



How modified landscapes filter rare species and modulate the regional pool of ecological traits?

Naraiana Loureiro Benone · Bruno Eleres Soares · Cleonice Maria Cardoso Lobato · Lidia Brasil Seabra · David Bauman · Luciano Fogaça de Assis Montag

Received: 15 February 2020 / Revised: 28 August 2020 / Accepted: 5 September 2020
© Springer Nature Switzerland AG 2020

Abstract Common and rare species differ in their level of dispersal ability and habitat specialization, and thus should respond to distinct assembly rules. Rare species are much more spatially restricted and usually show higher habitat specialization, so they can be much more vulnerable to landscape changes than common species. We simulated three species-loss scenarios to assess how different groups of stream fish species respond to environmental and spatial variables and how potential extinctions affected regional

functional richness and the average functional distinctiveness. Rare and common species contribute similarly to the global functional richness, but the loss of common species led to a marked decrease in local redundancy. Whilst intermediate and rare species are regulated by dispersal, dominant species respond to niche processes and are more affected by land-use changes. Therefore, common and rare species are under distinct assembly rules and may exhibit distinct responses in the face of environmental anthropization. Addressing rare species is often overlooked, despite constant claims regarding their importance and their frequently concerning conservation status. Accounting for their rarity can offer a more refined look at the responses of species to human modifications, providing valuable information on how to tackle biodiversity loss.

Naraiana Loureiro Benone and Bruno Eleres Soares are sharing co-first authorship.

Guest editors: David J. Hoeinghaus, Jaqueline O. Zeni, Gabriel L. Brejão, Rafael P. Leitão & Renata G. Frederico / Neotropical Stream Fish Ecology in a Changing Landscape

Electronic supplementary material The online version of this article (doi:<https://doi.org/10.1007/s10750-020-04405-9>) contains supplementary material, which is available to authorized users.

N. L. Benone (✉) · C. M. C. Lobato · L. B. Seabra · L. F. de Assis Montag
Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará – UFPA, Belém, PA, Brazil
e-mail: nbenone@gmail.com

N. L. Benone
Universidade do Estado de Minas Gerais – UEMG, Unidade Passos, Passos, MG, Brazil

Keywords Species loss · Land-use changes · Dispersal ability · Environmental filtering · Extinction

B. E. Soares
Laboratório de Limnologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro – UFRJ, Rio de Janeiro, RJ, Brazil

D. Bauman
Oxford University Centre for the Environment, Oxford, UK

Introduction

Land-use changes promote high rates of deforestation (Stabile et al., 2020), affecting terrestrial and aquatic ecosystems by the reduction of the connectivity amongst local communities and by the increase in vulnerability to local environmental pressures (Heino, 2013; Pérez-Mayorga et al., 2017; Montag et al., 2019). In lotic systems, deforestation leads to numerous changes in channel structure and energy sources (Hagen et al., 2010; Leal et al., 2016), which have direct effects on habitat suitability and dispersal of organisms. These changes are important drivers of the local community structure of fishes (Leitão et al., 2018; Montag et al., 2019).

Human-modified areas are characterized by lower richness and higher dominance than forested areas (Sykes et al., 2019). In addition to diversity loss, deforested areas usually exhibit differences in species composition (Brejão et al., 2018; Virgilio et al., 2018) associated with the homogenization of riparian vegetation, changes in microhabitat composition, and reduction of the water column due to increased sedimentation and silting (Ramalho et al., 2014; Montag et al., 2019). These changes are related to species-specific traits and have a marked effect on the functional structure of communities. For example, local deforestation reduces substrate heterogeneity, streambed stability and wood volume, and thus have negative effects on species that explore the stream bottom and highly structured microhabitats, such as those with broad pectoral fins and dorsal eyes (Leitão et al., 2018; Zeni et al., 2019).

Deforestation also reduces spatial connectivity amongst streams and hinder the movement of organisms (Perkin & Gido, 2012; Zeni et al., 2019; Lo et al., 2020). Riverscape fragmentation changes the structure of communities by the loss of species that depend on large areas to survive, such as large-sized carnivorous fishes (Leitão et al., 2018), and by reducing recolonization and tracking of suitable areas (Perkin & Gido, 2012; Edge et al., 2017). That way, modified landscapes do not affect fish communities only by niche-related processes but also by dispersal-related

processes, and therefore may be fitted in a metacommunity framework (Leibold et al., 2004).

The strength of dispersal and environmental filtering may be strongly linked to species niches and regional occupancy (Leibold et al., 2004; Pérez-Mayorga et al., 2017), which may produce varying outcomes. Common species may be generalists adapted to use a wide range of environmental variation, thus being primarily constrained by dispersal-related processes, whilst rare species may be specialists responding primarily to niche-related processes (Pandit et al., 2009). Alternatively, common species may be good dispersers, being able to reach habitats with proper conditions and being structured by environmental constraints, whilst rare species may be weaker dispersers and be strongly constrained by spatial variables (Leibold & Chase, 2018).

Deforestation reduces connectivity and changes local-scale features, modifying metacommunity dynamics and the strength of dispersal (Heino, 2013). Rare species may be especially vulnerable if they are habitat specialists and/or are unable to disperse efficiently through the modified landscape (Pérez-Mayorga et al., 2017), thus could be prone to regional extinction. Common species may contribute the most to ecosystem functioning as they concentrate abundance, biomass, and number of interactions (Grime, 1998; Smith and Knapp, 2003; Chapman et al., 2018). On the other hand, rare species may play crucial roles in ecosystem functioning by different mechanisms, such as by holding unique combinations of traits (e. g., close association to specific substrates) (Mouillot et al., 2013; Leitão et al., 2016). Nevertheless, the importance of rarity to functional diversity is constrained by land use and common species may be functionally unique in pristine environments (Chapman et al., 2018).

For decades, human disturbances have been changing the landscape of natural habitats and subjecting species to new types of environmental filters. The Brazilian Amazon exhibits about 80% of the original forest cover (Mapbiomas, 2019), and the current legislative framework is unable to appropriately conserve streams and their fish communities (Leal et al., 2018). Given the intensifying rates of land-use changes in the Amazonian rainforest (Barlow et al., 2019), stream fishes are at risk, but common and rare species may have to face different structuring processes in altered landscapes.

D. Bauman
Laboratoire d'Écologie Végétale et Biogéochimie, CP
244, Université Libre de Bruxelles, Brussels, Belgium

Herein, we intend to fill a gap on the intersection of how modified landscapes may impose different filters on fish species depending on their occupancy and local abundance and the possible consequences to local and regional functional structures. Specifically, we analyse (i) the importance of niche-related and dispersal-related processes for common and rare stream fish species and (ii) how the loss of common and rare species affects the regional functional diversity. We expect that common species will show a greater influence of dispersal processes, whilst rare species will be more affected by local habitat and land-use change. We also expect that rare species have higher contributions to the regional functional pool, since they should possess a more unique combination of traits.

Materials and methods

Study area

Surveyed streams are distributed in the Acará and Capim river basins, located in the northeast of Pará state, Eastern Amazon (Fig. 1). The region is covered by an ombrophilous *terra firme* forest. According to the Köppen classification, the climate is of the sub-type “Af”, defined as tropical humid, with a well-defined dry season from September to November (Peel et al., 2007; Alvares et al., 2013). The average annual temperature of the river basins ranges from 25 to 27 °C and the average annual rainfall is approximately 2,000 mm (Barthem et al., 2004). The altitudes vary between 100 and 150 metres. This region stands out for being in the “arc of deforestation”, characterized by extensive land use modifications, such as the implementation of industrial projects, high levels of logging, and large-scale agricultural and livestock activities (Gardner et al., 2013; Nepstad et al., 2014). The occupation process in the Capim River basin region started in the late 1950s (Leal et al., 2016) and in the 1990s, land use with logging and cattle ranching began to rise (Loureiro, 2012). The Acará basin region has a history of use since the 1980s, with the cultivation of oil palm and livestock (Nahum & Santos, 2013).

Sampling design and local habitat variables

We sampled 104 streams ranging from 1st to 3rd order during the dry season from 2012 to 2015. The chosen period aimed to avoid seasonal variation in the physical habitat structure in the fish assemblage (Peck et al., 2006). At each sampling site, a 150-m reach was divided into ten 15-m longitudinal sections by 11 equidistant cross-sections. Each stream was sampled once during the day. We used an adapted version (Callisto et al., 2014) of the U.S. Environmental Protection Agency protocol (Kaufmann et al., 1999; Peck et al., 2006), which is used for the assessment of physical stream habitats to determine the structure of the environment in each location. We measured 13 variables and converted them into z-scores. See Supplementary Material for more details on habitat variables and measurements (Supplementary Material 1, Appendix 1, Table S1, and Table S2).

Fish sampling

Fish were sampled with 55-cm diameter sieve nets made with 3 mm metallic mesh. A sampling effort of six hours was established for each stream, divided amongst collectors and longitudinal sections. The specimens were killed with lethal doses of eugenol, fixed in 10% formalin, and after 48 h, preserved in 70% ethanol. We identified the specimens at the lowest possible taxonomic level using taxonomic keys in the literature complemented by guidance from specialists. The UFPA Ethics Committee approved the sampling of fish specimens (CEUA no. 8293020418). We deposited specimens in the Zoology Museum at the Universidade Federal do Pará, in Belém, Brazil.

We sampled 35,766 individuals, distributed in five orders, 24 families, and 102 species (Supplementary Material 1, Table S3). Previous papers described the taxonomic structure of part of our data (Ferreira et al., 2018; Montag et al., 2019).

Land use classification

The dimensions of land use in the landscape were identified by Digital Image Processing in 30 by 600 m buffers on each side of the drainage network. This format was based on the specialized literature (Frimpong et al., 2005) and the Brazilian Forest Code (Federal Law No. 12651/12), which request a

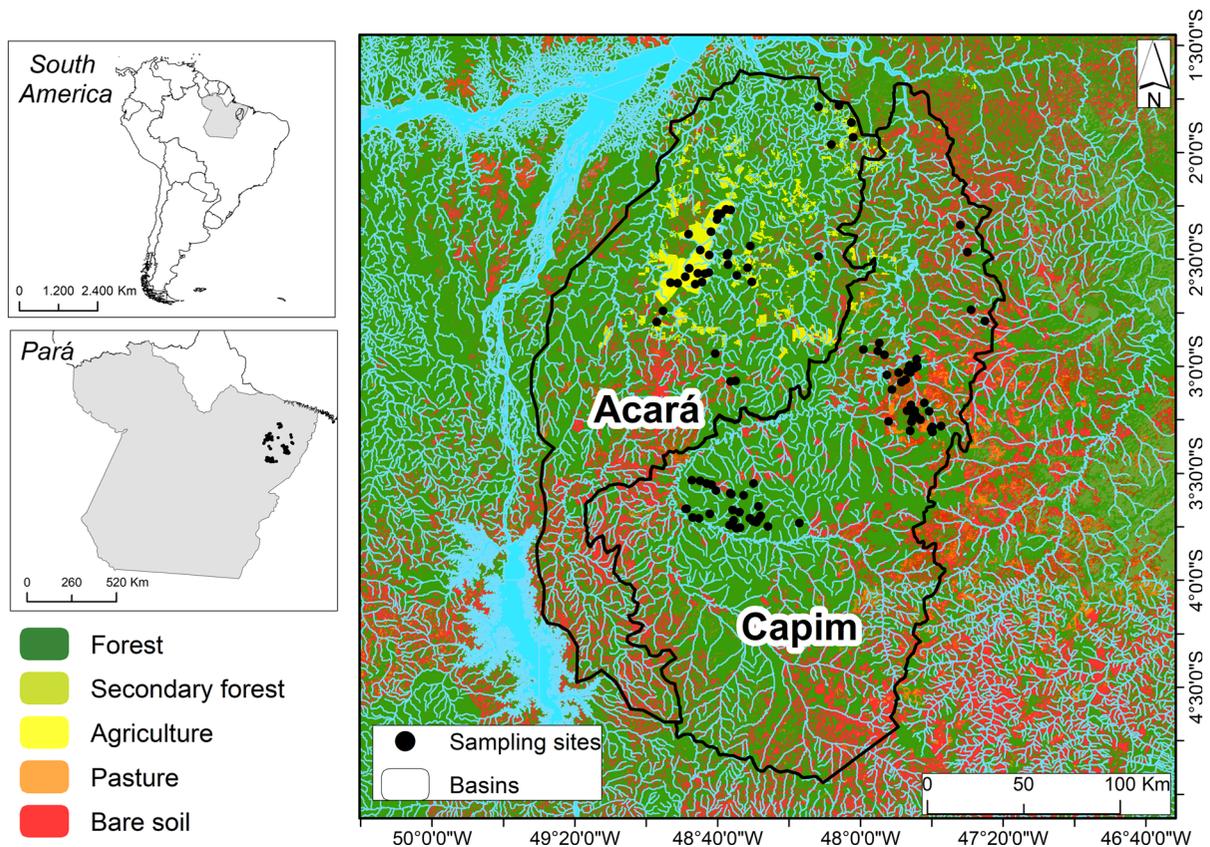


Fig. 1 Distribution of the 104 streams sampled in the Eastern Amazon. Colours indicate the types of land-use changes present in the region

permanent preservation area of 30 m on each river bank for lotic waterbodies up to 10 metres wide. Land-use was classified through digital image processing of the RapidEye Earth Imaging System (REIS) optical sensor. REIS sensor images have a 5-m spatial resolution and 5-band spectral resolution, ensuring greater precision in the classification of land use. Images were selected from the same year that the field surveys were conducted (see Montag et al., 2019). First, images were grained and orthorectified, then they were subjected to atmospheric correction (Richards & Jia, 1999). This image processing was performed with PCI Geomatics 2015 software using the ATCOR Ground Reflectance module. After the atmospheric correction of the images, a mosaic of REIS scenes was compiled using the OrthoEngine module and the REIS mosaic was submitted to object-oriented classification using eCognition 9 software. We validated the classification by comparing with TerraClass 2014 images provided by the Instituto

Nacional de Pesquisas Espaciais (Almeida et al., 2016). We identified the proportion of the following land cover on the landscape: primary forest (or forest in an advanced stage of succession), secondary forest, pasture, exposed soil and others (for shadows, clouds and imperfections) (Supplementary Material 1, Table S2).

Spatial variables

We used Moran's Eigenvector Maps (MEMs; Dray et al., 2006) to generate a set of spatial eigenvectors (MEM variables) aiming to capture both simple (e.g. gradients) and complex multi-scale spatial patterns in the fish community composition across the sampled streams. We followed the optimization method described in Bauman et al. (2018b), to ensure the selection of both the spatial weighting matrix (SWM) and the subset of spatial eigenvectors best capturing the spatial structures in our data. The SWM

optimisation and selection of a subset of spatial predictors can strongly influence statistical power, accuracy as well as the overall type I error rate, mostly for irregular sampling designs like ours (Bauman et al., 2018a, b). It has been recommended to integrate field-related knowledge (e.g. studied organisms biology, site topography) into the design of the candidate spatial weighting matrices used for the optimised selection of a subset of MEM variables (Dray et al., 2006; Bauman et al., 2018b). Here, we tested two schemes to define amongst-stream connectivity (Gabriel graph, and relative neighbourhood graph) and two types of weighting matrices (binary and linearly decreasing as a function of between-streams distance). We edited the connexions amongst streams on both candidate connectivity matrices to only reflect plausible links based on the basin hydrology and natural physical barriers. To reflect the fish biology, amongst-stream distances were calculated following the actual river course. We optimised the selection of a subset of spatial predictors from these four candidate spatial weighting matrices using Bauman et al. (2018b) method with the forward selection with double-stopping criterion option (Blanchet et al., 2008; Bauman et al., 2018a), focusing on MEM variables associated to patterns of positive spatial autocorrelation only. The optimisation procedure applied a Sidak correction for multiple tests to the p-values of the global permutation tests of significance for each spatial weighting matrix. Details, illustrations, and R code regarding the generation of the spatial predictors and inclusion of field knowledge in the spatial weighting matrices are provided in Appendix 8. Twelve MEM variables were selected to best capture the significant multi-scale spatial patterns present in the fish community data. We performed this selection with package *adespatial* (Dray et al., 2020).

Functional traits

Functional traits were obtained from five individuals of similar size of each species to avoid ontogenetic effects (Pagotto et al., 2011). For species with sexual dimorphism, we selected only female individuals for presenting less accentuated changes during the reproductive period (Ribeiro et al., 2016). In our study, only 2.9% of the measured species had marked sexual dimorphism. We measured 14 quantitative characteristics that resulted in 12 functional traits related to

locomotion, vertical position in the water column, and oral orientation of the species following Watson & Balon (1984) and Ohlberger et al. (2006) (Table 1). Further details on morphological measurements are described in Santos et al. (2019) and in the Supplementary Material (Supplementary Material 1, Appendix 2). We assigned the species to seven trophic guilds based on the literature (Table S3). When information was not available at the species level, we extrapolated from the genus.

The functional structure of the fish assemblages responds to selective habitat pressures. Landscape variables act mainly indirectly on functional attributes, mediated by changes in the conditions of local variables since anthropogenic changes in the landscape (e.g. deforestation and land use) alter the microclimate of the local habitat (Juen et al., 2016; Leal et al., 2016). Local conditions, such as variation in substrate composition, riparian cover, presence of large woody fragments, channel morphology, and channel habitat units, are the characteristics that most influence the functional structure of fish assemblages, mainly related to head length, pectoral fins, and body shape (Leitão et al., 2018; Santos et al., 2019).

The functional identity of the ichthyofauna in deeper and slower-flowing streams is characterized by traits of nektonic species, which exploit autochthonous resources, such as fish and invertebrates. In fast-flowing streams, they are associated with functional characteristics related to benthic fish with varied eating habits, including characteristics of periphytivorous and invertivorous species (Santos et al., 2019). Narrow and shaded streams are associated with nektonic species that exhibit functional traits adapted to explore resources in the marginal vegetation (Santos et al., 2019).

Data analysis

Since landscape variables were expressed as proportions of the buffers, they are all dependent on each other. To reduce them to orthogonal variables, we computed a Principal Components Analysis (PCA) and selected the two first axes. All variables were previously scaled. The two axes were combined with the habitat variables to set the environmental matrix.

Our functional traits matrix was composed of numerical and nominal traits, so we computed functional dissimilarities between species using Gower

Table 1 Ecomorphological indices based on 14 morphological measures of Amazon fish

Trait	Code	Calculation	Interpretation
Compression index of body	CI	MBH/MBW	High values indicate compressed fish which prefer habitats with slow flows
Relative body depth	RH	MBH/SL	Low values are related to fish inhabiting faster waters and lower capacity of vertical turns
Relative length of caudal peduncle	RLCP	LCP/SL	High values are associated to higher swimming capacity or fishes inhabiting faster waters, but not necessarily nektonic, able to realize propulsion at short distances
Compression index of caudal peduncle	CICP	MHCP/MWCP	Higher values indicate fish with compressed peduncles, typical of fish with slow swimming and low manoeuvrability
Index of ventral flattening	IVF	HBM/MBH	Lower values indicate fish adapted to fast waters, which can maintain position without swimming, typical of benthic species
Relative area of pectoral fin	RAPF	PFA/SL ²	High values are related to slow swimming species with good manoeuvrability or fish adapted to fast waters that live closer to the bottom
Aspect ratio of pectoral fin	ARPF	LPF/PFA	Higher ratios are associated to continuous high-speed swimmers that prefer pelagic regions
Relative length of head	RLH	HL/SL	Fish with larger heads ingest larger preys; thus, this index is more related to piscivores
Relative position of eyes	RPE	HEM/HH	High values indicate dorsal eyes, typical of benthic species
Relative width of mouth	RWM	MW/MBW	Higher values are associated to fish that ingest larger preys, such as piscivorous species
Mouth orientation	MO	Radian (mouth angle)	High values are related to fish that feed closer to the surface. Code: ventral = 0°; inferior = 10° to 80°; terminal = 90°; superior = 100 to 170°
Fineness coefficient	FC	SL/√MBH × MBW	This index evaluates the influence of body shape on swimming efficiency. Values of 2 to 6 indicate reduced drag, optimum ratio is 4.5

All indices followed Watson and Balon (1984) and Ohlberger et al. (2006)

distance. Then, following the framework of Violle et al. (2017), we combined the distance matrix with the species relative abundance matrix to calculate three components of rarity: (1) *Functional distinctiveness* assesses how functionally different a species is compared to the other species in the assemblage. This index is weighted by species abundance. (2) *Taxon restrictedness* is inversely related to the number of sites a species occurs given the total number of sites. (3) *Taxon scarcity* is inversely related to the abundance of the species on the site. We calculated a mean value for functional distinctiveness and taxon scarcity per site.

We used a Principal Coordinates Analysis (PCoA) to extract the two first orthogonal axes representing functional variation between species. We used the function `envfit` to evaluate the correlation of functional

traits with the ordination axes. Trophic guilds were represented by nominal variables, but `envfit` calculated R^2 as a single variable. We plotted the trophic guilds and the components of functional rarity in the ordination graph (Grenié et al., 2018). To evaluate the relationship between average functional distinctiveness and taxon restrictedness and taxon scarcity, we used Spearman's correlation.

We assessed how different groups of species respond to environmental and spatial variables in three species-loss scenarios following Leitão et al. (2016). The three scenarios sequentially removed species (i) from the rarest to the most dominant species, (ii) from the most dominant to the rarest, and (iii) independently from species rarity (i.e. randomly, in 999 null scenarios with shuffled order of species). Therefore, we evaluate how the coefficients of

explanation of pure environment, pure space, and space joined with environment change in successively smaller groups of species containing less (i) rare species, (ii) dominant species, and (iii) random species. To detect the influence of environmental and spatial variables on Hellinger-transformed species abundance, we first ran a forward selection procedure with each set of predictors to retain the most important variables. Then we used partial Redundancy Analysis (partial RDA) to calculate the isolated and shared influence of environment and space on species abundance. We used adjusted R^2 values to interpret the results. These steps were repeated in the two first species-loss scenarios, and 999 times in null scenarios. We used the mean value between taxon restrictedness and taxon scarcity as the criterion of rarity since they varied more amongst species.

We assessed how potential extinctions affected regional functional richness (FRic) and distinctiveness (FDist) in the same three earlier described species-loss scenarios. The random scenario included 10000 null scenarios with shuffled order of species. Functional diversity measures were calculated in each species-loss step to evaluate how the different scenarios of functional erosion differently affected functional structure. FRic is the amount of functional space filled by the regional pool of species, whilst FDist measures local functional redundancy. For the calculations, all quantitative traits were previously standardized, whilst qualitative traits were assigned as nominal. We kept the number of axes necessary to maintain a high-quality representation of the functional structure. We used the same criterion of rarity of the previous analyses.

All analyses were performed in R software (R Core Team, 2019) using packages *funrar* (Grenié et al., 2017), *FD* (Laliberté et al., 2014), *FactoMineR* (Lê et al., 2008), and *vegan* (Oksanen et al., 2019). We adopted a significance threshold of $\alpha < 0.05$.

Results

The two first axes of PCA for landscape variables explained 60.7% of the variation (Fig. 2). The first axis shows a continuum from primary forest to land-use cover. The second axis exhibited the differences amongst types of anthropogenic modifications, with

pasture close to the secondary forest and agriculture close to exposed soil.

The two first PCoA axes for species functional variation explained 46.7% of the functional variation (Fig. 3a). From the 13 functional traits, 11 were correlated with the PCoA ordination (Table 2). The first axis shows a gradient from species with high swimming efficiency (FC), inhabiting fast waters that can realize propulsion at short distances (RLCP) to fishes adapted to life in slow waters, capable to perform vertical turns (RH). The latter have bigger heads (RLH) and mouths (RWM) and eat larger prey. Diet changed from periphytivores and autochthonous invertivores to allochthonous invertivores and omnivores. The second axis differentiated fish that are either slow swimmers with high manoeuvrability or benthic species living in fast waters (RAPF), with large heads (RLH) and dorsal eyes (RPE) from flattened species that prefer slow flows (CI), with compressed peduncles, slow swimming, and low manoeuvrability (CICP), that with upturned mouths (MO). In this axis, diet changed from omnivores to general invertivores. We describe details on the association between species and functional traits and provide all values for the indices of rarity in Supplementary Material 1, Appendix 3, Fig. S1 and Table S4.

Most species are functionally rare, which is a result of low levels of functional distinctiveness (Fig. 3b) and high levels of taxon scarcity (Fig. 3c) and taxon restrictedness (Fig. 3d). Functional distinctiveness showed no correlation with taxon restrictedness (Spearman's $\rho = 0.15$, $P = 0.11$; Fig. 4a) and taxon scarcity (Spearman's $\rho = 0.17$, $P = 0.07$; Fig. 4b).

Scenarios of species removal highlighted that losing rare species first did not change spatial and environmental effects on the overall community whilst losing dominant species first led to marked changes in community responses to spatial and environmental variables. Groups of intermediate species (after the loss of the most dominant species) exhibited first an increase in the explanation of spatial variables and a decrease in the explanation of environmental variables. For the rarest species, the pure spatial signal and the shared effect of environment and space declined, although remained significant. This shows that intermediate and rare species are indeed under different assembly rules than dominant species, being more constrained by space than by environment (Fig. 5a–c).

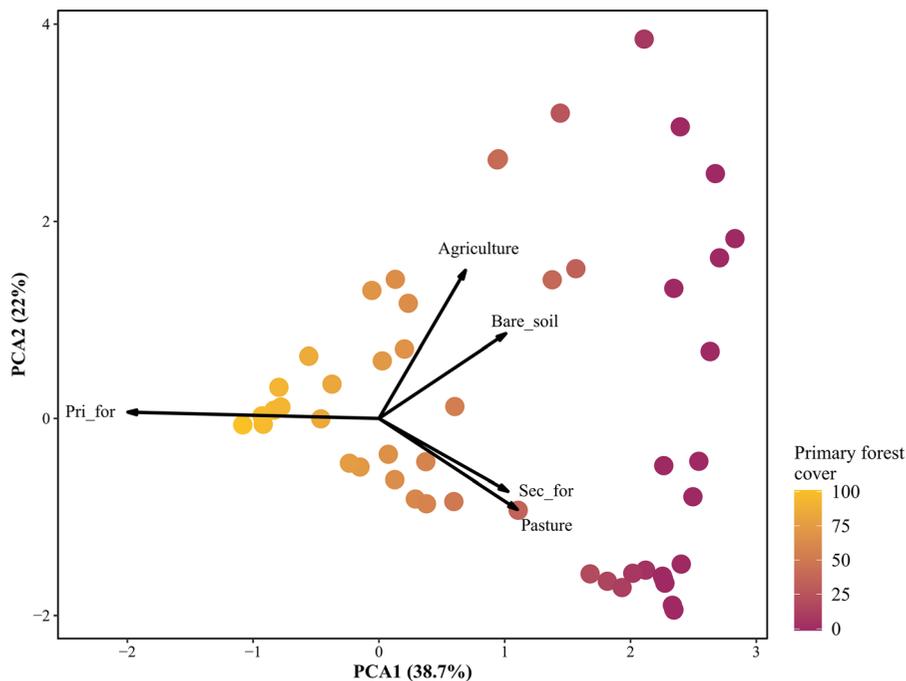


Fig. 2 Ordination of landscape variables for 104 streams as a result of principal component analysis. Codes for variables are in Supplementary Material 1, Table S1

The forward selection showed that local variables were more associated with dominant and rare species than landscape variables (Table 3), such as % undercut banks, % roots, and thalweg depth. However, landscape variables showed steady importance for the dominant species, which was not observed for rare species.

Despite being assembled by different rules, the species-loss scenarios highlighted that losing dominant or rare species first were not different from a random species-loss scenario when it comes to the regional functional erosion (functional richness) (Fig. 5d). Losing 30% of the most dominant species led to a reduction to 83.4% of the initial functional richness, whilst losing 30% of the rarest species led to a reduction to 67.4%, and null models had an average reduction to 70.3% of the initial functional richness. On the other hand, it affects the local functional structure (functional distinctiveness). The sequential loss of the most dominant species led to an increase in FDist, characterizing an increasing loss of local functional redundancy (Fig. 5e). The sequential loss of the rarest species did not differ from null expectations at first, but in a strongly depauperated regional fauna, it led to marked redundant communities.

Discussion

One of the few laws in ecology is that few species are common and most are rare. Despite this universal pattern, most of what we know from community ecology is biased towards common species (Lennon et al., 2011). Classifying species according to their rarity can give us an insight into the contribution of species to functional diversity and how they respond to assembly rules. Our results show that stream fish species are highly redundant and rarity is mostly a product of geographical taxon restrictedness and taxon scarcity than of functional distinctiveness. Rare and common species contribute similarly to the global functional richness, but rare species show a higher level of functional distinctiveness. These groups are structured by different assembly rules: whilst intermediate and rare species are regulated by dispersal, dominant species respond to niche processes. This is exactly the opposite of our hypothesis, highlighting the complexity of ecological communities and the difficulty to establish predictions on how communities will respond to human modifications.

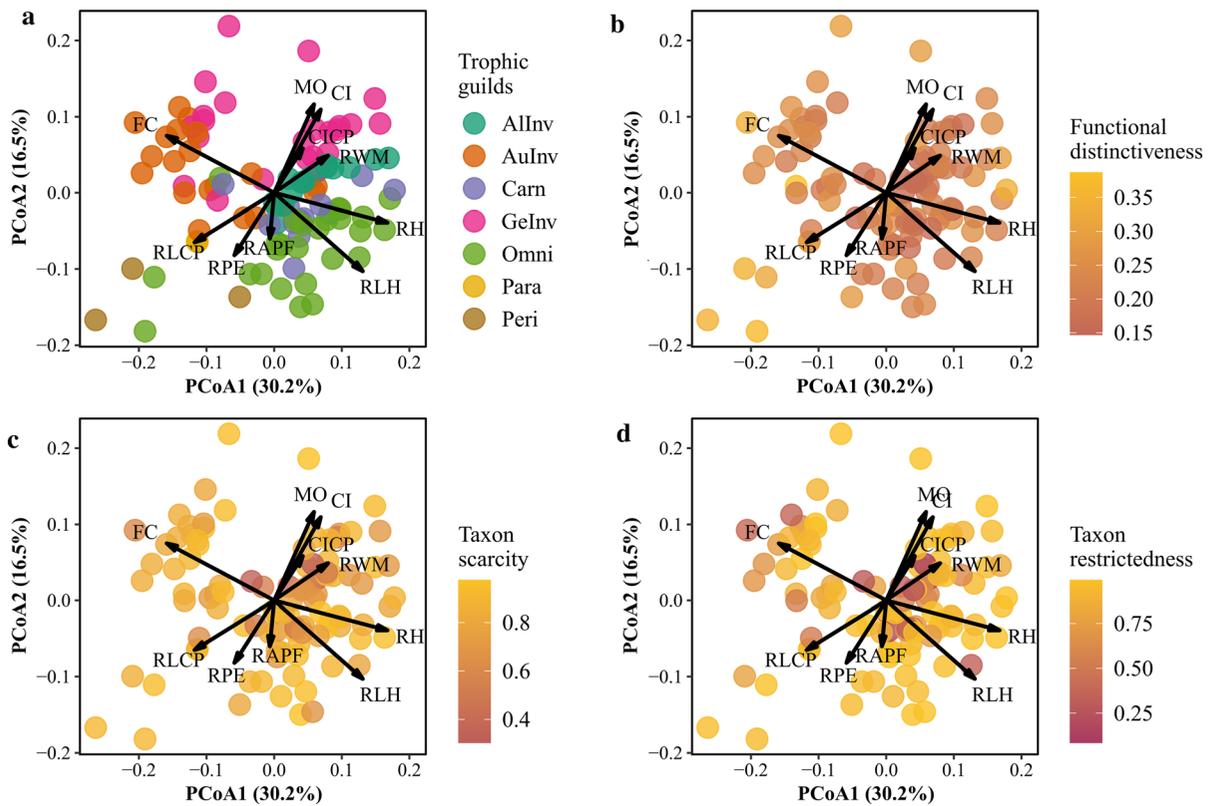


Fig. 3 Ordination of functional space of fish traits obtained through Principal Coordinates Analysis. Species are coloured by **a** trophic guilds, **b** functional distinctiveness, **c** taxon scarcity, and **d** taxon restrictedness. *AllInv* allochthonous invertivores,

AuInv autochthonous invertivores, *Carn* carnivores, *GeInv* general invertivores, *Para* parasites, *Omni* omnivores, *Peri* periphytivores. Codes for functional traits are in Table 2

Table 2 Correlation of functional traits to the ordination of functional space of PCoA

Trait	Code	PCoA1	PCoA2	R ²	P-value
Compression index	CI	0.53	0.85	0.42	< 0.01
Relative height	RH	0.97	- 0.23	0.74	< 0.01
Relative length of caudal peduncle	RLCP	- 0.88	- 0.48	0.45	< 0.01
Compression index of caudal peduncle	CICP	0.59	0.81	0.13	< 0.01
Index of ventral flattening	IVF	- 0.75	- 0.67	0.05	0.07
Relative area of pectoral fin	RAPF	- 0.11	- 0.99	0.09	0.01
Aspect ratio of pectoral fin	ARPF	0.94	- 0.34	0.04	0.16
Relative length of head	RLH	0.79	- 0.62	0.69	< 0.01
Relative position of eyes	RPE	- 0.58	- 0.81	0.25	< 0.01
Relative width of mouth	RWM	0.85	0.52	0.22	< 0.01
Mouth orientation	MO	0.45	0.89	0.43	< 0.01
Fineness coefficient	FC	- 0.9	0.43	0.77	< 0.01
Trophic guild	Guild	-	-	0.5	< 0.01

The envfit analysis does not calculate a value of correlation for each axis for nominal variables, such as trophic guilds

Bold values indicate significance at $\alpha = 0.05$

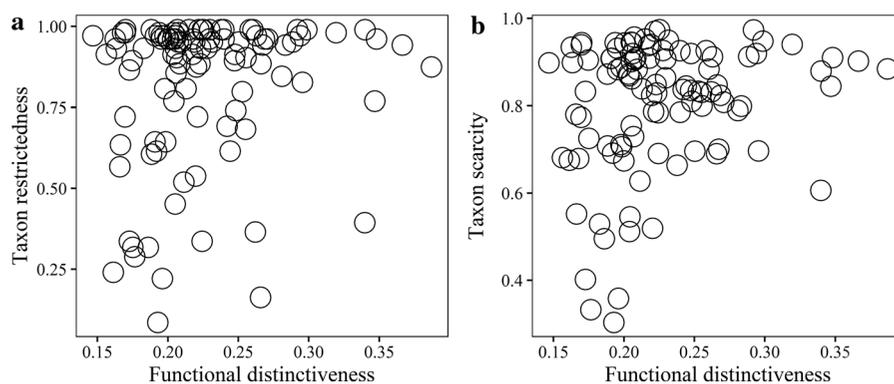


Fig. 4 Plots between mean functional distinctiveness and **a** taxon restrictedness and **b** taxon scarcity showed no sign of correlation

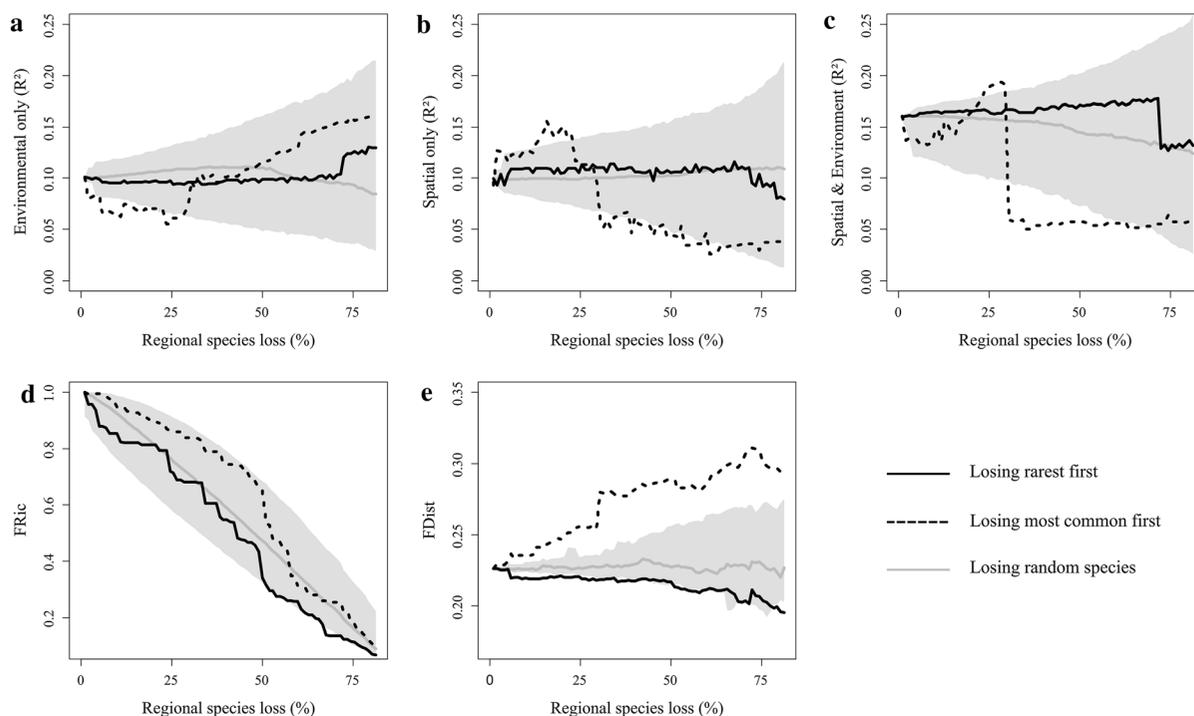


Fig. 5 Impact of regional species extinction on ecological filters (environmental and spatial variables) structuring fish assemblages in the Eastern Amazon and on the functional

structure regionally (FRic) and locally (FDist). The 95% confidence intervals are shown by the shaded area

Contributions of rare and common species

The regional loss of common species led to an accentuated decrease in local functional redundancy, highlighting the role of common species to maintain the local functional structure of fish communities. Local communities are dominated by common species and generally exhibit only a few functionally redundant species; therefore, the loss of common species

greatly affects the average functional distinctiveness as it decreases local redundancy in numerous communities at once. Nevertheless, both rare and common species contribute similarly to the regional functional richness, which may provide the capacity of this system to replace lost functions. Many studies showed that rare species provide unique combinations of traits because of their specialized habits and restricted habitat breadths (Coux et al., 2016; Leitão et al.,

Table 3 Environmental variables associated with fish assemblages in scenarios of progressive loss of dominant or rare species

Iteration	Losing most common first			Losing rarest first		
	Variables	Adj. R^2 Cum.	P -value	Variables	Adj. R^2 Cum.	P -value
All species	XFC_UB	0.076	0.001	XFC_UB	0.076	0.001
	XDEPTH_T	0.144	0.001	XDEPTH_T	0.144	0.001
	XFC_RO	0.192	0.001	XFC_RO	0.192	0.001
	XFC_CL	0.211	0.001	XFC_CL	0.211	0.001
	XFC_NAT	0.227	0.002	XFC_NAT	0.227	0.001
	PCT_FAST	0.239	0.001	PCT_FAST	0.239	0.003
	XC	0.248	0.013	XC	0.248	0.013
	Land2	0.255	0.014	Land2	0.255	0.021
	SEQ_FLO_1	0.260	0.035	SEQ_FLO_1	0.260	0.043
10 species removed	XFC_RO	0.063	0.001	XFC_UB	0.072	0.001
	XFC_UB	0.126	0.001	XDEPTH_T	0.141	0.001
	XDEPTH_T	0.159	0.001	XFC_RO	0.191	0.001
	XC	0.173	0.002	XFC_CL	0.209	0.001
	Land2	0.183	0.014	XFC_NAT	0.226	0.001
	XFC_CL	0.193	0.011	PCT_FAST	0.239	0.001
	PCT_FAST	0.205	0.008	XC	0.247	0.009
	Land1	0.210	0.043	Land2	0.255	0.009
40 species removed				SEQ_FLO_1	0.260	0.029
	XFC_UB	0.083	0.001	XFC_UB	0.074	0.001
	XFC_CL	0.117	0.001	XDEPTH_T	0.143	0.001
	XFC_NAT	0.137	0.002	XFC_RO	0.195	0.001
	XDEPTH_T	0.154	0.002	XFC_CL	0.212	0.002
				XFC_NAT	0.229	0.001
				PCT_FAST	0.243	0.001
				XC	0.251	0.004
				Land2	0.259	0.017
				SEQ_FLO_1	0.265	0.04
80 species removed	XFC_UB	0.122	0.001	XDEPTH_T	0.085	0.001
	XFC_CL	0.190	0.001	XFC_UB	0.156	0.001
	XDEPTH_T	0.215	0.005	XFC_RO	0.185	0.001
				XFC_CL	0.208	0.001
				XFC_NAT	0.226	0.001
				PCT_FAST	0.236	0.013
				XC	0.245	0.011
				Land2	0.254	0.011

The complete tables are available in Supplementary Material 2. Codes for variables are in Table S1. Land1 and Land2 refer to the axes of the PCA for landscape variables showed in Fig. 2

2016). However, as pointed by Chapman et al. (2018), common species also must hold a unique combination of traits, which allows them to achieve high

abundances, support larger habitat breadths, and occupy a wider portion of the geographic region.

The functionally rare species showed to be isolated and at the outer portion the functional space (Fig. 3).

The species that showed the highest values of functional rarity were the catfishes *Acanthodoras cataphractus* (Linnaeus, 1758) (Doradidae) and *Tetranematichthys barthemi* Peixoto and Wosiacki, 2010 (Auchenipteridae), and the electric fish *Brachyhypopomus sullivanii* Crampton, de Santana, Waddell and Lovejoy, 2017 (Hypopomidae). *A. cataphractus* has a nocturnal habit and is frequent in large rivers, swamps e mangroves (Boujard et al., 1997). The small size of *A. cataphractus* (11.5 cm; Sabaj & Ferraris, 2003) and its adaptation to complex environments allows it to occasionally enters small streams, like the observed in this study. *A. cataphractus* is an omnivorous species that seeks mainly organic waste by digging the sediment (Boujard et al., 1997). *T. barthemi* is also nocturnal, but little is known regarding its natural history and biology. Yet, based on the knowledge of its congeners (*Tetranematichthys wallacei* Vari & Ferraris, 2006 and *Tetranematichthys quadrifilis* (Kner, 1858)), we believe they are carnivores, with preferences for small fish, and their registries of occurrence indicate they are associated with shallow rainforest streams, with sandy bottoms and slow water flow (Vari & Ferraris, 2006), a microhabitat not frequent in the streams evaluated here.

The electric fish *B. sullivanii* is a recently described species, and its biological and natural history data are still scarce. However, there are some ecological notes recorded in the species description (Crampton et al., 2016). *B. sullivanii*, like all fish of the genus *Brachyhypopomus*, has a morphological specialization of electroreception for night activity. It is an insectivorous species, restricted to forested streams and savannas, normoxic, with low conductivity and smooth flow (Crampton et al., 2008). This specificity to the normal environment restricts its occurrence, since because of the small size of the gills when compared to other *Brachyhypopomus* that occur in hypoxic systems, *B. sullivanii* needs well-oxygenated stream (Crampton et al., 2008).

At the other extreme, we have common species, such as *Hyphessobrycon heterorhabdus* (Ulrey, 1894) (Characidae), *Microcharacidium weitzmani* Buckup, 1993 (Crenuchidae), and *Apistogramma* gr. *regani* (Cichlidae). These species have already been reported in other paper as abundant in the streams of the Acará-Capim basins (Montag et al., 2019). *H. heterorhabdus* and *A. gr. regani* live close to backwater systems,

where they capture food items (Brejão et al., 2013). Some characteristics may explain why these species are so numerous in the region. *H. heterorhabdus* and *A. gr. regani* are omnivorous and generalist, and *M. weitzmani* is invertivorous. These species have opportunistic habits and can feed close to macrophytes and in slow-flowing portions of the stream (Brejão et al., 2013; van der Sleen & Albert, 2017), common in altered streams. Ferreira et al. (2018) demonstrated that *M. weitzmani* is abundant in streams with different degrees of environmental preservation.

The high levels of functional redundancy observed in our study indicate that a species could compensate for the loss of another species in terms of contribution to ecosystem processes. This, together with the distinct responses of species to environmental conditions, gives rise to an increase in ecosystem stability (insurance effect of biodiversity, Yachi & Loreau, 1999). The studied streams still share several similarities with least or non-disturbed conditions (Juen et al., 2016; Montag et al., 2019; Leão et al., 2020), so an increase in stability could favour the biological communities in face of landscape changes. This is particularly important considering that these streams are inserted in the arc of deforestation, a region subjected to intensive logging where the effects of climatic changes together with land use activities are expected to be severe (Souza et al., 2019). Since fish communities showed a high turnover (i.e., high geographical taxon restrictedness and scarcity), environmental impacts could lead to the local extirpations of several redundant species (Correia et al., 2020).

Niche and dispersal-related assembly rules

Rare species were controlled by space, whilst common species were controlled by the environment. Dispersal ability is expected to be high amongst common species, so the low importance of space to modulate the composition of dominant species is in accordance with the literature. If dispersal is not limiting, these species can track the most suitable environmental conditions (Heino et al., 2015). This result challenges the customary view that common species are always generalists since they demonstrated a higher level of environmental specialization (Siqueira et al., 2012). However, the higher environmental signal for common species should be interpreted with caution, since it was inside the confidence interval of the null

scenario. But since the loss of dominant species led to an immediate decrease in the environmental signal, we believe our interpretation is valid.

Low environmental signal together with high spatial signal suggest that intermediate and rare species are controlled by either high or limiting dispersal (Ng et al., 2009). Rare species usually are geographically restricted, as widely observed in the ecological literature (Pérez-Mayorga et al., 2017; Grenié et al., 2018; Sykes et al., 2019), which is also the case of our study. Thus, the composition of rare species is explained by a strong limiting dispersal that hampers a perfect species sorting (Ng et al., 2009). This may also be the case of the rarest species in our simulations, which showed the same level of environmental signal than the null scenario, but low levels of spatial and spatially structured environmental signal. Alternatively, the low environmental signal could be a result of stronger drift effects on small populations (Melbourne & Hastings, 2008) or of non-measured variables, because rare species could be regulated by environmental variables that are more difficult to evaluate (Lennon et al., 2011).

The anthropogenic modifications in the landscape were particularly important to the dominant species. Stream fish are closely linked with the quality of the riparian vegetation, as it is their main source of food and shelter. Man-induced habitat degradation drives profound alterations in the structure of fish assemblages, as abundantly reported (Gido et al., 2010; Brejão et al., 2018). Although most species are negatively affected by these changes, some can benefit from them and become common (Parody et al., 2001), such as those with a generalist diet and opportunistic habits. For example, Brejão et al. (2018) showed that some cosmopolitan species had increased abundances at extensive levels of human modification. Most streams in our study are largely covered by primary and secondary forest and are highly diversified in terms of fish fauna (18.25 ± 6.25 species/stream), but deforestation is increasing and may lead to depauperated and homogeneous communities (Budnick et al., 2019).

Landscape changes can also influence dispersal-related processes (Taylor, 1997; Warren & Pardew, 1998; Perkin & Gido, 2012). Road networks and small dams make up barriers to fish movement, and habitat degradation can also impose lower permeability (Edge et al., 2017). Although we did not measure the

proportion of road crossings, they are common in altered regions with human presence and can have a homogenizing effect in fish biodiversity and change the functional identity of assemblages (Leitão et al., 2018). This is a major concern for the limited-dispersal rare species, because low connectivity may prevent them from recolonising nearby streams, and thus they can become more prone to extinction (Whitney et al., 2016).

For the last decades, the Eastern Amazon is changing from being previously dominated by large forests to a mosaic of large pastures, monocultures, and roads with ever-smaller patches of vegetation (Stabile et al., 2020). Despite the conservation efforts over the last decades, deforestation increased again in the last years (Nepstad et al., 2014), culminating in huge fires in 2019 with potentially strong effects on the regional hydrological cycle (Lovejoy & Nobre, 2019) and thus on the sensitive dynamics of streams. Here we showed that classifying fish according to their rarity evidenced that each group is regulated by distinct assembly rules. Addressing rare species is often overlooked, despite constant claims regarding their importance and their frequently concerning conservation status (Mouillot et al., 2013; Leitão et al., 2016). Accounting for their rarity can offer a more refined look at the responses of species to human modifications, providing valuable information on how to tackle biodiversity loss.

Acknowledgements We are grateful to Naiara R. Torres for designing the map and for calculating landscape and spatial variables. We thank the following institutions for funding: Conselho Nacional para o Desenvolvimento Científico e Tecnológico (MCTIC/CNPq) (LFAM: 302406/2019-0, NLB: 300706/2019-7, BES: 151743/2019-3); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/MEC) (NLB: 88887.475625/2020-00, CMCL: 1660508/2016-11, LBS: 88882.445585/2019-01); Fundação Amazônia de Amparo a Estudos e Pesquisas (FAPESPA) (003/2011, 085/2014, 128/2014) and CNPq (481015/2011-6). Conservation International (CI-Brasil), Fundação de Amparo e Desenvolvimento da Pesquisa (FADESP), Cikel, 33 Forest, Hydro Norsk, and Agropalma Group provided logistic support.

References

- Almeida, C. A., A. C. Coutinho, J. C. D. M. Esquerdo, M. Adami, A. Venturieri, C. G. Diniz, N. Dessay, L. Durieux & A. R. Gomes, 2016. High spatial resolution land use and land cover mapping of the Brazilian Legal Amazon in 2008

- using Landsat-5/TM and MODIS data. *Acta Amazonica* 46: 291–302.
- Alvares, C. A., J. L. Stape, P. C. Sentelhas, J. L. M. Gonçalves & G. Sparovek, 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728.
- Barlow, J., E. Berenguer, R. Carmenta & F. França, 2019. Clarifying Amazonia's burning crisis. *Global Change Biology* 26: 319–321.
- Barthem, R. B., P. Charvet-Almeida, L. F. A. Montag & A. E. Lanna, 2004. Amazon basin, GIWA Regional Assessment 40b. University of Kalmar, Kalmar, Sweden.
- Bauman, D., T. Drouet, S. Dray & J. Vlemminckx, 2018a. Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography* 41: 1638–1649.
- Bauman, D., T. Drouet, M. J. Fortin & S. Dray, 2018b. Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. *Ecology* 99: 2159–2166.
- Blanchet, F. G., P. Legendre & D. Borcard, 2008. Forward selection of explanatory variables. *Ecology* 89: 2623–2632.
- Boujard, T., M. Pascal, F. J. Meunier & P.-Y. L. Bail, 1997. Poissons de Guyane: Guide écologique de l'Approuague et de la réserve des Nouragues. Editions Quae, Paris.
- Brejão, G. L., P. Gerhard & J. Zuanon, 2013. Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon. *Neotropical Ichthyology* 11: 361–373.
- Brejão, G. L., D. J. Hoenighaus, M. A. Pérez-Mayorga, S. F. B. Ferraz & L. Casatti, 2018. Threshold responses of Amazonian stream fishes to timing and extent of deforestation. *Conservation Biology* 32: 860–871.
- Budnick, W. R., T. Leboucher, J. Belliard, J. Soininen, I. Lavoie, K. Pound, A. Jamoneau, J. Tison-Rosebery, E. Tales, V. Pajunen, S. Campeau & S. I. Passy, 2019. Local and regional drivers of taxonomic homogenization in stream communities along a land use gradient. *Global Ecology and Biogeography* 28: 1597–1609.
- Callisto, M., C. B. M. Alves, J. M. Lopes & M. A. Castro (eds), 2014. Condições ecológicas em bacias hidrográficas de empreendimentos hidrelétricos. CEMIG, Belo Horizonte.
- Chapman, A. S. A., V. Tunnicliffe & A. E. Bates, 2018. Both rare and common species make unique contributions to functional diversity in an ecosystem unaffected by human activities. *Diversity and Distributions* 24: 568–578.
- Correia, I., E. R. Nascimento & S. F. Gouveia, 2020. Effects of climate and land-use gradients on avian phylogenetic and functional diversity in a tropical dry forest. *Journal of Arid Environments* 173: 104024.
- Coux, C., R. Rader, I. Bartomeus & J. M. Tylianakis, 2016. Linking species functional roles to their network roles. *Ecology Letters* 19: 762–770.
- Crampton, W. G. R., L. J. Chapman & J. Bell, 2008. Interspecific variation in gill size is correlated to ambient dissolved oxygen in the Amazonian electric fish *Brachyhyopomus* (Gymnotiformes: Hypopomidae). *Environmental Biology of Fishes* 83: 223–235.
- Crampton, W. G. R., C. D. Santana, J. C. Waddell & N. R. Lovejoy, 2016. A taxonomic revision of the Neotropical electric fish genus *Brachyhyopomus* (Ostariophysi: Gymnotiformes: Hypopomidae), with descriptions of 15 new species. *Neotropical Ichthyology* 14: e150146.
- Dray, S., D. Bauman, G. Blanchet, D. Borcard, S. Clappe, G. Guenard, T. Jombart, G. Larocque, P. Legendre, N. Madi & H. H. Wagner, 2020. *adespatial: Multivariate Multiscale Spatial Analysis*. R package version 0.3-8 edn.
- Dray, S., P. Legendre & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.
- Edge, C. B., M.-J. Fortin, D. A. Jackson, D. Lawrie, L. Stanfield & N. Shrestha, 2017. Habitat alteration and habitat fragmentation differentially affect beta diversity of stream fish communities. *Landscape Ecology* 32: 647–662.
- Ferreira, M. C., T. O. Begot, B. S. Prudente, L. Juen & L. F. A. Montag, 2018. Effects of oil palm plantations on habitat structure and fish assemblages in Amazon streams. *Environmental Biology of Fishes* 101: 547–562.
- Frimpong, E. A., T. M. Sutton, K. J. Lim, P. J. Hrodey, B. A. Engel, T. P. Simon, J. G. Lee & D. C. Le Master, 2005. Determination of optimal riparian forest buffer dimensions for stream biota landscape association models using multivariate and multivariate responses. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1–6.
- Gardner, T. A., J. Ferreira, J. Barlow, A. C. Lees, L. Parry, I. C. G. Vieira, E. Berenguer, R. Abramovay, A. Aleixo & C. Andretti, 2013. A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 20120166.
- Gido, K. B., W. K. Dodds & M. E. Eberle, 2010. Retrospective analysis of fish community change during a half-century of landuse and streamflow changes. *Journal of the North American Benthological Society* 29: 970–987.
- Grenié, M., P. Denelle, C. M. Tucker, F. Munoz & C. Violle, 2017. funrar: An R package to characterize functional rarity. *Diversity and Distributions* 23: 1365–1371.
- Grenié, M., D. Mouillot, S. Villéger, P. Denelle, C. M. Tucker, F. Munoz & C. Violle, 2018. Functional rarity of coral reef fishes at the global scale: hotspots and challenges for conservation. *Biological Conservation* 226: 288–299.
- Grime, J. P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Hagen, E. M., M. E. McTammany, J. R. Webster & E. F. Benfield, 2010. Shifts in allochthonous input and autochthonous production in streams along an agricultural land-use gradient. *Hydrobiologia* 655: 61–77.
- Heino, J., 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews* 88: 166–178.
- Heino, J., A. S. Melo & L. M. Bini, 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology* 60: 223–235.
- Juen, L., E. J. Cunha, F. G. Carvalho, M. C. Ferreira, T. O. Begot, A. L. Andrade, Y. Shimano, H. Leão, P. S. Pompeu & L. F. A. Montag, 2016. Effects of oil palm plantations on the habitat structure and biota of streams in Eastern Amazon. *River Research and Applications* 32: 2081–2094.
- Kaufmann, P. R., P. Levine, D. V. Peck, E. G. Robison & C. Seeliger, 1999. Quantifying physical habitat in wadeable

- streams. *Environmental Monitoring and Assessment Program, National Health and Environmental Effects Research Laboratory, Office of Research and Development*. US Environmental Protection Agency.
- Laliberté, E., P. Legendre & B. Shipley, 2014. *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12 edn.
- Lê, S., J. Josse & F. Husson, 2008. FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* 25: 1–18.
- Leal, C. G., P. S. Pompeu, T. A. Gardner, R. P. Leitão, R. M. Hughes, P. R. Kaufmann, J. Zuanon, F. R. de Paula, S. F. B. Ferraz, J. R. Thomson, R. M. Nally, J. Ferreira & J. Barlow, 2016. Multi-scale assessment of human-induced changes to Amazonian instream habitats. *Landscape Ecology* 31: 1725–1745.
- Leal, C. G., J. Barlow, T. A. Gardner, R. M. Hughes, R. P. Leitão, R. Mac Nally, P. R. Kaufmann, S. F. B. Ferraz, J. Zuanon, F. R. de Paula, J. Ferreira, J. R. Thomson, G. D. Lennox, E. P. Dary, C. P. Röpke & P. S. Pompeu, 2018. Is environmental legislation conserving tropical stream faunas? A large-scale assessment of local, riparian and catchment-scale influences on Amazonian fish. *Journal of Applied Ecology* 55: 1312–1326.
- Leão, H., T. Siqueira, N. R. Torres & L. F. A. Montag, 2020. Ecological uniqueness of fish communities from streams in modified landscapes of Eastern Amazonia. *Ecological Indicators* 111: 106039.
- Leibold, M. A. & J. M. Chase, 2018. *Metacommunity Ecology*. Princeton University Press, Princeton and Oxford.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau & A. Gonzalez, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.
- Leitão, R. P., J. Zuanon, S. Villéger, S. E. Williams, C. Baraloto, C. Fortunel, F. P. Mendonça & D. Mouillot, 2016. Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society B: Biological Sciences* 283: 20160084.
- Leitão, R. P., J. Zuanon, D. Mouillot, C. G. Leal, R. M. Hughes, P. R. Kaufmann, S. Villéger, P. S. Pompeu, D. Kasper, F. R. de Paula, S. F. B. Ferraz & T. A. Gardner, 2018. Disentangling the pathways of land use impacts on the functional structure of fish assemblages in Amazon streams. *Ecography* 41: 219–232.
- Lennon, J. J., C. M. Beale, C. L. Reid, M. Kent & R. J. Pakeman, 2011. Are richness patterns of common and rare species equally well explained by environmental variables? *Ecography* 34: 529–539.
- Lo, M., J. Reed, L. Castello, E. A. Steel, E. A. Frimpong, A. Ickowitz, 2020. The influence of forests on freshwater fish in the tropics: a systematic review. *BioScience* 70: 404–414. <https://doi.org/10.1093/biosci/biaa021>.
- Loureiro, V. R., 2012. The Amazon in the 21st century: new forms of development. *Revista Direito GV* 8: 527–552.
- Lovejoy, T. E. & C. Nobre, 2019. Amazon tipping point: last chance for action. *Science Advances*. <https://doi.org/10.1126/sciadv.aba2949>.
- Mapbiomas, 2019. *Coleção 4.1 da série anual de mapas de cobertura e uso de solo do Brasil*. In: <http://mapbiomas.org/>. Accessed 15 May 2020.
- Melbourne, B. A. & A. Hastings, 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454: 100–103.
- Montag, L. F. A., K. O. Winemiller, F. W. Keppeler, H. Leão, N. L. Benone, N. R. Torres, B. S. Prudente, T. O. Begot, L. M. Bower & D. E. Saenz, 2019. Land cover, riparian zones and instream habitat influence stream fish assemblages in the eastern Amazon. *Ecology of Freshwater Fish* 28: 317–329.
- Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, S. Lavergne, S. Lavorel & N. Mouquet, 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology* 11: e1001569. <https://doi.org/10.1371/journal.pbio.1001569>.
- Nahum, J. S. & C. B. Santos, 2013. Impactos socioambientais da dendeicultura em comunidades tradicionais na amazônia paraense. *Acta Geografica*. <https://doi.org/10.5654/actageo2013.0003.0004>.
- Nepstad, D., D. McGrath, C. Stickler, A. Alencar, A. Azevedo, B. Swette, T. Bezerra, M. DiGiano, J. Shimada & R. S. Motta, 2014. Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. *Science* 344: 1118–1123.
- Ng, I. S. Y., C. M. Carr & K. Cottenie, 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619: 133–143.
- Ohlberger, J., G. Staaks & F. Hölker, 2006. Swimming efficiency and the influence of morphology on swimming costs in fishes. *Journal of Comparative Physiology B* 176: 17–25.
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlenn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szocs & H. Wagner, 2019. *vegan: Community ecology package*. R package version 2.5-6 edn.
- Pagotto, J. P. A., E. Goulart, E. F. Oliveira & C. B. Yamamura, 2011. Trophic ecomorphology of Siluriformes (Pisces, Osteichthyes) from a tropical stream. *Brazilian Journal of Biology* 71: 469–479.
- Pandit, S. N., J. Kolasa & K. Cottenie, 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.
- Parody, J. M., F. J. Cuthbert & E. H. Decker, 2001. The effect of 50 years of landscape change on species richness and community composition. *Global Ecology and Biogeography* 10: 305–313.
- Peck, D. V., A. T. Herlihy, B. H. Hill, R. M. Hughes, P. R. Kaufmann, D. J. Klemm, J. M. Lazorchak, F. H. McCormick, S. A. Peterson, P. L. Ringold, T. Magee & M. R. Cappaert, 2006. Environmental monitoring and assessment program—surface waters western pilot study: Field operations manual for wadeable streams. *EPA 600/R-06/003*. U.S. Environmental Protection Agency, Washington.

- Peel, M. C., B. L. Finlayson & T. A. McMahon, 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11: 1633–1644.
- Pérez-Mayorga, M. A., L. Casatti, F. B. Teresa & G. L. Brejão, 2017. Shared or distinct responses between intermediate and satellite stream fish species in an altered Amazonian River? *Environmental Biology of Fishes* 100: 1527–1541.
- Perkin, J. S. & K. B. Gido, 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications* 22: 2176–2187.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Ramalho, W. P., M. S. Susçuarana, J. J. López-Rojas, L. V. Rocha, E. C. Keppeler & L. J. Soares Vieira, 2014. Impacto do assoreamento sobre a diversidade de peixes em igarapés de um complexo vegetacional de campinarana no noroeste do Acre, Brasil. *Neotropical Biology and Conservation* 9: 105–114.
- Ribeiro, M. D., F. B. Teresa & L. Casatti, 2016. Use of functional traits to assess changes in stream fish assemblages across a habitat gradient. *Neotropical Ichthyology* 14: e140185.
- Richards, J. A. & X. Jia, 1999. Remote sensing digital image analysis: An introduction, 3rd ed. Springer, Berlin.
- Sabaj, M. H. & C. J. Ferraris Jr., 2003. Doradidae (Thorny catfishes). In Reis, R. E., S. O. Kullander & J. C. J. Ferraris (eds), *Checklist of the Freshwater Fishes of South and Central America*. EDIPUCRS, Porto Alegre: 456–469.
- Santos, L. L., N. L. Benone, B. E. Soares, R. B. Barthem & L. F. A. Montag, 2019. Trait-environment relationships in Amazon stream fish assemblages. *Ecology of Freshwater Fish* 28: 424–433.
- Siqueira, T., L. M. Bini, F. O. Roque, S. R. M. Couceiro, S. Trivinho-Strixino & K. Cottenie, 2012. Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 35: 183–192.
- Smith, M. D. & A. K. Knapp, 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* 6: 509–517.
- Souza, C. M., F. T. Kirchhoff, B. C. Oliveira, J. G. Ribeiro & M. H. Sales, 2019. Long-term annual surface water change in the Brazilian amazon biome: potential links with deforestation. *Infrastructure Development and Climate Change*. *Water* 11: 566.
- Stabile, M. C. C., A. L. Guimarães, D. S. Silva, V. Ribeiro, M. N. Macedo, M. T. Coe, E. Pinto, P. Moutinho & A. Alencar, 2020. Solving Brazil's land use puzzle: Increasing production and slowing Amazon deforestation. *Land Use Policy* 91: 104362.
- Sykes, L., L. Santini, A. Etard & T. Newbold, 2019. Effects of rarity form on species' responses to land use. *Conservation Biology* 34:688–696. <https://doi.org/10.1111/cobi.13419>.
- Taylor, C. M., 1997. Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* 110: 560–566.
- van der Sleen, P. & J. S. Albert, 2017. Field guide to the fishes of the Amazon, Orinoco, and Guianas, Vol. 115. Princeton University Press, New Jersey.
- Vari, R. P. & C. J. Ferraris Jr., 2006. The catfish genus *Tetranemachthys* (Auchenipteridae). *Copeia* 2006: 168–180.
- Violle, C., W. Thuiller, N. Mouquet, F. Munoz, N. J. B. Kraft, M. W. Cadotte, S. W. Livingstone & D. Moullot, 2017. Functional rarity: the ecology of outliers. *Trends in Ecology & Evolution* 32: 356–367.
- Virgilio, L. R., W. P. Ramalho, J. C. B. S. Silva, M. Silveira Suçuarana, C. H. Brito & L. J. S. Vieira, 2018. Does riparian vegetation affect fish assemblage? A longitudinal gradient analysis in three Amazonian streams. *Acta Scientiarum Biological Sciences* 40: e42562.
- Warren Jr., M. L. & M. G. Pardew, 1998. Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* 127: 637–644.
- Watson, D. J. & E. K. Balon, 1984. Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. *Journal of Fish Biology* 25: 371–384.
- Whitney, J. E., K. B. Gido, E. C. Martin & K. J. Hase, 2016. The first to arrive and the last to leave: colonisation and extinction dynamics of common and rare fishes in intermittent prairie streams. *Freshwater Biology* 61: 1321–1334.
- Yachi, S. & M. Loreau, 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences* 96: 1463–1468.
- Zeni, J. O., M. A. Pérez-Mayorga, C. A. Roa-Fuentes, G. L. Brejão & L. Casatti, 2019. How deforestation drives stream habitat changes and the functional structure of fish assemblages in different tropical regions. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29: 1238–1252.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.