

Research



Cite this article: Cantera I, Jézéquel C, Dejean T, Muriene J, Vigouroux R, Valentini A, Brosse S. 2023 Deforestation strengthens environmental filtering and competitive exclusion in Neotropical streams and rivers. *Proc. R. Soc. B* **290**: 20231130. <https://doi.org/10.1098/rspb.2023.1130>

Received: 23 May 2023

Accepted: 16 August 2023

Subject Category:

Ecology

Subject Areas:

ecology

Keywords:

functional diversity, assembly rules, tropical fish, null models, environmental DNA

Author for correspondence:

Isabel Cantera

e-mail: isa_cantera@hotmail.com

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6806558>.

Deforestation strengthens environmental filtering and competitive exclusion in Neotropical streams and rivers

Isabel Cantera^{1,2}, Céline Jézéquel², Tony Dejean³, Jérôme Muriene², Régis Vigouroux⁴, Alice Valentini³ and Sébastien Brosse²

¹Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 26, 20133 Milano, Italy

²Laboratoire Evolution et Diversité Biologique, UMR5174, Université Paul Sabatier, CNRS, IRD, 118 route de Narbonne, 31062 Toulouse, France

³SPYGEN, 17 rue du Lac Saint-André Savoie Technolac, BP 274, 73375 Le Bourget-du-Lac, France

⁴HYDRECO, Laboratoire Environnement de Petit Saut, BP 823, 97388 Kourou Cedex, French Guiana

IC, 0000-0003-3161-1878; AV, 0000-0001-5829-5479; SB, 0000-0002-3659-8177

Understanding how anthropization impacts the assembly of species onto communities is pivotal to go beyond the observation of biodiversity changes and reveal how disturbances affect the environmental and biotic processes shaping biodiversity. Here, we propose a simple framework to measure the assembly processes underpinning functional convergence/divergence patterns. We applied this framework to northern Amazonian fish communities inventoried using environmental DNA in 35 stream sites and 64 river sites. We found that the harsh and unstable environmental conditions characterizing streams conveyed communities towards functional convergence, by filtering traits related to food acquisition and, to a lower extent, dispersal. Such environmental filtering also strengthened competition by excluding species having less competitive food acquisition traits. Instead, random species assembly was more marked in river communities, which may be explained by the downstream position of rivers facilitating the dispersion of species. Although fish assembly rules differed between streams and river fish communities, anthropogenic disturbances reduced functional divergence in both ecosystems, with a reinforcement of both environmental filtering and weaker competitor exclusion. This may explain the substantial biodiversity alterations observed under slight deforestation levels in Neotropical freshwater ecosystems and underlines their vulnerability to anthropic disturbances that not only affect species persistence but also modify community assembly rules.

1. Introduction

Global changes are currently reshaping plant and animal assemblages throughout the world, making local communities a result of both natural and anthropogenic gradients. Understanding how anthropization impacts the assembly of species onto communities is thus pivotal to go beyond the observation of biodiversity changes.

Community structure results from a hierarchical filter in which species are progressively filtered from a regional pool by both deterministic [1] and stochastic processes [2], acting from regional to local spatial scales. First, regional variables (e.g. connectivity, the size of the regional species pool) and regional-scale processes (e.g. random colonization events, dispersal limitation) mainly determine the species' capacity to arrive in a community [3,4]. Then, candidate species are selected by environmental filters based on their ability to establish and persist given the local abiotic constraints. Finally, biotic interactions determine which species can coexist among the species capable of enduring the abiotic constraints. Those deterministic processes are expected

to shape predictable patterns of trait diversity in co-occurring species within a given community (i.e. functional diversity) [4,5]. The influence of those processes can be measured by the degree of deviance of the observed functional diversity in a local community from null expectations based on a potential pool of species (i.e. functional patterns under random species assembly). Hence, the strength of the processes will be reflected in the magnitude of functional divergence or functional convergence from random patterns. Functional divergence reflects that locally coexisting species are more functionally dissimilar than expected randomly. This pattern may arise from the competitive exclusion of species with similar ecological strategies leading to limiting similarity through niche differentiation [6]. Conversely, functional convergence occurs when coexisting species are more functionally similar than expected randomly, due to specific traits being selected over others. This pattern can be shaped by environmental filtering, which retains species sharing the same traits that make them adapted to the abiotic constraints in a given site, or by the competitive exclusion of species with traits associated with low competitive ability for the limiting resources [4,7]. Therefore, biotic interactions lead to species coexistence either because species are functionally dissimilar (functional divergence due to limiting similarity) or because they are functionally similar (functional convergence due to weaker competitor exclusion). The foregoing assembly rules operate simultaneously within a community but at different spatial scales [4,5,8]. Competition for resources is restricted to the spatial scale of individual home ranges, as interactions among all species are unlikely at broader spatial scales, where the environmental filtering of unsuitable traits occurs. Defining the type and/or strength of assembly processes requires defining the spatial scale at which processes should be tested, and therefore, determining the appropriate potential pool from which species are selected to create random communities [5,9]. Measuring environmental filtering strength must consider a regional pool of species able to thrive in very different environmental conditions and may have very different traits. By contrast, the detection of biotic interactions may consider a species pool based on species membership in a specific ecosystem, to exclude abiotic constraints [8,10].

Assembly rules simultaneously shape communities, but their relative importance varies along environmental gradients [11,12], particularly gradients of harshness. For instance, in plants and bees, environmental filtering is higher in high-altitude areas due to harsh environmental conditions compared to lower-altitude areas [12,13]. Progressive changes in the type and/or intensity of the processes shaping communities might occur along anthropogenic gradients. Through an expected loss of species, functional diversity can decrease more than expected under a random selection of the extirpated species. Consequently, anthropization may induce functional convergence [14–16] by filtering out species with similar traits, either due to a regional reinforcement of environmental filtering or to a local weaker competitor exclusion [4]. By contrast, disturbance can drive functional divergence between species by promoting limiting similarity [17].

The role of each assembly process varies across ecosystems [11] and, thus, how they are impacted by anthropization may also differ among ecosystems. Freshwater systems are hierarchical networks influenced by directional connectivity, integrating processes across multiple temporal and spatial

scales [18,19]. Because of this complexity, they are considered macro-systems comprising a series of connected and interacting ecosystems [18]. Streams are small entities located in the upstream parts of the hydrological network. They are isolated, strongly influenced by abiotic conditions (which are highly variable), and have severe hydrological regimes [20,21]. By contrast, large rivers exhibit larger environmental stability, habitat size and complexity [22]. The relative importance of processes shaping communities in these ecosystems may vary, as the abiotic differences between streams and rivers shape different diversity patterns of the aquatic fauna [23,24]. The network position hypothesis stipulates that stream communities are mainly assembled by environmental filtering [3], excluding functions not adapted to those harsh and unstable environments [25]. In opposition, river communities are less influenced by abiotic conditions and more influenced by stochastic processes [3,26]. Furthermore, weaker competitive exclusion may dominate in the harsh conditions of streams, while river conditions may promote limiting similarity. For instance, fish communities in Brazilian streams exhibited significant functional convergence, whereas functional divergence was found in river communities [27]. However, the processes underlying those patterns were not investigated. Besides integrating different potential species pools to elucidate the assembly rules across spatial scales, understanding how assembly processes vary along anthropization gradients needs to consider separately each ecosystem.

Amazonian streams and rivers host the most diverse freshwater fish fauna (*ca* 20% of global fish species diversity [28]) and provide significant goods and services [29]. Assessing how human impacts affect the assembly of aquatic communities in the region is highly important, as they are facing unprecedented levels of deforestation due to increasing agriculture, mining, and urbanization [29]. These activities are altering the hydrology and physico-chemical conditions of streams and rivers [29–32], consequently affecting the species composition [33–35], as well as taxonomic and functional diversities [32,35,36] of fish communities. However, the extent to which these biodiversity alterations are related to assembly rules remains unassessed. This study aims to define if the assembly processes underpinning convergence/divergence patterns of functional diversity in fish communities differ between streams and rivers (hereafter called ecosystem types) and vary along a deforestation gradient. Fish communities were sampled in 99 sites (64 belonging to rivers and 35 belonging to streams) across eight river basins in the northern Amazonian region (Guiana Shield; figure 1) using environmental DNA (eDNA) metabarcoding. This method has proven to be efficient and reliable in characterizing local fish communities in both streams and rivers in this region [36–40]. For each community, functional diversity was computed using morphological and ecological traits (electronic supplementary material, table S1), and the convergence/divergence of this diversity from null models was measured using standardized effect sizes (SES). This measure compares the functional diversity of sampled communities to that of communities randomly assembled from a species pool representing the regional fauna, which includes different environmental conditions (regional species pool), or the regional pool of species being able to persist in a specific environment (or ecosystem type), according to the investigated assembly process. We investigated environmental filtering by comparing observed communities to communities simulated

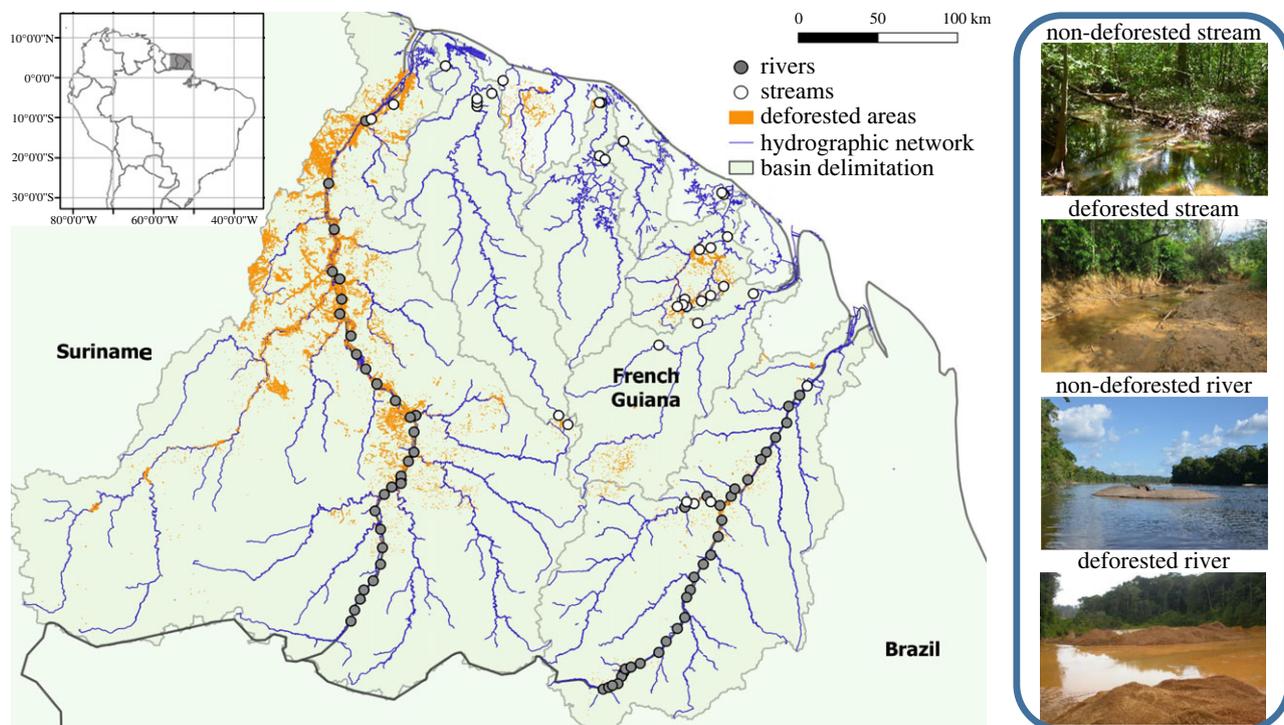


Figure 1. Study area indicating the 99 fish sampling sites. The grey and white circles indicate the sampling sites in streams ($n = 35$) and rivers ($n = 64$), respectively. The highlighted grey area in the inset map locates the study area in South America. Pictures illustrate non-deforested and deforested stream and river sites.

from a random selection of species from the entire species pool, including both stream and river species (hereafter called 'regional species pool'; table 1). In opposition, divergence/convergence patterns were assessed separately for each ecosystem, thus controlling environmental variability, to disentangle biotic processes (limiting similarity and weaker competitive exclusion). For this, communities were simulated from a random selection of species from either stream or river species pools (hereafter called 'ecosystem species pools'; table 1). Following this framework (see Material and methods), we first defined the governing processes in each ecosystem. Given the harsh conditions in streams, we expect (1) higher functional convergence in streams compared to rivers, due to both stronger environmental filtering and stronger weaker competitor exclusion (table 1). Then, we assessed how the specific processes of each ecosystem respond to deforestation. Here, we expect (2) functional convergence to increase with deforestation, driven by stronger environmental filtering and stronger weaker competitor exclusion, with deforestation effects being more marked in streams than in rivers, given that the conditions are harsher (table 1). Finally, within the same community, some traits can exhibit functional divergence while others functional convergence and patterns may remain undetected when multiple traits are combined [8,41]. Therefore, we assessed assembly processes by calculating functional diversity with all traits together (overall), and separately for traits related to three ecological functions: food acquisition, habitat use and dispersal (electronic supplementary material, table S1).

2. Material and methods

(a) Environmental DNA sampling

From 2016 to 2018, 99 sites were sampled during the dry season (September–November) across French Guiana (figure 1; electronic

supplementary material, table S2). Located in northeastern Amazonia *sensu lato* (including the Guiana Shield and the Amazon River drainage), the study area has a homogeneous equatorial climate and is covered by dense, uniform lowland primary rainforest [42]. The altitude is in the range of 0–860 m a.s.l. and annual rainfall ranges from 3600 mm in the northeast to 2000 mm in the southwest. eDNA was collected from water samples at 64 river sites along the main channel and the large tributaries of the Maroni and Oyapock rivers, and 35 stream sites across eight 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) [43]. Such distinction between stream and river sites is frequently used to characterize these two environments (or freshwater ecosystems) for which the fauna and environmental conditions markedly differ [34,44,45]. Sampling sites were selected to consider both undisturbed sites and sites under human disturbances such as urbanization, agriculture and gold-mining.

Following the protocol in Cantera *et al.* [37], we collected eDNA by filtering water for 30 min per site with one replicate for stream sites and two replicates for river sites. With this protocol in the same region, one replicate detected, on average, 87% of the site's expected species richness in streams, while, in rivers, two replicates detected around 77% of the site's richness. Moreover, the method provides similar or more complete inventories to those derived from gill-netting in the study region [37] and describes local fish communities within a spatial signal comparable to that of capture-based methods describing communities over a few hundred metres [38]. Details on eDNA collection, extraction, amplification with 'teleo' primers [46], bioinformatic analyses and taxonomic assignment using the reference database from Cantera *et al.* [38] (containing 265 Guianese fish species) are in the electronic supplementary material and followed the same protocol used by Cantera *et al.* [36,38].

(b) Measuring deforestation gradients using GIS data

For each fish sampling site, we calculated the percentage of deforested surfaces upstream from each site. In freshwater

Table 1. Theoretical framework for relating functional deviance from null models to assembly processes shaping communities. For each community, SES values were calculated by comparing observed functional diversity to that simulated by random assembly from a species pool, which varies according to the investigated process. Environmental filtering was assessed by simulating communities from a random selection of species from the entire species pool, including both stream and river species (regional pool). Limiting similarity and weaker competitor exclusion were assessed by simulating communities from either stream or river species pools (ecosystem pools).

process	species pool	pattern	hypotheses
environmental filtering (EF)	regional	functional convergence (SES <0)	(1) $EF_{\text{streams}} > EF_{\text{rivers}}$ (2) EF increases with deforestation
limiting similarity (LS)	ecosystem	functional divergence (SES >0)	(1) $LS_{\text{streams}} < LS_{\text{rivers}}$ (2) LS decreases with deforestation
weaker competitor exclusion (WE)	ecosystem	functional convergence (SES <0)	(1) $WE_{\text{streams}} > WE_{\text{rivers}}$ (2) WE increases with deforestation

systems, disturbances may accumulate because of the downstream transfer of matter and pollutants [36,47]. 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 [48]. For streams, upstream sub-basin areas were delineated at a distance of 0.5 km upstream from each sampling site because deforestation occurred near 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 [36].

At each site, we summed upstream deforested surfaces from Landsat satellite image datasets. Forest loss surfaces were obtained from the Global Forest Change dataset [49], 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. The deforestation before 2000 was limited (128 km²), accounting for 15.3% of the total deforested surfaces on the study area (833 km²) and mainly attributed to the gold rush that began between 1995 and 2000. Except for river courses, all pixels with less than 25% canopy closure were regarded as deforested. Finally, surfaces deforested by gold-mining activity in French Guiana, Suriname and northern Brazil were included [50,51]. We merged those datasets 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 [51]. Moreover, in the sites where human disturbance stopped, forest recovery remained limited due 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 [36]. 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 streams) or 30 km (for rivers) upstream from each sampling site and divided by the upstream sub-basin area. All the spatial analyses were performed on ArcGIS 10.8.

(c) Measuring functional diversity

Functional diversity captures the variety of morphological, ecological, behavioural and physiological traits among species within a community [52]. To measure the functional diversity of each community, we assigned traits to the detected species. We used the most detailed morphological and ecological traits available. For the morphological traits, nine measurements were made using side-view pictures collected over the past decade to compute nine unitless ratios (hereafter, traits) reflecting food acquisition and locomotion [52,53] (electronic supplementary material, table S1). The morphological traits (presenting correlation coefficients lower than 0.5; electronic supplementary material, figure S1) 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 dataset demonstrated that it was negligible compared to the among-species functional variation [53]. The maximum body length of each species obtained from FishBase represented the maximum body size for the species and was regarded as a synthetic functional trait [52]. We used qualitative traits related to trophy, behaviour (territoriality, gregariousness and motility), and habitat preference (substratum and position in the water column). Those traits were selected (electronic supplementary material, table S1) and collected from FishBase (www.fishbase.org) and the literature [54].

First, the 10 morphological traits (continuous) and the six ecological (categorical) traits were combined to build functional spaces and assess the ‘overall functional diversity’. Gower’s functional distances between species were calculated combining the species of both ecosystems (for the null model using the regional species pool) and for each ecosystem separately (for the null models using ecosystem pools). This parameter considers categorical and continuous traits, standardizes them, and handles missing data. The three distance matrices were ordinated into multi-dimensional spaces by a principal coordinate analysis (PCoA), which generates coordinates for all species within global functional spaces. To measure functional diversity, we used the ‘functional richness’ index [55]. The first three PCoA axes for streams and the first four PCoA axes for rivers were retained. This configuration maximized functional space quality [56] 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 that we found was 4 for streams and 30 for rivers). The resulting measure is the convex hull volume occupied by co-occurring species at each site in the functional space and is in the range of 0–1. Higher values reflect high volume occupation and, therefore, high functional diversity. Besides calculating the overall functional diversity for each community (combining the 16 available traits; see electronic

supplementary material, table S1), we also aggregated traits according to three ecological functions (food acquisition, habitat use, and dispersal; electronic supplementary material, table S1) and used the same approach to calculate functional diversity independently for each ecological functions.

(d) Null models to assess ecological processes

Three null models having specific species pools were used to measure, for each community, the degree of functional convergence/divergence of the observed functional diversity from random expectations [57]. First, to assess environmental filtering strength, we compared the observed functional diversity to the one simulated from a random sample of species from the regional species pool (including stream and river species). Then, two null models were used to distinguish between limiting similarity and weaker competitor exclusion. One compared the observed functional diversity of each stream site with the one simulated from a random sample of species from the stream species pool and the other compared the observed functional diversity of each river site with the one simulated from a random sample of species from the river species pool. This procedure was applied to the overall functional diversity calculated using all traits but also for each of the three considered ecological functions (food acquisition, habitat use, and dispersal; see electronic supplementary material, table S1, for details). This led the development of a total of 3 null models considering all traits, and 3 null models for each of the 3 ecological functions.

For the resulting 12 null models, the number of randomly selected species was equal to the observed species number in each site, and the species identities were randomized 999 times for all the species (regional pool) or considering separately stream and river fish species (ecosystem pools). By doing so, 999 null values of functional diversity were generated per site. Then, we compared observed functional diversity to the one expected by chance by calculating SES values per site. SES values correspond to the difference between the observed functional diversity and the mean of the 999 simulated values of functional diversity divided by the standard deviation of the 999 null values. Negative SES values indicate that the functional diversity is lower than expected by chance given the observed taxonomic diversity (functional convergence). By contrast, positive SES values indicate that functional diversity is higher than expected under random assembly (functional divergence). SES values not only indicate the direction of deviance (convergence/divergence) but also quantify the magnitude of the deviance.

(e) Statistical analyses

First, we assessed if SES values were outside of the 'neutral interval' ($-1.75 < \text{SES} < 1.75$), to describe the pattern of functional convergence/divergence specific of each community. Then, to retrieve the general trend of each trait group in each ecosystem, we used two-sided *t*-tests to estimate whether the mean of the SES values was significantly different from zero. If the mean was significantly different from zero, we assumed that the patterns tended to deviate from random expectations [8,10]. Overall significant convergence or divergence was assumed when the mean of the SES values was below or above zero, respectively. Finally, to compare convergence/divergence patterns between ecosystems, we used *t*-tests to assess if the SES values were statistically significant between the stream and riverine communities, for each group of traits.

Linear mixed models were used to test the effects of the percentage of deforested surfaces on the SES calculated for each ecosystem. For both stream and river ecosystems, the position in the upstream–downstream gradient influences environmental conditions [19]. To test the effect of deforestation while controlling possible environmental variations within each ecosystem,

we included the upstream–downstream gradient in the model using the log-transformed distance of the sampling site to the source in metres, considering that it increases from upstream to downstream. This variable correlated with other abiotic variables (electronic supplementary material, figure S2), suggesting that it is a synthetic variable representing different abiotic variations from upstream to downstream [19]. For each group of traits and each ecosystem, we used the SES values as response variables to build a specific model in which the upstream–downstream and deforestation gradients were scaled fixed independent variables. Basin identity was included as a random effect, to control for differences in fish species between river basins. Model validity was assessed by testing the normal distribution of the residuals with Shapiro's tests. The models were built using the *lmer* function from the *lme4* package in R (R Core Team 2016). Rivers and stream sites were considered separately. The variance explained per model was calculated using a coefficient of determination (R^2) with the *r.squaredGLMM* function in the *MuMIn* package of R.

3. Results

Overall, 184 fish species were detected; 158 and 119 species were detected across river and stream sites, respectively (see electronic supplementary material, tables S3 and S4, for species matrices per site). Species richness per site ranged from 4 to 56 (mean = 26, s.e. = 1.9) in stream sites and from 30 to 90 (mean = 57, s.e. = 1.6) in river sites. We did not find traits for *Hartiella longicauda* (detected in two stream sites); thus it was not included to measure functional diversity.

(a) Comparing functional diversity with random assembly from the regional pool of species

When measuring functional deviance from random expectations simulated from the regional species pool, significant functional convergence (SES values < -1.75) was observed in 26% of stream communities for overall functional diversity, while functional deviance was not observed in any river community. For food acquisition traits, significant functional convergence was observed in 11% of stream communities and 5% of river communities. For those two trait groups, no community showed significant functional divergence. Conversely, significant functional divergence was found in 48% of stream communities and 11% of river communities for habitat use traits, as well as in 5% of river communities for dispersal traits. No stream community displayed significant functional deviance for dispersal traits. Overall functional diversity and traits related to dispersal showed positive means of SES values (figure 2a,d), but they did not significantly differ from zero in river communities (overall: $t = 1.6$, d.f. = 63, $p = 0.1$; dispersal: $t = 2$, d.f. = 63, $p = 0.05$). However, they significantly deviated from zero in streams (overall: $t = -6$, d.f. = 34, $p < 0.001$; dispersal: $t = -5.2$, d.f. = 34, $p < 0.001$). Considering food acquisition and habitat use traits, the mean of SES values significantly differed from zero in both river (food acquisition: $t = -11$, d.f. = 63, $p < 0.001$; habitat use: $t = 8.3$, d.f. = 63, $p < 0.001$) and stream communities (food acquisition: $t = -10.5$, d.f. = 34, $p < 0.001$; habitat use: $t = 9$, d.f. = 34, $p < 0.001$) (figure 2b,c). In general, SES means differed significantly between ecosystems ($p < 0.02$; figure 2a,d). Streams exhibited consistent average deviation from 0 in both directions, depending on trait types. Specifically, the mean of SES values for habitat use traits

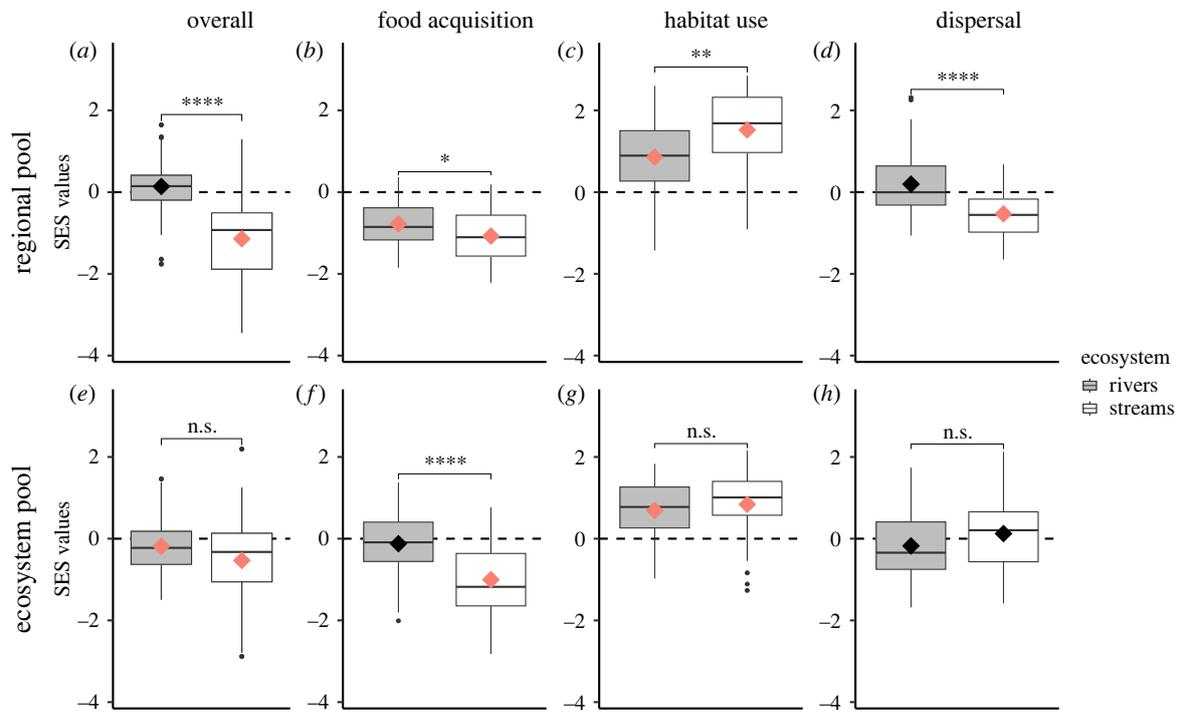


Figure 2. Ecosystem effect on SES comparing the observed functional diversity of a given community to the one obtained from random communities assembled from the regional (*a,b,c,d*) or ecosystem pools of species (*e,f,g,h*). See Material and methods for details. SES values were calculated for overall functional diversity (*a,e*), traits related to food acquisition (*b,f*), habitat use (*c,g*) and dispersal capacities (*d,h*). The SES sign indicates if the functional diversity is lower (SES < 0) or higher (SES > 0) than expected by chance, given the observed richness. Red and black diamonds indicate means differing significantly and not from zero, respectively (two-sided *t*-tests). Black dashed lines represent SES = 0. Statistically significant differences between stream and river communities were assessed using *t*-tests. *, ** and *** indicate statistical significance at the $p < 0.05$, $p < 0.01$, and $p < 0.001$ levels, respectively. 'ns' represents results that are not statistically significant.

was higher in streams than in rivers, whereas the means SES of the other types of traits were smaller in streams.

In streams, the percentage of deforested surfaces had a significant effect on SES values calculated for overall functional diversity and traits related to food acquisition and habitat use (table 2). Traits related to habitat use tended to functional divergence in streams with low deforestation levels, whereas highly deforested streams were more randomly assembled (figure 3*a*). Additionally, the extent of functional convergence increased along the deforestation gradient for overall functional diversity and traits related to food acquisition (figure 3*a*). In rivers, deforestation only had significant effects on the SES values calculated with traits related to habitat use (table 2), with a trend of decreasing functional divergence along the gradient (figure 3*b*).

The pattern towards functional divergence on habitat use traits characterizing streams at regional scales increased along the upstream–downstream gradient in streams (table 2; electronic supplementary material, figure S3*a*). For rivers, we found the opposite pattern (table 2; electronic supplementary material, figure S3*b*).

(b) Comparing functional diversity with random assembly from the ecosystem pool of species

Measuring functional deviance from random expectations independently for stream and river communities revealed significant functional convergence in 14% of stream communities for overall functional diversity, as well as for food acquisition traits in 20% of stream communities and 3% of river communities. Significant functional divergence was

observed in 9% of stream communities and 2% of river communities for habitat use traits, as well as in 6% of stream communities for dispersal-related traits. No significant deviance was obtained for river communities on overall functional diversity and for dispersal traits. For overall functional diversity and traits related to food acquisition, the means of SES values were negative (figure 2*e,f*). These means were not significantly different (or only marginally different) from zero for river communities (overall: $t = -2.2$, d.f. = 63, $p = 0.03$; food acquisition: $t = -1.3$, d.f. = 63, $p = 0.18$), while they differed significantly from zero in streams (overall: $t = -2.8$, d.f. = 34, $p = 0.007$; food acquisition: $t = -7.2$, d.f. = 34, $p < 0.001$). For both habitats, SES values for habitat use traits had positive means and differed significantly from zero (streams: $t = 5.7$, d.f. = 34, $p < 0.001$; rivers: $t = 8.2$, d.f. = 63, $p < 0.001$; figure 2*g*). Finally, the means of SES values calculated with dispersal traits were not significantly different from zero in both ecosystems (streams: $t = 0.8$, d.f. = 34, $p = 0.45$; rivers: $t = -1.8$, d.f. = 63, $p = 0.07$) (figure 2*h*). In general, SES values did not differ significantly between streams and river communities ($p > 0.1$; figure 2), except for food acquisition, where stream communities had on average significantly lower SES values ($p < 0.0001$; figure 2*f*).

In streams, we observed significant negative effects of the percentage of upstream deforestation on SES values calculated for overall functional diversity, food acquisition and habitat use traits (table 2). Traits related to habitat use tended to exhibit functional divergence at communities under low deforestation levels, while they tend to be close to random assembly at high deforestation levels (figure 3*c*). Traits related to food acquisition always exhibited functional

Table 2. Results of the linear mixed models testing the effects of upstream–downstream and deforestation gradients on SES values in each ecosystem for overall traits, traits related to food acquisition, habitat use and dispersal capacities. SES values were calculated by comparing observed functional diversity to that obtained from random communities assembled from either (a) the regional species pool or (b) the ecosystem species pool (see Material and methods). For each response variable, a specific mixed model was built with basin identity included as a random effect. Marginal R^2 (R_M^2) accounts for the variance explained only by fixed variables, while conditional R^2 (R_C^2) accounts for the variance explained by the entire model. Significant effects (p -value < 0.05) are highlighted in italics.

ecosystem	function	R_C^2	R_M^2	independent variables	slope	p -value
(a) regional species pool						
streams	overall (all traits together)	0.33	0.33	deforestation gradient	<i>−0.65</i>	<i>0.00</i>
				upstream–downstream gradient	0.05	0.78
	food acquisition	0.22	0.18	deforestation gradient	<i>−0.25</i>	<i>0.01</i>
				upstream–downstream gradient	0.07	0.49
	habitat use	0.33	0.33	deforestation gradient	<i>−0.45</i>	<i>0.00</i>
				upstream–downstream gradient	<i>0.35</i>	<i>0.02</i>
	dispersal	0.39	0.06	deforestation gradient	0.06	0.57
				upstream–downstream gradient	0.16	0.13
rivers	overall (all traits together)	0.41	0.04	deforestation gradient	<i>−0.18</i>	<i>0.06</i>
				upstream–downstream gradient	0.07	0.48
	food acquisition	0.07	0.05	deforestation gradient	<i>−0.14</i>	<i>0.11</i>
				upstream–downstream gradient	0.03	0.76
	habitat use	0.35	0.17	deforestation gradient	<i>0.23</i>	<i>0.03</i>
				upstream–downstream gradient	<i>−0.43</i>	<i>0.00</i>
	dispersal	0.35	0.02	deforestation gradient	<i>−0.12</i>	<i>0.26</i>
				upstream–downstream gradient	0.11	0.33
(b) ecosystem species pool						
streams	overall (all traits together)	0.2	0.2	deforestation gradient	<i>−0.48</i>	<i>0.01</i>
				upstream–downstream gradient	0.17	0.34
	food acquisition	0.25	0.18	deforestation gradient	<i>−0.33</i>	<i>0.02</i>
				upstream–downstream gradient	0.11	0.39
	habitat use	0.33	0.33	deforestation gradient	<i>−0.44</i>	<i>0.00</i>
				upstream–downstream gradient	0.24	0.07
	dispersal	0.5	0.09	deforestation gradient	0.10	0.49
				upstream–downstream gradient	<i>0.30</i>	<i>0.05</i>
rivers	overall (all traits together)	0.1	0.1	deforestation gradient	<i>−0.21</i>	<i>0.04</i>
				upstream–downstream gradient	<i>−0.01</i>	<i>0.89</i>
	food acquisition	0.19	0.02	deforestation gradient	<i>−0.02</i>	<i>0.85</i>
				upstream–downstream gradient	<i>−0.10</i>	<i>0.38</i>
	habitat use	0.43	0.18	deforestation gradient	<i>−0.07</i>	<i>0.35</i>
				upstream–downstream gradient	<i>−0.24</i>	<i>0.00</i>
	dispersal	0.38	0.11	deforestation gradient	0.06	0.56
				upstream–downstream gradient	<i>0.22</i>	<i>0.03</i>

convergence, but this convergence is reinforced under high deforestation levels (figure 3c). For overall functional diversity, communities shifted from random assembly at low deforestation levels to functional convergence in highly deforested sites, levelling the extent of functional convergence of food acquisition traits (figure 3c). In river communities, deforestation was only related to SES calculated for overall functional diversity (table 2), reflecting a

shift from prevailing random patterns at low deforestation levels to a trend towards functional convergence at high deforestation levels (figure 3d).

Along the upstream–downstream gradient in streams, functional convergence decreased for all trait categories, but the effect was only significant for traits related to dispersal (table 2; electronic supplementary material, figure S3c). In river communities, the upstream–downstream gradient had

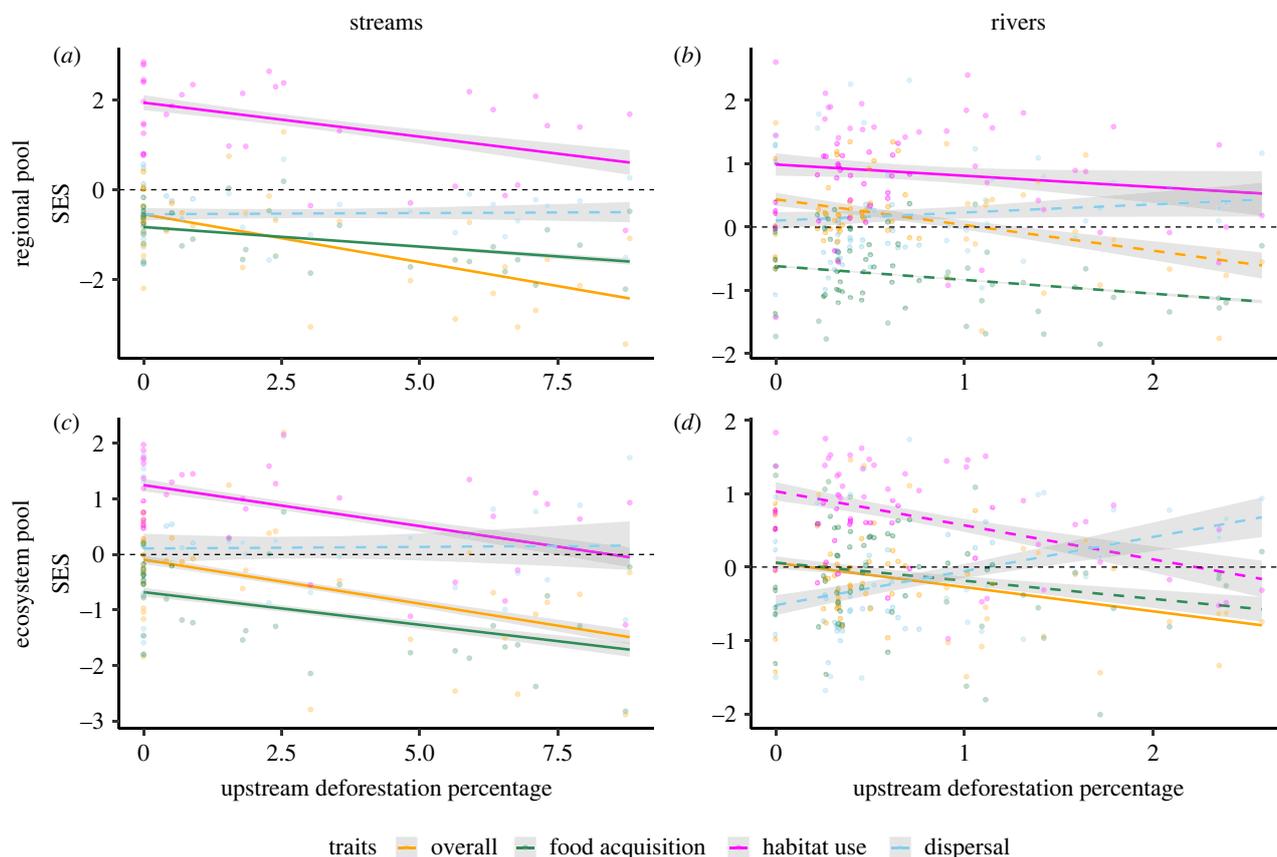


Figure 3. Effects of the percentage of deforested surfaces on SES values of functional diversity for each group of traits in (a,c) stream communities ($n = 35$) and (b,d) river communities ($n = 64$). SES values were calculated by comparing observed functional diversity with the one obtained from random assembly from either the ecosystem or regional pools (see Material and methods) for all the traits together (overall functional diversity), traits related to food acquisition, habitat use and dispersal capacities. Fitted values of the mixed models (see Material and methods) are shown with solid and dashed lines indicating significant and non-significant effects, respectively. The shaded areas represent the 95% confidence intervals. The dashed horizontal black line indicates $SES = 0$. For a better representation, the percentage of upstream deforestation was square-root-transformed; raw values ranged from 0 to 77.4% for streams and 0 to 6.6% for river sites. See electronic supplementary material, figures S4 and S5, for details.

significant but opposite effects on SES values calculated with habitat use and dispersal traits (table 2). Dispersal traits tend to shift from functional convergence in upstream rivers to no deviance from null expectations in downstream rivers (electronic supplementary material, figure S3d). Conversely, habitat use traits tended to shift from functional divergence to random assembly along this gradient (electronic supplementary material, figure S3d).

4. Discussion

(a) Assembly rules in stream and river ecosystems

The quantification of environmental filtering strength in streams by comparing observed functional diversity to the one expected under a random assembly of the regional species pool did not provide complete support for the network position hypothesis. Despite obtaining significant trends towards functional convergence (mean SES being negative and significantly different from zero for all trait groups, except habitat use), most communities had functional diversity values similar to the ones under random assembly. This pattern contrasts with the one known in temperate rivers and might be underlined by dispersal limitation prevailing over environmental filtering in both stream [58] and river [33] fish communities in the Amazonian region, where natural environmental conditions poorly explain species

composition [33,45]. Nevertheless, for overall functional diversity, stream communities deviated from randomness on more occasions than river communities (26% of communities versus 0%); and comparing SES values between ecosystems revealed trends towards a higher functional convergence in streams than in rivers. Compared to rivers, environmental filtering still plays a considerable role in some streams, particularly those located in mountainous areas characterized by harsh environmental conditions [59–62]. Specifically, we only obtained negative SES values for traits related to food acquisition and, to a lesser extent, dispersal (figure 2b,d), which suggests that species may be mostly filtered based on those traits. Mountain stream ecosystems host few fish species [45], often sharing traits such as small body size and low dispersal abilities. For instance, mountain stream fishes share morphological attributes providing them the ability to pass rapids and waterfalls (e.g. low caudal peduncle throttling) but reducing their swimming endurance [52], thus making them poor dispersers. However, these stream faunas still belong to distinct lineages, including benthic algae browsers feeding on rocks (e.g. *Lithoxius* sp.) and woods (e.g. *Guianancistrus* sp.), benthic (*Characidium* sp.) and surface (*Bryconamericus* sp.) insectivores belonging to the Crenuchidae and Characidae families, and even sand dwelling Siluriforms (*Ituglanis* sp.). This can explain the trend towards a higher divergence for habitat use traits compared to river faunas, a tendency more pronounced in stream

sites located downstream of the drainage basins (electronic supplementary material, figure S3a).

Comparing observed functional diversity to the one expected from a random assembly of species belonging to either streams or rivers showed that trends of functional deviance did not significantly differ between rivers and streams, except for traits related to food acquisition. For those traits, streams tended to exhibit, on average, more negative SES values; with 20% of communities deviating significantly from random assembly. This reflects a more marked tendency to functional convergence, which may result from a higher effect of competitive exclusion of weaker competitors for food resources than in rivers. Streams are known to be less productive and offer less diverse resources than rivers [19,63], making feeding competition harsher and favouring species with highly competitive traits for feeding. This process appears to be particularly marked in most upstream streams where habitat harshness and isolation reinforce exclusion effects, especially on dispersal-related traits (table 2; electronic supplementary material, figure S3c). Given their isolated condition, upstream streams are particularly suited to priority effects (i.e. first colonizers dominate a given site and limit the establishment of other species that could also survive in the site [64]). Consequently, priority effects can also explain the convergence on dispersal-related traits in upstream streams, as the dominant species can exclude other species, regardless of their trait similarity. Exploring priority effects requires abundance data to assess positive frequency dependence patterns, but eDNA metabarcoding is still limited in providing relevant abundance data [65]. Further studies might, therefore, investigate the potential of eDNA to provide fish abundance [66,67], which will provide a finer assessment of community assembly, functional structure and the impact of human activities [68,69].

Our study suggests that the harsh and unstable conditions characterizing streams may filter traits related to food acquisition and, to a lesser extent, dispersal. Nonetheless, those conditions might not only exclude species that are not able to persist in those ecosystems but might also increase the competition strength, thereby excluding species having less competitive food acquisition traits. Instead, according to the network position hypothesis, the downstream position of rivers facilitates the dispersion of species [3], which may explain the lower functional deviance observed in river ecosystems.

(b) Assembly rules under anthropization

In streams, the percentage of deforested surfaces upstream from the fish sampling sites ranged from 0 to 77% (mean = 17%, s.e. = 4.1; electronic supplementary material, table S2) and resulted in negative effects on the SES values of most trait groups, conveying those communities towards functional convergence. Although functional convergence induced by anthropization has already been observed in temperate streams for both fish and invertebrate communities [14,16], we here show that this trend might be concomitantly ruled by two distinct ecological processes acting at different spatial scales. The trends towards functional convergence in both regional null models (generally negative SES means for most trait groups) and ecosystem null models (generally negative SES means for overall functional diversity and food acquisition traits) in streams increased under high

deforestation levels. Thus, declines in functional diversity due to deforestation can be related not only to an increase in environmental constraints that strengthen environmental filtering but also to a decline in resource availability that increases competition strength, resulting in the exclusion of the less competitive species. The additive effects of increased environmental filtering and increased competitive exclusion might explain the drastic impacts of deforestation reported in the streams from the Amazonian region [31,32,70]. Such impacts are induced by deforestation, which is mainly associated with gold-mining development, an activity generating detrimental effects on stream physico-chemical conditions and streambed physical structure [44] and thus disproportionately affecting the benthic compartment. For instance, gold-mining was reported to increase the turbidity and fine particle siltation in streams [31,70], leading to negative effects on algal growth [71] and thereby reducing food availability for algae feeders. These physical changes may thus reduce habitat availability and food resources for benthic species and algae grazers (e.g. Loricaridae), thereby strengthening both the abiotic and biotic filtering of those species.

For river communities, the percentage of deforested surfaces upstream from the sites was lower (ranging from 0 to 7%; mean 0.1%; s.e. = 0.2; electronic supplementary material, table S2) compared to streams, but it was extended over a larger part of the upstream drainage basin, as we accounted for deforested surfaces located in the upstream sub-basin area delineated at a distance of 30 km from each river site [36]. Null models comparing observed communities to simulated communities from the regional pool of species (figure 3b) showed that only habitat use traits were significantly linked to deforestation. Even if SES values were always above zero for this function, the extent of deviance from null expectations decreased with deforestation. Therefore, as in streams, deforestation may be reinforcing environmental filters that retain species with specific traits allowing them to thrive in those conditions. Deviance from ecosystem null models (simulations based on the species pool exclusive to rivers; figure 3d) increased towards negative SES values. This pattern might be underpinned by an increase in competitive interactions that leads to species exclusion in communities highly impacted by deforestation. As in streams, algae browsers, but also detritivorous species, are shrinking in sites impacted by deforestation, and the species persisting in impacted sites are opportunistic and highly competitive (e.g. *Hypostomus* sp.) [36]. In addition, more sensitive species naturally confined to particular habitats, and probably less competitive, tend to disappear from impacted sites (e.g. *Otocinclus* sp. or *Guyanancistrus* sp.) [36]. As in streams, these results offer insights into the processes underlying the biodiversity responses to human impacts on large rivers. Those processes are still modulated by environmental changes through the river upstream-downstream gradient, with downstream rivers exhibiting less functional convergence than upstream sites for dispersal-related traits (electronic supplementary material, figure S3d). This can be explained by the high dispersal rates characteristic of large rivers, which allow mass effects [3]. Under high colonization rates, species can temporarily occupy habitat patches that are not suitable for them, thereby partly counterbalancing the environmental constraints induced by deforestation. Answering this hypothesis is currently difficult because, once again, abundance data are needed to detect

mass effect processes. On the other hand, a possible methodological issue in large rivers might be the downstream drift of eDNA, as at least one study claimed that eDNA could be detected far downstream from its emission to the environment [72]. However, studies explicitly addressing how this method characterizes spatial patterns of aquatic taxa showed more limited distances [38,73,74]. For instance, a cage study showed that eDNA concentrations become strongly reduced 2 km downstream from the emission source [75]. In addition, eDNA provided fish inventories and species spatial patterns comparable to those of local samples using capture methods in the rivers sampled in this study [38], testifying for a local description of communities that does not exceed a few kilometres. These short detection distances might be explained by the accelerated eDNA degradation at warm water temperatures (26–30°C) [76] and the gentle topography of the rivers, which both restrict downstream eDNA transport. Although we cannot exclude that the eDNA of some species, probably the most abundant ones, can be transported over long distances [77], it might be limited to a few species in our samples, as this potential DNA drift does not blur spatial patterns of whole fish communities [38].

5. Conclusion

Understanding the differential responses of different types of traits across spatial scales, ecosystems, and anthropogenic gradients may help build a general theory of community assembly by assessing functional convergence/divergence patterns. The key point here was to consider null models based on a regional species pool to evaluate environmental filtering effects, while null models constructed using the ecosystem-specific pools of species allowed assessing biotic interactions (limiting similarity and weaker competitor exclusion). This simple theoretical framework (table 1), should be applied to overall trait approaches. It also deserves to be detailed for each ecological function because, as shown here, a general functional trend can hide idiosyncratic assembly processes for specific functions, highlighting the complexity of the assembly rules in the Neotropics. More generally, our approach is transposable to any kind of biological model or ecosystem. In Guianese freshwater communities, it revealed that fish assembly rules in streams differed from those ruling river communities. The significant effects of deforestation were more pronounced in streams than in rivers (higher slopes; table 2) and the functions affected by deforestation differed between streams and rivers. Assessing

anthropization effects on rivers is more challenging than in streams due to their complexity, spatial heterogeneity and cumulative impacts over longer distances, suggesting that the deforestation gradient may be underestimated in rivers [78,79]. Nevertheless, anthropogenic disturbances affected assembly processes in similar ways in both ecosystems, with a reinforcement of both environmental filtering and competition. This probably explains the observed steep declines in biodiversity under slight deforestation levels (less than 3% on average in [36]), as well as the biotic homogenization of fish communities observed in anthropized localities across the region [33]. Thus, this study underlines the vulnerability of Neotropical ecosystems to anthropic disturbances that not only affect species persistence but also modify community assembly rules.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Site information and SES values for each community calculated for each trait type and species pool are provided in electronic supplementary material, table S2 [81]. Matrices of detected species by site are provided in electronic supplementary material, tables S3 and S4, for rivers and streams, respectively. Raw sequencing data are provided at <https://doi.org/10.5061/dryad.pvmcvdnmr> [80] for samples collected in rivers and at <https://doi.org/10.6084/m9.figshare.13129703.v1> [82] for samples collected in streams. The sequencing codes in electronic supplementary material, table S2 [81], can be used to extract the runs used for this study.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. I.C.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; C.J.: data curation, writing—review and editing; T.D.: methodology, writing—review and editing; J.M.: resources, writing—review and editing; R.V.: resources; A.V.: data curation, methodology, writing—review and editing; S.B.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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

Funding. Funding was provided by CEBA (ANR-10-LABX-25-01), DRIIHM (ANR-11-LABX-0010), TULIP (ANR-10-LABX-0041), DEAL Guyane, OEG and VIGILIFE Sentinel Rivers.

Acknowledgments. We thank Kévin Cilléros for his comments on the manuscript; the PAG, Michel Aloïke, Hydreco and SPYGEN staff for field and laboratory support. Pierre Joubert provided gold-mined areas in Surinam and Guiana. Guyane Wild Fish provided some fish pictures for morphological measures.

References

- Keddy PA. 1992 Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3**, 157–164. (doi:10.2307/3235676)
- Connor EF, Simberloff D. 1979 The assembly of species communities: chance or competition? *Ecology* **60**, 1132–1140. (doi:10.2307/1936961)
- Schmera D *et al.* 2018 Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshw. Biol.* **63**, 74–85. (doi:10.1111/fwb.12973)
- Münkemüller T *et al.* 2020 Dos and don'ts when inferring assembly rules from diversity patterns. *Glob. Ecol. Biogeogr.* **29**, 1212–1229. (doi:10.1111/geb.13098)
- de Bello F *et al.* 2012 Functional species pool framework to test for biotic effects on community assembly. *Ecology* **93**, 2263–2273. (doi:10.1890/1-1394.1)
- MacArthur R, Levins R. 1967 The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385. (doi:10.1086/282505)
- Grime JP. 2001 *Plant strategies, vegetation processes, and ecosystem properties*. Oxford, UK: Wiley.
- Troia MJ, Gido KB. 2015 Functional strategies drive community assembly of stream fishes along

- environmental gradients and across spatial scales. *Oecologia* **177**, 545–559. (doi:10.1007/s00442-014-3178-1)
9. Botta-Dukát Z, Czúcz B. 2016 Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods Ecol. Evol.* **7**, 114–126. (doi:10.1111/2041-210X.12450)
 10. Saar L, de Bello F, Pärtel M, Helm A. 2017 Trait assembly in grasslands depends on habitat history and spatial scale. *Oecologia* **184**, 1–12. (doi:10.1007/s00442-017-3812-9)
 11. Cornwell WK, Ackerly DD. 2009 Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.* **79**, 109–126. (doi:10.1890/07-1134.1)
 12. Ulrich W, Sewerniak P, Puchalka R, Piwczynski M. 2017 Environmental filtering triggers community assembly of forest understorey plants in Central European pine stands. *Sci. Rep.* **7**, 274. (doi:10.1038/s41598-017-00255-z)
 13. Thakur D, Chawla A. 2019 Functional diversity along elevational gradients in the high altitude vegetation of the western Himalaya. *Biodivers. Conserv.* **28**, 1977–1996. (doi:10.1007/s10531-019-01728-5)
 14. Kuczynski L, Grenouillet G. 2018 Community disassembly under global change: evidence in favor of the stress-dominance hypothesis. *Glob. Change Biol.* **24**, 4417–4427. (doi:10.1111/gcb.14320)
 15. Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F. 2009 Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* **12**, 22–33. (doi:10.1111/j.1461-0248.2008.01255.x)
 16. Gutiérrez-Cánovas C, Sánchez-Fernández D, Velasco J, Millán A, Bonada N. 2015 Similarity in the difference: changes in community functional features along natural and anthropogenic stress gradients. *Ecology* **96**, 2458–2466. (doi:10.1890/14-1447.1)
 17. Teresa FB, Casatti L. 2012 Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams. *Ecol. Freshw. Fish* **21**, 433–442. (doi:10.1111/j.1600-0633.2012.00562.x)
 18. McCluney KE, Poff NL, Palmer MA, Thorp JH, Poole GC, Williams BS, Williams MR, Baron JS. 2014 Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. *Front. Ecol. Environ.* **12**, 48–58. (doi:10.1890/120367)
 19. Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980 The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**, 130–137. (doi:10.1139/f80-017)
 20. Poff NL, Allan JD. 1995 Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* **76**, 606–627. (doi:10.2307/1941217)
 21. Olden JD, Poff NL, Bestgen KR. 2006 Life-history strategies predict fish invasions and extirpations in the Colorado river basin. *Ecol. Monogr.* **76**, 25–40. (doi:10.1890/05-0330)
 22. Willis SC, Winemiller KO, Lopez-Fernandez H. 2005 Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia* **142**, 284–295. (doi:10.1007/s00442-004-1723-z)
 23. Munepeerakul R, Bertuzzo E, Lynch HJ, Fagan WF, Rinaldo A, Rodriguez-Iturbe I. 2008 Neutral metacommunity models predict fish diversity patterns in Mississippi–Missouri basin. *Nature* **453**, 220–222. (doi:10.1038/nature06813)
 24. Altermatt F. 2013 Diversity in riverine metacommunities: a network perspective. *Aquat. Ecol.* **47**, 365–377. (doi:10.1007/s10452-013-9450-3)
 25. Jackson DA, Peres-Neto PR, Olden JD. 2001 What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* **58**, 157–170. (doi:10.1139/f00-239)
 26. Brown BL, Swan CM. 2010 Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* **79**, 571–580. (doi:10.1111/j.1365-2656.2010.01668.x)
 27. Carvalho RA, Tejerina-Garro FL. 2015 Environmental and spatial processes: what controls the functional structure of fish assemblages in tropical rivers and headwater streams? *Ecol. Freshw. Fish* **24**, 317–328. (doi:10.1111/eff.12152)
 28. Lévêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedesco PA. 2008 Global diversity of fish (Pisces) in freshwater. *Hydrobiologia* **595**, 545–567. (doi:10.1007/s10750-007-9034-0)
 29. Castello L, Macedo MN. 2016 Large-scale degradation of Amazonian freshwater ecosystems. *Glob. Change Biol.* **22**, 990–1007. (doi:10.1111/gcb.13173)
 30. Dezécache C, Faure E, Gond V, Salles J-M, Vieilledent G, Hérault B. 2017 Gold-rush in a forested El Dorado: deforestation leakages and the need for regional cooperation. *Environ. Res. Lett.* **12**, 034013. (doi:10.1088/1748-9326/aa6082)
 31. Hammond DS, Gond V, Thoisy B de, Forget P-M, DeDijn BPE. 2007 Causes and consequences of a tropical forest gold rush in the Guiana Shield, South America. *AMBIO J. Hum. Environ.* **36**, 661–670. (doi:10.1579/0044-7447(2007)36[661:CACOAT]2.0.CO;2)
 32. Leitão RP *et al.* 2018 Disentangling the pathways of land use impacts on the functional structure of fish assemblages in Amazon streams. *Ecography* **41**, 219–232. (doi:10.1111/ecog.02845)
 33. Coutant O, Jézéquel C, Mokany K, Cantera I, Covain R, Valentini A, Dejean T, Brosse S, Muriene J. 2023 Environmental DNA reveals a mismatch between diversity facets of Amazonian fishes in response to contrasting geographical, environmental and anthropogenic effects. *Glob. Change Biol.* **29**, 1741–1758. (doi:10.1111/gcb.16533)
 34. Allard L, Popée M, Vigouroux R, Brosse S. 2016 Effect of reduced impact logging and small-scale mining disturbances on Neotropical stream fish assemblages. *Aquat. Sci.* **78**, 315–325. (doi:10.1007/s00027-015-0433-4)
 35. Arantes CC, Winemiller KO, Petrere M, Castello L, Hess LL, Freitas CEC. 2018 Relationships between forest cover and fish diversity in the Amazon River floodplain. *J. Appl. Ecol.* **55**, 386–395. (doi:10.1111/1365-2664.12967)
 36. Cantera I *et al.* 2022 Low level of anthropization linked to harsh vertebrate biodiversity declines in Amazonia. *Nat. Commun.* **13**, 3290. (doi:10.1038/s41467-022-30842-2)
 37. Cantera I, Cilleros K, Valentini A, Cerdan A, Dejean T, Iribar A, Taberlet P, Vigouroux R, Brosse S. 2019 Optimizing environmental DNA sampling effort for fish inventories in tropical streams and rivers. *Sci. Rep.* **9**, 3085. (doi:10.1038/s41598-019-39399-5)
 38. Cantera I, Decotte J, Dejean T, Muriene J, Vigouroux R, Valentini A, Brosse S. 2022 Characterizing the spatial signal of environmental DNA in river systems using a community ecology approach. *Mol. Ecol. Resour.* **22**, 1274–1283. (doi:10.1111/1755-0998.13544)
 39. Cilleros K *et al.* 2018 Unlocking biodiversity and conservation studies in high-diversity environments using environmental DNA (eDNA): a test with Guianese freshwater fishes. *Mol. Ecol. Resour.* **19**, 27–46. (doi:10.1111/1755-0998.12900)
 40. Jerde CL, Wilson EA, Dressler TL. 2019 Measuring global fish species richness with eDNA metabarcoding. *Mol. Ecol. Resour.* **19**, 19–22. (doi:10.1111/1755-0998.12929)
 41. Lamouroux N, Poff NL, Angermeier PL. 2002 Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* **83**, 1792–1807. (doi:10.1890/0012-9658(2002)083[1792:ICOSFC]2.0.CO;2)
 42. Hansen A *et al.* 2019 Global humid tropics forest structural condition and forest structural integrity maps. *Sci. Data* **6**, 232. (doi:10.1038/s41597-019-0214-3)
 43. Strahler A. 1957 Quantitative analysis of watershed geomorphology. *Eos Trans. Am. Geophys. Union* **38**, 913–920. (doi:10.1029/TR038i006p00913)
 44. Dedieu N, Vigouroux R, Cerdan P, Céréghino R. 2015 Invertebrate communities delineate hydro-ecoregions and respond to anthropogenic disturbance in East-Amazonian streams. *Hydrobiologia* **742**, 95–105. (doi:10.1007/s10750-014-1969-3)
 45. Cilleros K, Allard L, Vigouroux R, Brosse S. 2017 Disentangling spatial and environmental determinants of fish species richness and assemblage structure in Neotropical rainforest streams. *Freshw. Biol.* **62**, 1707–1720. (doi:10.1111/fwb.12981)
 46. Valentini A *et al.* 2016 Next-generation monitoring of aquatic biodiversity using environmental DNA metabarcoding. *Mol. Ecol.* **25**, 929–942. (doi:10.1111/mec.13428)
 47. Pringle CM. 2001 Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecol. Appl.* **11**, 981–998. (doi:10.1890/1051-0761(2001)011[0981:HCCATM]2.0.CO;2)
 48. NASA. 2013 NASA Shuttle radar topography mission global 1 arc second [Data set]. *NASA EOSDIS Land*

- Process. DAAC* **20**. (doi:10.5067/MEaSURES/SRTM/SRTMGL1.003)
49. Hansen MC *et al.* 2013 High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853. (doi:10.1126/science.1244693)
50. WWF. 2016 Gold-mining deforestation in French Guiana in 2015. See <https://www.geoguyane.fr/geonetwork/srv/fre/catalog.search#/metadata/9ecded9c-9849-47aa-8d88-cffd905dca6c>.
51. Rahm M *et al.* 2015 *Monitoring the impact of gold mining on the forest cover and freshwater in the Guiana Shield*. Guiana Shield Project and WWF Guianas.
52. Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ. 2017 Functional ecology of fish: current approaches and future challenges. *Aquat. Sci.* **79**, 783–801. (doi:10.1007/s00027-017-0546-z)
53. Toussaint A, Charpin N, Beauchard O, Grenouillet G, Oberdorff T, Tedesco PA, Brosse S, Villéger S. 2018 Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. *Ecol. Lett.* **21**, 1649–1659. (doi:10.1111/ele.13141)
54. Planquette P, Keith P, Le Bail PY. 1996 *Atlas des poissons d'eau douce de Guyane (tome 1)*. Paris, France: IEBG–MNHN, INRA, CSP, Min. Env.
55. Villéger S, Mason NWH, Mouillot D. 2008 New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301. (doi:10.1890/07-1206.1)
56. Maire E, Grenouillet G, Brosse S, Villéger S. 2015 How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces: assessing functional space quality. *Glob. Ecol. Biogeogr.* **24**, 728–740. (doi:10.1111/geb.12299)
57. Gotelli NJ, Graves GR. 1996 *Null models in ecology*. Washington, DC: Smithsonian Institution.
58. Cilleros K, Allard L, Grenouillet G, Brosse S. 2016 Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages. *J. Biogeogr.* **43**, 1832–1843. (doi:10.1111/jbi.12839)
59. Brosse S, Melki F, Vigouroux R. 2019 Fishes of the Mitaraka mountains (French Guiana). *Zoosystema* **40**, 131. (doi:10.5252/zoosystema2019v41a8)
60. Brosse S, Montoya-Burgos JI, Grenouillet G, Surugue N. 2013 Determinants of fish assemblage structure in Mount Itoupé mountain streams (French Guiana). *Ann. Limnol. Int. J. Limnol.* **49**, 43–49. (doi:10.1051/limn/2013037)
61. Alonso LE, Mol JH. 2007 *A rapid biological assessment of the Lely and Nassau plateaus, Suriname (with additional information on the Brownsberg plateau)*. RAP Bulletin of Biological Assessment.
62. Mol JH, Wan Tong You K, Vrede I, Flynn A, Ouboter PE, Van der Lugt F. 2007 Fishes of Lely and Nassau mountains, Suriname. In *A rapid biological assessment of the Lely and Nassau plateaus, Suriname (with additional information on the Brownsberg plateau)* (eds ME Alonzim, JH Mol). RAP Bulletin of Biological Assessment.
63. Allan JD, Castillo MM. 2021 *Stream ecology: structure and function of running waters*. Cham, Switzerland: Springer Nature.
64. Little CJ, Altermatt F. 2018 Do priority effects outweigh environmental filtering in a guild of dominant freshwater macroinvertebrates? *Proc. R. Soc. B* **285**, 20180205. (doi:10.1098/rspb.2018.0205)
65. Yao M, Zhang S, Lu Q, Chen X, Zhang S, Kong Y, Zhao J. 2022 Fishing for fish environmental DNA: ecological applications, methodological considerations, surveying designs, and ways forward. *Mol. Ecol.* **31**, 5132–5164. (doi:10.1111/mec.16659)
66. Zinger L *et al.* 2020 Advances and prospects of environmental DNA in neotropical rainforests. *Adv. Ecol. Res.* **62**, 331–373. (doi:10.1016/bs.aecr.2020.01.001)
67. Pont D *et al.* 2023 Quantitative monitoring of diverse fish communities on a large scale combining eDNA metabarcoding and qPCR. *Mol. Ecol. Resour.* **23**, 396–409. (doi:10.1111/1755-0998.13715)
68. Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR. 2013 A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**, 167–177. (doi:10.1016/j.tree.2012.10.004)
69. Cadotte MW, Tucker CM. 2017 Should environmental filtering be abandoned? *Trends Ecol. Evol.* **32**, 429–437. (doi:10.1016/j.tree.2017.03.004)
70. Dedieu N, Allard L, Vigouroux R, Brosse S, Céréghino R. 2014 Physical habitat and water chemistry changes induced by logging and gold mining in French Guiana streams. *Knowl. Manage. Aquat. Ecosyst.* **415**, 02. (doi:10.1051/kmae/2014026)
71. Tudesque L, Grenouillet G, Gevrey M, Khazraie K, Brosse S. 2012 Influence of small-scale gold mining on French Guiana streams: are diatom assemblages valid disturbance sensors? *Ecol. Indic.* **14**, 100–106. (doi:10.1016/j.ecolind.2011.07.018)
72. Deiner K, Fronhofer EA, Mächler E, Walsler J-C, Altermatt F. 2016 Environmental DNA reveals that rivers are conveyor belts of biodiversity information. *Nat. Commun.* **7**, 12544. (doi:10.1038/ncomms12544)
73. Civade R, Dejean T, Valentini A, Roset N, Raymond J-C, Bonin A, Taberlet P, Pont D. 2016 Spatial representativeness of environmental DNA metabarcoding signal for fish biodiversity assessment in a natural freshwater system. *PLoS ONE* **11**, e0157366. (doi:10.1371/journal.pone.0157366)
74. Jo T, Yamanaka H. 2022 Meta-analyses of environmental DNA downstream transport and deposition in relation to hydrogeography in riverine environments. *Freshw. Biol.* **67**, 1333–1343. (doi:10.1111/fwb.13920)
75. Van Driessche C, Everts T, Neyrinck S, Brys R. 2022 Experimental assessment of downstream environmental DNA patterns under variable fish biomass and river discharge rates. *Environ. DNA* **5**, 102–116. (doi:10.1002/edn3.361)
76. Eichmiller JJ, Best SE, Sorensen PW. 2016 Effects of temperature and trophic state on degradation of environmental DNA in lake water. *Environ. Sci. Technol.* **50**, 1859–1867. (doi:10.1021/acs.est.5b05672)
77. Pont D *et al.* 2018 Environmental DNA reveals quantitative patterns of fish biodiversity in large rivers despite its downstream transportation. *Sci. Rep.* **8**, 10361. (doi:10.1038/s41598-018-28424-8)
78. Lindberg TT, Bernhardt ES, Bier R, Helton AM, Merola RB, Vengosh A, Di Giulio RT. 2011 Cumulative impacts of mountaintop mining on an Appalachian watershed. *Proc. Natl Acad. Sci. USA* **108**, 20929–20934. (doi:10.1073/pnas.1112381108)
79. Vörösmarty CJ *et al.* 2010 Global threats to human water security and river biodiversity. *Nature* **467**, 555–561. (doi:10.1038/nature09440)
80. Cantera I. 2021 Data for characterizing the spatial signal of environmental DNA in river systems using a community ecology approach. Dryad, Dataset. (doi:10.5061/dryad.pvmcndnmr)
81. Cantera I, Jézéquel C, Dejean T, Murielle J, Vigouroux R, Valentini A, Brosse S. 2023 Deforestation strengthens environmental filtering and competitive exclusion in Neotropical streams and rivers. Figshare. (doi:10.6084/m9.figshare.c.6806558)
82. Coutant O, Cantera I, Cilleros K, Dejean T, Valentini A, Murielle J, Brosse S. 2022 Detecting fish assemblages with environmental DNA: does protocol matter? Figshare. (doi:10.6084/m9.figshare.13129703.v1)