ii for rivers, Fig. 1B, C) but not in stream sites. In contrast, deforestation significantly affected the functional evenness of stream communities (validating hypothesis iii for streams, Fig. 1D), resulting in stream communities, where benthic herbivore species are under-represented compared to undisturbed sites. Our findings strongly support that part of the vulnerable traits supported by the species located out of the core of the functional space are declining in the deforested sites, leaving the related functions unaccomplished or jeopardized by a decline in functional redundancy. Such functional changes could severely hamper the functioning and stability of ecosystems (Naeem 1998; Pillar et al. 2013). Moreover, we here show that considering the multiple facets of functional diversity allows to detect deep functional changes induced by human disturbances. We, therefore, appeal considering not only the overall range of functional traits (i.e., functional richness) but also the position of communities in the functional space (functional identity) and the internal structure of the functional spaces (functional evenness and divergence) to obtain a comprehensive image of the functional consequences of human disturbances. We thus advocate that human impacts on the functional structure of communities should be assessed in a multifaceted way to better inform management and conservation targets.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-023-00463-8.

Additional file 1: Table S1. Site information with geographical locations, basin and ecosystem membership, the number of detected taxa for each site, sampling date, deforestation percentages and abiotic variables measured at each site.

Additional file 2: Contains Tables S2 and S5. Table S2. Morphological and ecological traits and measures used to assess functional diversity. Their corresponding functions are indicated. See Su et al. (2019), Toussaint et al. (2016) and Villéger et al. (2010) for details on morphological measures. **Table S5.** Results of the linear mixed models testing the effects of deforestation and the upstream-downstream gradient on the Standardized Effect Size (SES) values calculated for each index (see Methods). For each response variable, a specific mixed model was built with basin identity included as a random effect. Marginal R^2 (R^2_M) accounts for the variance explained only by fixed variables, while conditional R^2 (R^2_C) accounts for the variance explained by the entire model. Significant effects (P <0.05) are highlighted in bold.

Additional file 3: Table S3. Matrix of detected species by site for river sites.

Additional file 4: Table S4. Matrix of detected species by site for stream sites.

Additional file 5: Table S6. Coordinates of the stream fish species on the PCoA axes.

Additional file 6: Table S7. Coordinates of the river fish species on the PCoA axes.

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Author contributions

IC and SB conceived the ideas, designed methodology and led the writing of the manuscript; SB, IC, JM, and RV collected the data; IC, analyzed the data; CJ performed the GIS analyses. AV, and TD, conducted the laboratory work and bioinformatic analyses. All authors contributed critically to the drafts.

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Availability of data and materials
The data generated in this study are provided in Additional files 1, 3 and 4 (Tables S1, S3 and S4) and under accession codes in archived repositories for raw sequencing data. For samples collected in rivers, the data can be found at https://doi.org/10.5061/dryad.pvmcvdnmr and for samples collected in streams, the data can be found at https://doi.org/10.6084/m9.figshare.13129703.v1. The site labels in Table S1 can be used to extract the runs used for this study.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
A.V. and T.D. are research scientists in a private company specialized in the use of eDNA for biodiversity monitoring, with some patent technologies (SPYGEN). The remaining authors declare no competing interests.

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