ORIGINAL ARTICLE

Historical stability promoted higher functional specialization and originality in Neotropical stream fish assemblages

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Abstract

Aim: Disturbances are events that influence the structure of biological assemblages, yet how historical disturbances have affected the functional structure of recent assemblages is still poorly known. We used species functional traits to investigate the effects of historical disturbances, such as past climate change (aridification), on the current structure of stream fish assemblages.

Location: Amazon Basin and Brazilian Northeast streams.

Methods: We used measures of functional specialization and originality to assess the effects of historical disturbances on the structure of fish assemblages in streams with similar local environmental conditions in each biome (Amazonia and Caatinga). For this, we measured 15 traits related to locomotion, feeding and habitat use for each species sampled. We then compared the functional structure of each assemblage expressed as functional richness (FRic) and evenness (FEve) between biomes. We also used structured and random simulations of species extinctions to identify the influence of the loss of original and specialized species due to historical disturbance.

Results: We found high levels of functional specialization in Amazonia (historically more stable) and redundancy in Caatinga (higher frequency of historical disturbances) regional assemblages, regardless of the inter-biome differences in species richness. These results were also detected in local assemblages, suggesting that the effect of historical disturbances influences the structure of fish assemblages, both at small and large spatial scales.

Main conclusions: The historical stability in Amazonian fish assemblages may have favoured a higher taxonomic and FRic, as well as greater functional specialization and originality, compared to Caatinga assemblages. Our results reinforce the importance of understanding and evaluating the evolutionary history of ecosystems in order to describe the current functional structure of species assemblages.

KEYWORDS
functional biogeography, functional structure, historical factors, ichthyofauna, Neotropical freshwaters, species loss

1 | INTRODUCTION

Disturbances are important events that modify the structure and diversity of biological communities. In many cases, they promote species loss (Ernst, Linsenmair, & Rödel, 2006), while in others they may constitute key factors in allowing species persistence (Pickett & White, 1985), or even new establishments (Mori, 2011). The level of species loss or persistence is related to the frequency and intensity of disturbances, with severe events normally followed by the extinction of less resilient species (Thomas et al., 2004). However, our knowledge of how disturbance operates comes predominantly from studies over short time-scales, and focusing on the taxonomic facet of biodiversity (Ives & Carpenter, 2007; Medeiros & Maltchik, 2001; Tilman, Reich, & Knops, 2006). Although obviously relevant, such studies have often been criticized for not incorporating measures based on species functional traits, and for not evaluating the possible effects of previous historical disturbances (Reiss, Bridle, Montoya, & Woodward, 2009). Understanding the long-term importance of natural historical disturbance in influencing the structure of biological assemblages may help to define better conservation strategies by considering the functional requirements and responses of species assemblages to ongoing global changes (Buisson, Grenouillet, Villéger, Canal, & Laffaille, 2013; Díaz & Cabido, 2001; Violle, Reich, Pacala, Enquist, & Kattge, 2014).

An alternative way to understand the effects of future changes in biological systems is to investigate how past events have influenced biological diversification and the structure of present assemblages. Historical events (i.e. mountain uplifts, glaciation, marine incursions and climatic changes) have produced natural disturbances that have shaped the evolutionary history of ecosystems, and their effects can still be observed in the functional structure of current assemblages (Gonzalez & Loreau, 2009). Assemblages subject to severe or repeated disturbances tend to contain proportionally more stress-tolerant species, and a structure that is simplified in terms of trait diversity (Zimov et al., 1995). Decreased species functional originality (FOri) (i.e. the inverse of redundancy, representing the isolation of a species in a functional space occupied by a given assemblage; sensu Mouillot, Graham, Villéger, Mason, & Bellwood, 2013) and functional specialization (i.e. the mean distance of a species in a functional space from the rest of the species pool; sensu Mouillot et al., 2013) are considered to be key consequences of this process. However, it remains unclear how historical disturbances can shape the structure of modern assemblages, although it has been shown that changes in functional specialization and originality may also be related with alterations in local conditions at an ecological time-scale (Leitão et al., 2018).

In order to help decouple the contribution of historical disturbances and current local conditions, it is possible to apply appropriate environmental condition controls; for instance, by selecting similar sites in terms of local attributes but located within different biogeographic zones (Cilleros, Allard, Grenouillet, & Brosse, 2016). Such an aim can be reached complementarily by assessing how levels of species originality and specialization affect the functional structure of assemblages (e.g. functional trait richness and evenness). This scenario allows us to hypothesize that, if historical factors are

more important than local environmental conditions, then different levels of specialization and originality will be found even in assemblages that occur under similar environmental conditions. For example, assemblages located in historically stable regions would be expected to exhibit higher levels of functional specialization due to the greater time available for diversification (Ricklefs, 2006). Such specialization will promote greater changes in assemblage functional structure because specialized species tend to occupy the boundaries of the functional space (extreme trait combinations) and generally have few neighbouring species (higher levels of originality). On the other hand, less extensive changes in functional structure would be expected to occur at sites within historically unstable regions, due to lower levels of both originality (high redundancy) and specialization.

Here, we compare the functional structure of stream fish assemblages from two Neotropical biomes that have experienced contrasting disturbance regimes since the Plio-Pleistocene. To test the effect of past stability on current patterns of the assemblages' functional structure, we assessed this at both local and the regional spatial scales. It is not possible to replicate biomes, but we selected streams with similar topographical (altitude, size and order) and general environmental conditions to control for local environmental effects. Firstly, we investigated the differences in functional structure between biomes taking into account the variation in local species richness. After this, we investigated the contribution of specialist and original species to the functional structure of each biome by generating simulations of species extinction.

2 | MATERIALS AND METHODS

2.1 | Biogeographic history of Caatinga and Amazonia

The current study was based on fish inventories of headwater streams from two Neotropical biomes: Amazonia, where sample sites drain into tributaries of the middle and lower Amazon Basin; and Caatinga, where sample sites drain into tributaries of the Jaguaribe and Coreaú Basins, north-eastern Brazil (Figure 1). Species assemblages from each biome were shaped under essentially different past conditions. During the past of Amazonia, the climate has been relatively stable (Peres et al., 2010), while the Caatinga region has been impacted by several disturbances (Pôrto, Cabral, & Tabarelli, 2004). In addition to marine incursions throughout its coastal regions some 5 Myr ago, a critical driver of changes in Caatinga landscapes was the set of huge climatic alterations that resulted in changes from tropical to semi-arid conditions (i.e. aridification process) during the Plio-Pleistocene (Pôrto et al., 2004). As a result, while the Amazonian ichthyofauna experienced long-term climatic stability, fish species assemblages from Caatinga experienced intense and frequent historical disturbances.

2.2 | Fish sampling and data selection

Fish sampling was conducted between 2011 and 2015 following a standardized protocol (Mendonça, Magnusson, & Zuanon, 2005;
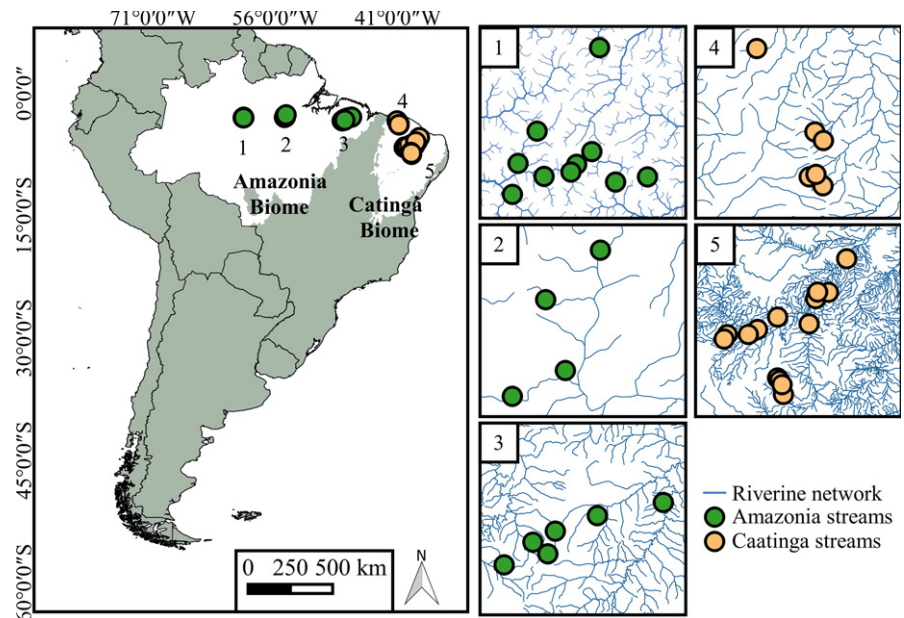
FIGURE 1 Geographical locations of sampled stream sites in the Brazilian Caatinga (20) and Amazonia (20) biomes

see Appendix S1 for details). To minimize the potential influence of anthropogenic disturbances on our results, the majority of stream sample sites were located within officially protected areas, or at least occurred within catchments with high environmental integrity (Leitão et al., 2018; Rodrigues-Filho et al., 2016).

In each stream, several environmental descriptors were measured, including channel depth and width, current velocity, canopy cover, temperature, pH and substrate composition in a 50-m stretch (see Appendix S1 for details of measures). Local environmental conditions, altitudinal gradients and stream order are often considered the main drivers structuring fish assemblages at local scales (Erős, Heino, Schmera, & Rask, 2009; Hoeinghaus, Winemiller, & Birnbaum, 2007; Mendonça et al., 2005; Rodrigues-Filho, Gurgel-Lourenço, Lima, de Oliveira, & Sánchez-Botero, 2017). To control for the effects of current local habitat on the fish assemblage functional structure, we then selected 20 streams in each biome with similar environmental conditions, a procedure that involved permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) and multivariate dispersion (PERMDISPER; Anderson, Ellingsen, & McArdle, 2006) (Figure S1.1 of Appendix S1).

2.3 | Functional structure of fish assemblages

We conducted an ecomorphological analysis to assess the functional structure of fish assemblages by characterizing all species for three key functions: food acquisition, locomotion and habitat preferences. Body mass and morphometric measures were taken from 3–10 adult individuals per species, and then combined into 15 ecomorphological traits (see Appendix S2 for details). To allow comparisons at the species level, we used the mean values for each trait measured across individuals. The traits measured have

been used canonically to describe the functional structure of freshwater ichthyofaunas (see Toussaint, Charpin, Brosse, & Villéger, 2016 for a worldwide scale example, and Leitão et al., 2018 for the Amazon). Although resulting in reduced accuracy, indirectly inferring function based on morpho-anatomical features is especially useful for species-rich regions where basic knowledge on fish ecology is largely lacking (Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017).

After standardizing and centralizing (mean zero and one standard deviation) values for the 15 traits, all species from the pool (Amazonia and Caatinga) were ordered in a multidimensional functional space using a Principal Component Analysis (PCA). Decisions concerning the number of dimensions that should be retained in order to adequately represent the initial functional distance between species pairs followed Maire, Grenouillet, Brosse, and Villéger (2015). We kept the first four PCA axes, as this was the minimum number of axes that provided a high-quality functional space, explaining 67.9% of the accumulated variance. We also verified that species ordination was not driven by a few functional traits; for example, different traits had correlations >0.7 on the four axes (Table S2.2), confirming the complementarity of information within the selected trait set. From this functional space, functional structure indices were then calculated.

We used functional richness (FRic) and functional evenness (FEve) to describe assemblage functional structure. FRic is the volume of the convex hull polygon occupied by all species of an assemblage within the defined functional space (Cornwell, Schwilk, & Ackerly, 2006). We standardized FRic values for each assemblage by expressing them as a proportion of the volume filled by the global pool of species. FEve indicates the regularity of species abundance distributions in functional space, and is constrained between 0 and 1, increasing when species and their

abundances are more evenly distributed (Villéger, Mason, & Mouillot, 2008).

2.4 | Data analysis

We compared the species assemblage structure between biomes at both regional (species pool from each biome) and local (streams) scales. The latter comparison was conducted with a Student *t* test using as response variable the values of species richness and functional structure (FRic and FEve). To take into account the effects of species richness on FRic and FEve in each biome, we conducted an analysis of covariance (ANCOVA), with species richness and biome (factor) as predictor variables. This framework provided an interpretation of the relationship between local species richness values and between biome variance in assemblage functional structure. Given that the two biomes have contrasting evolutionary histories, the use of ANCOVA allowed to evaluate the influence of the regional species pool (selected across the evolutionary history of each biome) on the functional patterns at the local streams to be tested.

To determine how historical disturbances influenced the functional structure of assemblages *via* trait diversification between species (specialization or originality), we conducted a set of species loss simulations. We first calculated the FOri and specialization (FSpe) values for each species. Both indexes were standardized between 0 and 1, dividing the value of each species by the respective maximum values for FOri and FSpe derived for the total species pool. FOri is expressed as the distance between each species and its nearest neighbour in a given multidimensional functional space; species will be functionally less original when showing combinations of traits similar to another species (Mouillot et al., 2013). Functional specialization (FSpe) is expressed by the Euclidean distance between each species and the centroid of the functional space (Mouillot et al., 2013). Lower FSpe indicates that the generalist species (species closer to the centre of the functional space) are more representative than specialist species within a given assemblage. We then evaluated to what extent the loss

of more original and specialized species (higher values of FOri and FSpe) promoted changes in FRic and FEve. To do this, we sequentially removed the species with the highest FOri and FSpe values, and then calculated the remaining FRic and FEve values for each regional assemblage. The observed changes in functional structure are informative in themselves, but to investigate if they were greater than expected by chance, we also compared those scenarios to null models where species were randomly removed (irrespective to their level of originality and specialization) before calculating FRic and FEve (999 times).

Functional diversity indexes were calculated with the functions *convhulln* (FRic, "geometry" package) and *dbFD* (FEve, "FD" package) (Laliberté & Legendre, 2010). The packages "geometry" (Habel, Grasman, Stahel, & Sterratt, 2014) and "cluster" (Maechler, Rousseew, Struyf, Hubert, & Hornik, 2016) were used to calculate nearest neighbour distances, using R 3.4.2 (The R Foundation for Statistical Computing, 2017).

3 | RESULTS

3.1 | Functional structure of fish assemblages between biomes

A total of 109 species were collected from 40 sampled streams (32 in Caatinga and 83 in Amazonia, with six species present in both biomes), distributed across six orders and 15 families (Table S3.1 of Appendix S3). The proportion of species within each fish order was similar between biomes, with exception of Gymnotiformes that occurred only in the Amazonian streams (Figure S3.1). Species of the orders Characiformes and Siluriformes showed greatest occupation of multifunctional space (Figure S3.2-3).

Taxonomic and FRic was higher in Amazonian streams than in those from Caatinga (Figure 2). This was largely due to the great influence of traits correlated with PC 2 and PC 3 of the functional space (Figure 3), such as fins surface to body size ratio, transversal body shape and mass (Table S2.2). On the other hand, regularity of
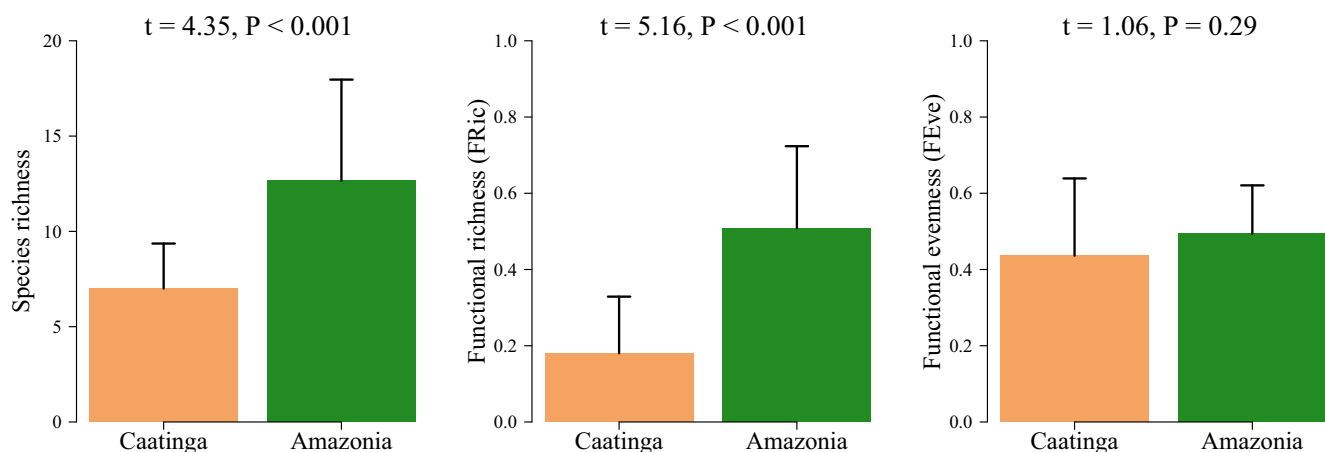

FIGURE 2 Species richness, Functional Richness (FRic) and Functional Evenness (FEve) of local stream fish assemblages from Caatinga (n = 20) and Amazonia (n = 20). Bars represent an above-average standard deviation. The Student *t* test values of $p < .05$ were considered significant
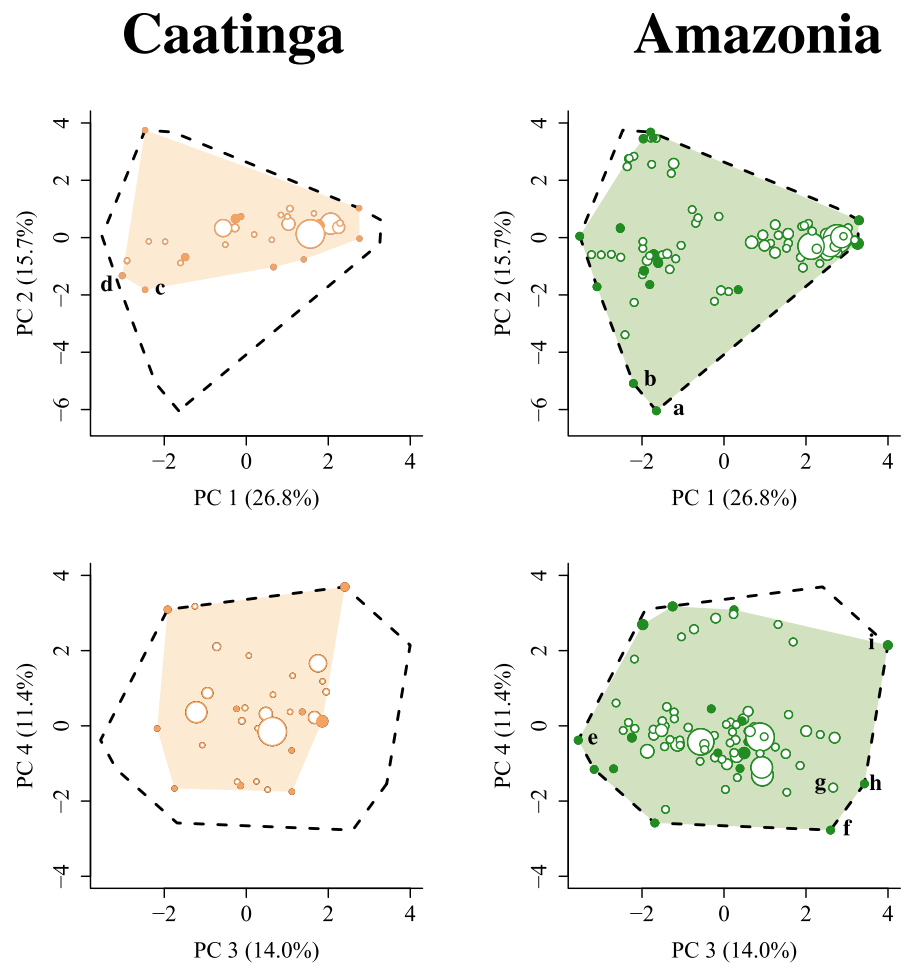
Caatinga   Amazonia

FIGURE 3 Multidimensional space of stream fish ecomorphological traits from regional assemblages of Caatinga and Amazonia, represented by the first four axes of a Principal Component Analysis (PC). Dots correspond to each species, with size proportional their total abundance in each biome. Filled dots correspond to species located on the border of the functional space for each regional assemblage. The volume of the functional space occupied by each regional assemblage is represented by the polygons. The dotted line represents the functional volume occupied by the global pool of species. Letters indicate species particularly cited in the Discussion section

functional space occupation (FEve) did not differ between biomes (Figure 2). The number of species in stream sites explained the variation only on FRic ($F = 10.22$; $p = .003$). On the other hand, there was no effect of biome on FRic ($F = 0.55$; $p = .43$) and FEve ($F = 2.80$; $p = .10$) (Figure 4).

3.2 | Impacts of losing functional specialists and original species

The species loss simulations revealed that, for both Amazonian and Caatinga regional assemblages, FRic decreased much faster with the removal of the most functionally original and the most specialized species than via random loss (Figure 5a,b). This decrease was especially acute in Amazonia, where FRic dropped by 80% with the loss of only the 15% most original and specialized species. During simulations, FSpe had greater influence in Amazonia, while FOri was more important in Caatinga for changes in FEve (Figure 5c,d). FEve values were lower than expected by chance after the loss of the 50% most original species in Caatinga streams, while the loss of approximately 55% of the most specialized species resulted in lower FEve than expected by chance in Amazonia. Similar patterns were observed after controlling for the effects of species richness on the functional structure of the assemblages (see Appendix S4 for details).
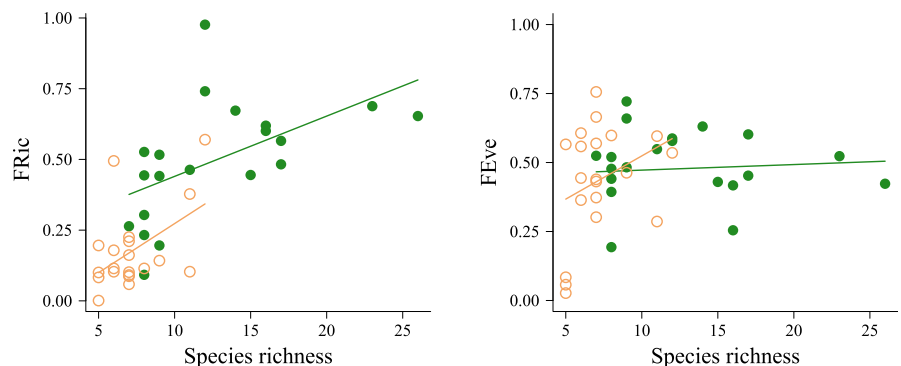

FIGURE 4 Linear relationships between species richness and functional richness—FRic (left) and functional evenness—FEve (right) for stream fish assemblages from Caatinga (open) and Amazonia (filled)
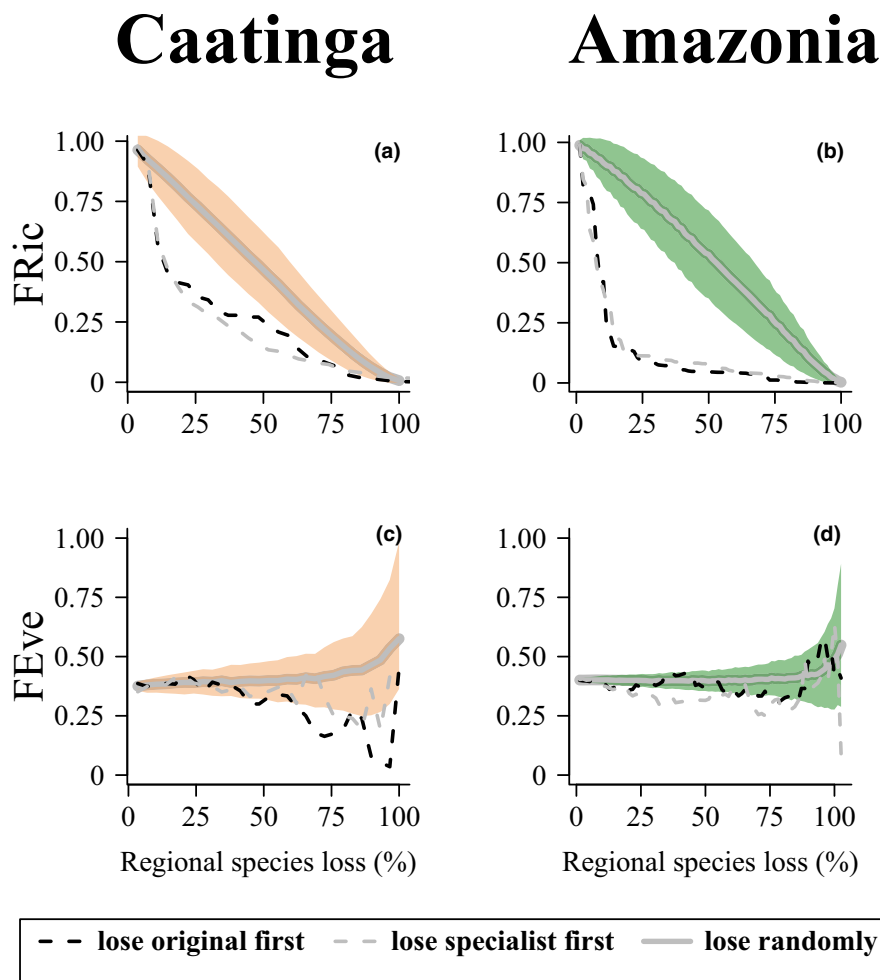
Caatinga   Amazonia

FIGURE 5 Impact of losing original and specialist species on the functional richness (FRic) and functional evenness (FEve) of regional stream fish assemblages from Caatinga (a, c) and Amazonia (b, d). Each scenario was tested against random loss of species (grey line and shaded area indicate, respectively, the mean and the 95% confidence interval of the null models)

4 | DISCUSSION

It has been well documented that almost all kinds of current disturbances have profound impacts on the structure of species assemblages (Hooper et al., 2012; Kulakowski & Veblen, 2007). However, how historical disturbances have affected the functional structure of current assemblages is still poorly known, especially for the species-rich tropical ecosystems. We analysed the contrasting consequences of historical disturbances on stream fish assemblages from two Neotropical biomes. Taxonomic and FRic were higher in the more historically stable one (Amazonia), at both local and regional scales. At the regional scale, species extinction simulations revealed that assemblages subjected to higher frequency and intensity of disturbances (Caatinga) have higher levels of functional redundancy, whereas historically stable assemblages (Amazonia) have proportionally more species with unique and extreme traits combinations. Therefore, losing species would cause greater erosion of FRic in Amazonia than in Caatinga. Differences in the level of niche packing between regions influenced by different levels of historical stability could explain these results. In simulated extinction analysis, increases in niche specialization in the historically stable region resulted in a stronger effect on assemblage functional structure. The same patterns were observed after controlling for species

number (Figure S4.1), indicating that the functional responses of the fish assemblages were not directly dependent on taxonomic richness.

4.1 | Functional characterization of species between biomes

Despite the high overlap in functional space filled by fish species from the two biomes, the amount of space filled by the Amazonian species, especially in the second and third PC axes, explained their higher FRic values. In practice, such morphological diversification may represent a wide range of possibilities in terms of feeding resource use and stream habitat occupation (Leitão et al., 2016). For example, two exclusive Amazonian species of the family Loricariidae (*Rineloricaria madeira* and *R. lanceolata*; letters **a** and **b** in Figure 3), positioned at the lower extreme of PC2, have highly specialized phenotypes that reduce drag and increase propulsion capacity, allowing movement and survival in extremely strong currents. In the Caatinga, representatives of this same family (*Parotocinclus haroldoi* and *P. cearensis*; **c** and **d** in Figure 3) also have negative values in PC2, but with lower levels of specialization. Such species have a periphyton-grazing habit and the peculiar shape of the body allows them to exploit rocky bottoms in rapids, roots, and trunks (Pagotto, Goulart, Oliveira, & Yamamura, 2011).

Similarly, species with extreme PC3 values were found exclusively in Amazonian streams. The main characteristic distinguishing between these species is body mass (higher and lower values found respectively in the negative and positive extremes of PC3). For instance, among all studied species, the heaviest is a member of the family Acestrorhynchidae (*Acestrorhynchus falcatus*; letter **e** in Figure 3). It is a high-speed and diurnal predator, feeding exclusively on fish and being one of the main organisms responsible for the top-down control in these systems (Clark, Ostrand, & Bonner, 2017). Extreme positive PC3 scores occur for highly specialized small-body species capable of exploiting highly specific microhabitats and diets, such as the miniature catfish *Pygidianops amphioxus* (**f** in Figure 3), which spends its entire life buried in the sand feeding nocturnally on small benthic invertebrates (Carvalho, Zuanon, & Ferreira, 2014). Other habitat-specialists are the crenuchids *Microcharacidium weitzmani* and *M. eleotrioides* (**g** and **h** in Figure 3), with respectively maximum body length of 12 and 21 mm (Buckup, 1993), which occupy temporary ponds associated with streams or the bottom of the main channel, where they feed on small autochthonous insects dragged by the current (J. Zuanon, pers. obs.). Another example is the killifish *Laimosemion kirovskyi* (**i** in Figure 3), which has the striking ability to reach shallow temporary ponds by jumping movements across dry land, escaping from stream predators and using allochthonous resources available in these marginal systems (Espírito-Santo, Rodríguez, & Zuanon, 2013).

Increased specialization and originality may be related to evolutionary mechanisms that promote the use of different habitats and new feeding resources (Micheli & Halpern, 2005; Mouillot, Dumay, & Tomasini, 2007). This can be observed at a regional scale (biomes), suggesting that the high FRic of fish assemblages in Amazonian streams results from unique combinations of traits associated with species that are not found in the Caatinga. In fact, in a long-term experiment, Reich et al. (2012) have shown that environmental disturbances leads to functional impoverishment of assemblages. Moreover, recent findings have shown that the most unique and extreme combinations of traits are disproportionately supported by rare species, which often have greater sensitivity to disturbances (Leitão et al., 2016). Our results agreed with this pattern, as the most specialized species (those that are at the margins of functional space) were least abundant, especially in Caatinga (filled circles on Figure 3). Possible explanations for low functional specialization in the Caatinga may thus include higher extinction rates of less abundant species with restricted spatial distributions.

4.2 | Historical processes and assemblage functional structure

The different patterns observed for the structure of stream fish assemblages between Amazonia and Caatinga may have their roots in the evolutionary trajectories of the two regions during the last 2 Myr, approximating to the start of the Caatinga aridification process (Pôrto

et al., 2004). In the last 2 Myr the Amazon biome had a relatively stable climate (few large-scale disturbances), while the Caatinga experienced marine incursions across the coastal sector, and the regional climate changed dramatically from humid to semi-arid following the last glacial period (Pôrto et al., 2004). These large-scale historical events promoted a drastic reduction in the drainage area of the Caatinga and probably promoted a variety of extinction events in the regional ichthyofauna (Hugueny, Movellan, & Belliard, 2011). These extinctions would have reduced the overall taxonomic richness of the biome and, together with the climatic severity, may particularly favoured species less sensitive to the current semi-arid conditions.

Other factors may also have influenced current patterns of the stream fish assemblages functional structure between Amazonia and Caatinga, such as the total area of the biomes and the dispersal history of the species involved (Blanchet et al., 2010). Fish dispersal capacity can be inferred in several ways, including such morphological traits as body size, mass and transversal surface (Tedesco et al., 2012). Although we found larger sized stream fish species in Amazonia, the overall pattern for the Neotropical region is of species with low dispersal capacity (Dias et al., 2014), which leads to important implications. For the Amazon, the large drainage area (*c*. 7 million km^2) makes it impossible for most species to colonize the most distant sites. This, together with historical stability, favours higher rates of diversification (Peres et al., 2010). In contrast, the Caatinga has a smaller drainage area, but the aridification process has resulted in numerous water disconnection events (Datry, Larned, & Tockner, 2014). In contrast to the situation in the Amazon (spatially separated sites due to the larger drainage area), the discontinuity events in the Caatinga tend to result in assemblages with high levels of redundancy. Indeed, Dias et al. (2014) found that connected water systems have higher diversification values. Consequently, we believe that historically stable regions with larger drainage areas tend to have stream fish assemblages with higher values of functional specialization and originality due to lower extinction rates and high dispersal limitation.

Large changes in functional diversity may occur if an already stressed community is disturbed by a new factor (Paine, Tegner, & Johnson, 1998). This prediction has been confirmed in short-term studies looking at the synergistic effects of habitat degradation and introduced species (Flynn et al., 2009; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2015), as well as modelled scenarios of the effects of future climatic changes on stream fish assemblages (Buisson et al., 2013). The collapse of the late Quaternary megafauna is a good example of how historical events can influence the structure of real assemblages (Johnson, 2009; Zimov et al., 1995). The loss of its interactions with regional vegetation caused numerous changes in ecosystem dynamics, most notably biotic homogenization and changes in the fire regimes due to the accumulation of combustible vegetative material (Johnson, 2009). This is one of the best-documented examples of how biodiversity loss can directly affect ecosystem functionality, and can serve as a model for the likely consequences and directions of future climatic changes. Thus, the chronological components of such results (past, present and future projections) can serve to warn us about the potential of disturbances, acting at a variety of spatial scales,

to control the diversification process (specialization and originality) in biological assemblages.

4.3 | Study limitations and perspectives

Although current assemblages commonly show signatures of their past (Ricklefs, 2006), we must be careful when interpreting modern patterns based solely on historical events. In this context, an important factor to be considered is the different magnitude of current human pressure between Amazonia and Caatinga, especially in relation to the more degraded landscape conditions and the significantly higher level of fish introductions found in the latter (Pereira et al., 2017). We recognize that these factors cannot be completely ruled out as having had an impact on the analysed systems. However, stream sites were carefully selected precisely to mitigate the impacts of this possible analytical noise, with chosen sites having the smallest possible amount of habitat degradation and small (or zero) numbers of introduced species (in terms of total abundance per assemblage).

Second, although this approach has been extensively studied and is well-established in the literature (e.g. Leitão et al., 2016; Toussaint et al., 2016; Villéger et al., 2017), we described the functional structure of the fish assemblages using only morphometric traits. The inclusion of other types of traits, such as species life history (Espírito-Santo et al., 2013; Winemiller & Rose, 1992) and environmental tolerance (Teresa & Casatti, 2012), would certainly add additional information on the possible effects of historical disturbances. However, such information is extremely scarce for the stream ichthyofauna from both Amazonia and Caatinga, so that currently it is only available for a very small portion of the studied species. In consequence, we fully support the calls for an urgent improvement on the knowledge of basic biological and ecological aspects of tropical stream ichthyofaunas (e.g. Leitão et al., 2018), as well as for a more complete and standardized protocol of fish functional trait assessment (e.g. Thorson, Munch, Cope, & Gao, 2017; Villéger et al., 2017).

5 | CONCLUSIONS

We studied two regional assemblages with very distinct evolutionary histories, which resulted in a large-scale natural experiment concerning the effects of environmental disturbances on the structure of stream fish assemblages. Our results may have great relevance for understanding the long-term effects of climate and landscape changes across the Neotropical region. In addition, understanding the natural dynamics of each assemblage and its consequences for the local and regional functional structure may be important starting points for delineating appropriate conservation strategies (Cardinale et al., 2007; Wallington, Hobbs, & Moore, 2005). Although we used stream fish assemblages as study models, the patterns found herein should be observable in other taxonomic groups. This serves as a warning about how intensification of disturbances in many ecosystems on Earth can affect the functional structure of biological assemblages in the near future.

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BIOSKETCH

Carlos Rodrigues-Filho is interested in understand how local, regional and historical forces shape the taxonomic and functional structure of biological assemblages. This article is a product of Rodrigues-Filho' MSc thesis, conducted at the Ecology Graduate Program of Brazil's National Institute for Amazon Research (INPA).

Author contributions: C.R.F., R.P.L., J.Z. and F.B.B. conceived the ideas; C.R.F., R.P.L., J.I.S.B. and J.Z. conducted the fieldwork and collected the data with additional material from collaborators; C.R.F., F.B.B. and R.P.L. analysed the data; and C.R.F. led the writing with assistance from R.P.L., J.Z., J.I.S.B. and F.B.B.

SUPPORTING INFORMATION

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